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Effects of Moose, *Alces alces*, on Aquatic Vegetation in Sibley Provincial Park[1], Ontario

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The effect of Moose (*Alces alces*) on aquatic vegetation was studied in Sibley Provincial Park, Ontario. Two small exclosures were built in preferred feeding lakes to protect vegetation from Moose. Both exclosures developed a dense growth of plants. In one, species palatable to Moose were much more abundant than in unprotected areas. The other lake supported very little vegetation outside the exclosure. Aquatic vegetation in a large preferred lake underwent a series of changes from the 1960's to 1980. *Nuphar variegatum* and *Potamogeton filiformis* largely disappeared, leaving the lake sparsely vegetated in some years and dominated by annuals in others. With recent reductions in Moose activity, *Nuphar* is becoming re-established. In the 23 lakes studied, *Nuphar variegatum* was absent or scarce in areas heavily used by Moose, but *Potamogeton foliosus*, an annual, was most common in such sites.

Key Words: Moose, *Alces alces*, aquatic plants, feeding behaviour.

With their remarkable appetite for twigs, Moose (*Alces alces*) can have a profound effect on the forest communities that provide the bulk of their diet (e.g., Janke 1976). Much less is known, however, about the influence of Moose on their aquatic habitats.

Isle Royale provides some of the best documentation. Evidently Water Lilies (Nymphaeaceae) were plentiful on the island in the early 1900's before Moose became established. By 1930, when Moose were particularly abundant, aquatic vegetation was greatly depleted: Water Lilies were "practically gone" and pondweeds (Zosteraceae) were scarce (Murie 1934). Aquatic vegetation had apparently recovered somewhat by 1960 (Krefting 1974), but was again depleted around 1970 (Jordan et al. 1973), corresponding to fluctuations in Moose numbers described by Peterson (1977).

Similar evidence was provided by Wright (1956) in New Brunswick. He used aerial photographs to estimate the abundance of Water Lilies in areas where Moose were common, and concluded that the plants were depleted in lakes accessible to Moose. He also recorded a depletion of Water Lilies around 1912 when Moose had been particularly abundant in the province.

In an experimental study, Aho and Jordan (1979) used exclosures to protect sections of ponds from Moose. At the end of the growing season, the standing crop was much greater in protected than unprotected areas. The only apparent effect on plant species composition was a relative increase in *Potamogeton pusillus* and *Lemna minor* in the protected parts of one pond.

While studying aquatic feeding by Moose, we realized that the animals had an important influence on both the abundance and species composition of aquatic vegetation. Here we describe this influence by reporting (1) a study using exclosures in two ponds heavily used by Moose, (2) plant succession in a well used lake, and (3) species composition of 23 lakes in relation to Moose activity.

Study Area

The study was done in Sibley Provincial Park, Ontario (48° 20′N, 88° 45′W), a 243-km^2 peninsula of principally boreal forest on the north shore of Lake Superior. The Park is closed to hunting and trapping, and supports conspicuous populations of Moose, White-Tailed Deer (*Odocoileus virginianus*), Black Bears (*Ursus americanus*), Beavers (*Castor canadensis*), and some Timber Wolves (*Canis lupus*). The Park includes 37 named lakes, plus numerous small, unnamed lakes and ponds. Most of the water bodies are <50 ha in surface area and have soft organic sediments; many are <2 m deep. Rock outcropping in the peninsula consists mainly of Precambrian sediments which impart a higher mineral content to the lake water than is common in granitic areas of the Precambrian Shield. Total alkalinity of the water is typically 15 to 150 ppm $CaCO_3$, with pH from 6.5 to 8.5.

