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SIZE-SELECTIVE PREDATION ON UNIONID CLAMS BY MUSKRATS

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Abstract: We collected shells of the northern floater (*Anodonta grandis simpsoniana*) from muskrat (*Ondatra zibethicus*) middens on the shore of a small lake in the boreal forest zone of Alberta. Muskrats ate a mean of 228 ± 23.6 (SE) clams/day or 1.4 ± 0.15 kg/day (soft body mass measured as wet wt) from 22 July to 1 September 1986. The overall length and age distributions of clams eaten (median length = 64.3 mm, median age = 7.5 yr) were larger and older ($P < 0.001$) than a random sample of clams from the lake (median length = 49.1 mm, median age = 6.2 yr). Muskrats may have a significant effect on the size and age distributions of clams in the lake.

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The muskrat is a herbivore that occasionally eats animal matter (Enders 1932, Smith 1938, Bellrose 1950). Most studies of muskrat diet have reported only the plant species in their diet (Butler 1940, Takos 1947, Danell 1978) because most studies of muskrat diets are conducted in marshes where plant matter is abundant relative to suitable animal prey. A few studies noted the consumption of animal prey (e.g., crayfish, fish, insects, snails, young birds, other muskrats, frogs, turtles, salt- and freshwater mussels) (Errington 1941, Bellrose 1950, Triplet 1983). In addition, muskrats have been accused of destroying mussel beds (Headlee 1906, Van Cleave 1940, Joy 1985) based on the observation of shells discarded on feeding platforms. However, prey selection and consumption rates of clams by muskrats have not been documented. The goals of our study were to determine the size and age distributions of clams consumed by muskrats, to test for spatial and temporal variation in their size and age distributions, and to determine whether the size and age distributions of clams eaten differed from the size and age distributions of clams in the lake.

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METHODS

We collected intact valves of unionid clams from muskrat middens along the shore of Narrow Lake (54°34′N, 113°37′W), a small (1.14 km^2), deep ($\bar{x}$ depth = 14.2 m), moderately productive ($\bar{x}$ total phosphorus = 12.9 mg/m^2) lake

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We sent shells to the
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in the boreal forest zone of central Alberta. The northern floater was the only unionid clam in the lake (Hanson et al. 1988). Unionid clams are found throughout the littoral zone (0–6 m) of the lake except that part of the southern basin where there are dense beds of macroalgae (*Chara* spp.) (Hanson et al. 1988). We collected shells from middens along 68.6% of the shoreline of the north basin of the lake at 3–4-day intervals from 22 July to 2 September 1986. Collection sites were marked with surveyor's tape. We studied the north basin of the lake because it was a distinct basin, was least disturbed by human activity, and was the only basin with extensive muskrat activity during 1986. Each intact shell was assumed to represent 1 clam consumed, but this is an underestimate of the consumption rate because muskrats occasionally break both valves and some shells were probably missed because they were buried or hidden under roots or in burrows. We were unable to estimate the size of the muskrat population on the study site because these muskrats live in bank burrows.

We sent shells to the laboratory where encrusting debris was removed, they were air dried, and sprayed with clear lacquer to prevent breakage. The total length of each shell was recorded to the nearest 0.1 mm. Shells were aged by counting annuli. Clams of the genus *Anodonta* show clear growth rings and false annuli are easily distinguished from true annuli (Ghent et al. 1978, Haukioja and Hakala 1978, McCuaig and Green 1983). A subsample of 100 shells was aged independently by 2 people and results compared. The few discrepancies (4) were due to a less experienced reader missing the first annulus. We consider errors in aging to be minimal throughout this study.

The minimum daily rate of clam consumption by muskrats was estimated for 3 intervals by summing the number of clams collected over the actual number of days in the interval. Consumption rates were divided by 0.686 (proportion of basin sampled) to yield an estimate for the entire north basin of the lake.

We collected data from 6 sites and 3 intervals of approximately 14 days (22 Jul–3 Aug, 4 Aug–18 Aug, 19 Aug–1 Sep 1986) to test (*G*-test) for temporal and spatial variation in the length and age distributions of clam shells. All data on length and age of shells from muskrat middens were grouped and tested for differences from the length and age distributions of clams collected from the north basin of the lake. The method of collecting clams from the lake is described by Hanson et al. (1988).

RESULTS

In Narrow Lake, we observed muskrats diving for clams and carrying clams to shore in their forepaws. Muskrats appeared to open clam shells by inserting their lower incisors between the ventral edges of the valves and prying upwards, breaking the upper valve and allowing access to the body of the clam. Once consumed, the shells, usually with 1 valve remaining intact, were discarded in discrete refuse piles or middens. Middens were identified easily; they were ≤ 1 m^2 and some contained $>1,000$ shells. When shells were collected at 3–4-day intervals, the piles were smaller, having a maximum area of about 0.25 m^2 and containing ≤ 100 shells.

We collected 6,053 shells from middens over the 6-week study that represents 8,824 clams eaten for the entire north basin of the lake. The minimum rate of consumption of clams by the muskrat population over each of the 3 sampling intervals was 138, 235, and 250 clams/day for 22 July–3 August, 4–18 August, and 19 August–1 September, respectively.

The length and age distributions of clams consumed by muskrats differed among the 3 sampling intervals and among the 6 sites around the basin. The length-frequency distributions of shells from the middens differed among dates ($\chi^2 = 144$, 12 df, $P < 0.001$) and among sites ($\chi^2 = 528$, 30 df, $P < 0.001$). The length-distributions for each site differed among sampling dates ($\chi^2 = 1,651$, 10 df, $P < 0.01$). Although the length distributions differed, the median length of shells did not: 63, 65.3, and 64.2 mm for 22 July–3 August, 4–18 August, and 19 August–1 September, respectively. The differences among size-distributions most likely reflect the large sample sizes and were not significant in a biological sense. The age-frequency data were very similar; there was a significant date effect ($\chi^2 = 158$, 12 df, $P < 0.001$), site effect ($\chi^2 = 873$, 30 df, $P < 0.001$), and date × site interaction ($\chi^2 = 1,627$, 10 df, $P < 0.001$), but the median age of clams eaten by muskrats varied little (7.4–7.6 yr) among sampling intervals. Consequently, all data (dates and sites) were combined to compare length- and age-frequency distributions of the shells collected from middens with those of clams collected from the north basin of the lake.