Methods

During June 1978, a sturdy exclosure was built in each of two small lakes, called Lakes 7B and 24A, that were heavily used by Moose. (Locations on the UTM Grid are 5369100 m N, 370500 m E for Lake 7B, and

5358100 m N, 369800 m E for Lake 24A). Each exclosure covered 4.5 m^2 of lake bottom in about 50 cm of water. They consisted of steel pipes driven into the lake sediment, with cross bars secured by scaffolding clamps. The structure was covered in welded wire screening with openings 3 × 3 cm.

Exclosures were inspected several times in 1978 to 1980. Plants growing inside were harvested on 12 July 1979 and 29 July 1980 for Lakes 24A and 7B respectively. Lake bottom inside the exclosures was divided into 12 plots each 61 × 61 cm. The vegetation in each plot was uprooted by hand. It was then sorted by species; roots and rhizomes were removed from all species except *Eleocharis acicularis* (which has a very small root system); the number of stems was counted for all species except *E. acicularis* and the Characeae; and the wet weight of each species was recorded after the vegetation had drained in the air for 5 sec.

A strip of five control plots, also 61 × 61 cm, was marked out on each side of the exclosures in water of similar depth and over a similar type of substrate extending 1-4 m from the exclosure. Plants in these plots were harvested and treated in the same way. Plants elsewhere in the lake were examined to ensure that control plots were typical of similar parts of the lake.

Moose activity was studied from 1976 to 1980 in Joeboy Lake (UTM Grid 5370000 m N, 372500 m E), a known feeding area for Moose. Observations each year consisted of five to eight 3-h shifts between mid-June and mid-July, with half the shifts from 0600 to 0900 and half from 1800 to 2100. During shifts, an observer at a fixed shoreline location scanned the lake every 15 min and recorded the number of moose seen.

Cobus (1972) also studied Moose behaviour in Joeboy Lake in 1971. He recorded the number of Moose present in the lake in scans at 15-min intervals throughout daylight hours about 2 days per week. Because he presented his data by time of day for the early summer (his Fig. 3), it was possible to calculate the mean number of moose seen per scan from 0600 to 0900 and from 1800 to 2100. His results are based on about 12 mornings and 12 evenings from 1 June to 14 July.

In 1975 to 1979, we made occasional notes on the vegetation in Joeboy Lake in spring and early summer, and did a quantitative survey during 1 or 2 days during late summer (26 July to 3 September). Each survey was based on 342 to 410 non-permanent plots at about 3 m intervals along four transect lines which were traversed by canoe. Approximately the same lines were used each year. In each 75 × 75 cm plot, the observer estimated the percentage of lake bottom covered by each plant species as if seen from above. In 1980, the four lines were traversed more quickly, and notes were made on plant abundance.

Our entire study included 24 lakes in Sibley Provincial Park. Detailed information on Moose activity, lake surface area, mean water depth, shoreline type, organic content of the sediment, water chemical composition, and plant abundance will be given in a separate report. Briefly, preliminary study indicated that the relative amount of aquatic feeding in a lake could be assessed at the end of the feeding season from the amount of Moose tracks, trails, summer dung piles, and other signs around the lake perimeter. Therefore, Moose activity on the 24 lakes was rated subjectively from high (5) to none (0) based on these signs in August and early September, 1977. Records of moose sightings at the more accessible lakes generally agreed with the subjective ratings. Abundance of different species of aquatic plants was also estimated in each lake in late summer of 1977. A canoe or boat was paddled near the shoreline and in several lines criss-crossing the lake. Areas with <2 m of water were divided into convenient sections. Abundance of each plant species was estimated in each section as the approximate percentage of lake bottom covered by the plants as if seen from above without interference of other vegetation. Estimates from the sections were then combined to give estimated abundance in shallow water areas (<2 m) for each lake.

To determine the effect of Moose activity on vegetation, we did stepwise multiple regressions of the abundance of each plant species (expressed as percentage of all vegetation in the lake) on the Moose activity rating and other variables. Only plant species represented in 10 or more lakes were included. Logarithmic transformations were used to reduce skew in the distributions. One lake (Calcite Lake) was omitted because the indirect and direct measures of Moose activity did not agree. Because the many variables gave considerable opportunity for chance associations, the 1% level of statistical significance was used.

For all plants listed, voucher specimens were pressed and are located in the herbarium of the University of Waterloo, Waterloo, Ontario. Plant names follow Fernald (1950).

Results

Exclosures

Lake bottom inside the exclosures was trampled during construction in June 1978. In the Lake 24A exclosure, numerous small *Potamogeton alpinus* and *P. epihydrus* were growing by late summer of 1978, apparently from rhizomes which had grown into the exclosure from outside. When harvested in July 1979, the exclosure was crowded with plants. Expressed as weight per plot, the exclosure contained 10 to 20 times more *Potamogeton alpinus*, *P. epihydrus*, and Characeae than control plots, but similar amounts of *Eleocharis acicularis* (Table 1). Plots in the exclosure also

TABLE 1. Mean ± SD weight (g) of aquatic plants harvested from 12 plots in the exclosure and 10 unprotected control plots in Lake 24A.

Species	Exclosure	Control	P[1]
Eleocharis acicularis	169 ± 83	190 ± 119	n.s.
Potamogeton alpinus	121 ± 93	5 ± 4	<0.002
Characeae	35 ± 20	3 ± 3	<0.002
P. epihydrus	27 ± 27	3 ± 3	<0.05
P. foliosus	5 ± 4	0 ± 0	<0.002
Najas flexilis	3 ± 3	2 ± 2	n.s.
Myriophyllum verticillatum	2 ± 4	0 ± 0	n.s.
Hippuris vulgaris	0 ± 0	1 ± 3	n.s.
P. berchtoldi	0 ± 0	1 ± 1	n.s.

[1]Statistical significance of the difference by the Mann-Whitney U test, 2-tailed.

contained more stems of *P. alpinus* and *P. foliosus* than plots outside ($P < 0.002$).

P. alpinus and *P. epihydrus* from the exclosure were more mature and had greater weight per stem. Exclosure plants had generally grown to the water surface and had developed floating leaves and fruit. Those outside were shorter, with only submersed leaves.

By July 1978, the 7B exclosure had developed a dense growth of *Potamogeton foliosus*. The rest of the lake was sparsely vegetated, mainly with small clumbs of the same plant. In 1979, the expected crop of *P. foliosus* failed to develop in Lake 7B and in several other lakes. The exclosure contained a sparse growth of Characeae, similar to the rest of the lake, plus a few stems of *Sparganium chlorocarpum* and *Sagittaria latifolia*. By July 1980, the last two species formed a dense growth in the exclosure, but the rest of the lake had almost no vegetation. Plant weights per plot averaged 1890 ± 920 g (mean ± SD) for *Sparganium chlorocarpum* and 30 ± 60 g for *Sagittaria latifolia* in the exclosure. There was almost no vegetation in the 10 control plots.

Joeboy Lake

There was a pronounced decline in Moose activity on Joeboy Lake between 1971 and the later years (Table 2). Cobus (1972) noted that Moose activity was highest in mid-June to mid-July. Therefore the inclusion of early June in his results, in contrast to our later results, could not account for the higher values in 1971.

TABLE 2. Number of 3-h observation shifts on Joeboy Lake during mornings and evenings, first and last dates of shifts, and mean number of Moose seen during scans of the lake in six years.

Year	Shifts	Dates	Mean no.
1971[1]	24	1 Jun-14 Jul	5.0
1976	5	21 Jun- 1 Jul	2.6
1977	8	21 Jun-14 Jul	0.4
1978	8	17 Jun-16 Jul	1.9
1979	7	25 Jun-17 Jul	0.7
1980	8	19 Jun-15 Jul	0.4

[1]Recalculated from Cobus (1972, Figure 3).

Residents of the area report an abundant growth of yellow Water Lilies (*Nuphar variegatum*) in the lake in the 1960s. Subsequently the plant was almost eliminated. Cobus (1972) considered *Potamogeton filiformis* the most abundant and preferred plant in the lake in 1971. He presented a map showing "dense beds" of the plant covering about 30% of the lake (his Fig. 1), and noted that Moose concentrated on these beds. Cobus listed the larger pondweeds (*P. amplifolius* and *P. richardsonii*) as second in importance to Moose in the lake, and *Nuphar variegatum* as third. Our 1975 survey showed only 6% of the lake's surface to be covered in vegetation. The dense beds of *P. filiformis* previously mapped by Cobus were largely devoid of vegetation, and the species was judged to cover less than 0.1% of the lake. Most specimens of *Nuphar* were very small (leaf diameter about 3 cm) and may have been seedlings.

Najas flexilis and *Potamogeton foliosus*, which grew as annuals, played a large but variable part in subsequent years. The 1975 survey estimated 6 to 7% plant cover. *N. flexilis* was the most common plant with 3% cover, followed by the large pondweeds at 2%. In 1977 and 1978, plant cover exploded to 42% and 55% respectively because of an abundant growth of *P. foliosus* and *N. flexilis* which together accounted for most of the vegetation. The larger pondweeds were next at 3%. *P. filiformis*, covering 1% of the lake, was much more common than in 1975 and 1976.

In 1979 there was a poor crop of pondweeds and an almost total failure of *P. foliosus* in several lakes. Reasons for this are unknown, but the late spring may have contributed. Plant cover in Joeboy was 4%. However, there were many large specimens of *Nuphar variegatum* (leaf diameter of 20-30 cm). In 1980, large *N. variegatum* were judged to cover 1% of the lake, and Moose were seen feeding steadily on the species for the first time since our observations began in 1976.

Based on the description by Cobus (1972), average water depth appeared not to have changed from 1971 to 1980. However, water depth declined from spring to late summer by 10-20 cm in most years, causing shallow shoreline areas to become exposed mud.

Comparison of Lakes

The abundance of *Nuphar variegatum* in the 23 lakes was closely related to Moose activity (Table 3). In the six lakes heavily used by Moose, *N. variegatum* comprised only 0.4 ± 0.8% of the vegetation (mean ± SD), compared to 7.1 ± 6.2% in the other 17

TABLE 3. Moose activity rated from high (5) to none (0), and abundance of two plant species expressed as percent of all aquatic vegetation in the lake for 23 lakes.

Lake	Moose activity	*Nuphar variegatum* (%)	*Potamogeton foliosus* (%)
7B	4.6	0.0	82.0
24A	4.4	2.0	4.0
Joeboy	4.3	0.1	56.0
Gardner	4.0	0.1	30.0
15D	3.7	0.0	13.0
Talus	3.1	0.01	0.0
Lizard	2.5	19.0	0.03
Ferns	1.6	2.0	12.0
Norma	1.6	8.0	0.0
Pickerel	1.5	7.0	2.0
7A	1.3	17.0	2.0
15A	1.3	0.7	3.0
Kay	1.2	5.0	0.0
Legend	1.0	0.6	0.0
Grassy	0.8	0.2	0.4
Holt	0.8	1.0	0.0
Sawbill	0.8	7.0	6.0
1A	0.6	3.0	2.0
Rita	0.6	13.0	0.01
13A	0.5	10.0	0.02
Helen	0.4	17.0	0.0
1B	0.3	5.0	0.1
Norwegian	0.3	5.0	9.0

lakes. Most specimens from heavily used lakes had small leaves (3-10 cm diameter), spindly petioles, and they rarely flowered. Conspicuous beds of *N. variegatum* were confined to lakes with little Moose activity. The Moose activity rating was the only factor included in the stepwise multiple regression ($r = -0.56$, $P<0.01$).

Potamogeton foliosus was most abundant in the heavily used lakes (Table 3). It comprised 31 ± 32% of the vegetation in the six heavily used lakes (mean ± SD), but only 2 ± 4% in the other 17 lakes. Stepwise multiple regression included the Moose activity rating as the first factor ($r = 0.61$, $P<0.01$), and total phosphorus in the water as the second factor ($r = 0.52$, $P < 0.01$) related to abundance of the plant.

Abundance of the other plant species was not significantly related to Moose activity. Relationships between plant abundance and other lake variables will be reported separately.

Discussion

These studies suggest that Moose have a complex influence on aquatic vegetation.

In some cases, presumably, the animals simply remove preferred food items by grazing. The dense growth of *Potamogeton alpinus* and *P. epihydrus* in one exclosure, and the initial growth of *P. foliosus* in the other, contrasted sharply with the sparse development of the same species in unprotected areas. Since these species are highly palatable to Moose (D. Fraser, unpublished data), their depletion outside the exclosure was likely due to grazing. *Eleocharis acicularis* is not a preferred food item, and was about equally abundant in protected and unprotected areas.

Some species are probably depleted by Moose through mechanical disturbance rather than grazing. Emergent species such as *Sparganium chlorocarpum* and *Sagittaria latifolia* normally contain substantially less sodium than submersed or floating-leafed plants (Boyd 1978), and do not appear to be eaten a great deal by Moose. Suppression of these species in the unprotected areas of Lake 7B was probably caused by repeated disturbance when Moose sought preferred vegetation. In some areas, Moose activity may also influence plant growth by increasing the turbidity of the water (Aho and Jordan 1979), or by causing disturbed sediments to settle on the vegetation.

Some plants appear to be particularly vulnerable to disturbance. Depletion of *Nuphar variegatum* by concentrated aquatic feeding has been mentioned repeatedly in the past and is fully supported here. Although not the most preferred species of aquatics (D. Fraser, unpublished data), *Nuphar* seem greatly affected by herbivory. For example, Seton (1953: 172) describes killing a bed of Water Lilies by repeated clipping of the leaves and petioles. Many other aquatic species, however, seem to survive substantial removal by herbivores (Aho and Jordan 1979).

In contrast to *Nuphar*, *Potamogeton foliosus* flourished in preferred feeding areas even though it is readily eaten by Moose (D. Fraser, unpublished data). Unlike most other pondweeds that usually developed from rhizomes or winter buds, *P. foliosus* commonly grew annually from fruit. This probably imparted a competitive advantage in areas where rhizomes are continually disturbed by Moose. Once the disturbance is removed, as in the exclosure in Lake 7B, *P. foliosus* would presumably be choked out by perennials.

In Joeboy Lake, the rapid changes of vegetation may have been influenced by the exceptionally shallow water and soft sediment as well as the activities of Moose. However, the depletion of *Nuphar variegatum* and the trend toward annuals (*Potamogeton foliosus* and *Najas flexilis*) are consistent with the apparent effects of Moose observed in other lakes.

Moose seem particularly attracted by lakes with a mineral soil substrate such as the clay-bottomed Lake 7B and the silt-bottomed Lake 24A (cf. Fraser et al. 1980). Such sites can be puzzling when first encountered. The intense Moose activity at Lakes 7B and 24A was obvious from tracks and trails, but 7B had very little vegetation, and 24A was dominated by *Eleocharis acicularis* which Moose rarely appear to eat. At first glance, one might suppose that these sites were unproductive aquatic habitat, and that Moose were attracted by something other than aquatic plants.

The exclosures show, however, that these are fertile sites that would be crowded with aquatic plants but for the devastating effect of the Moose. We suggest that Moose continue to use these areas despite their depleted vegetation because of some superior quality of the plants imparted by the mineral soil bottom. Science belatedly came to recognize that the sediment is important in the nutrition of aquatic plants (Hutchinson 1975: 276). Moose probably knew this long ago.

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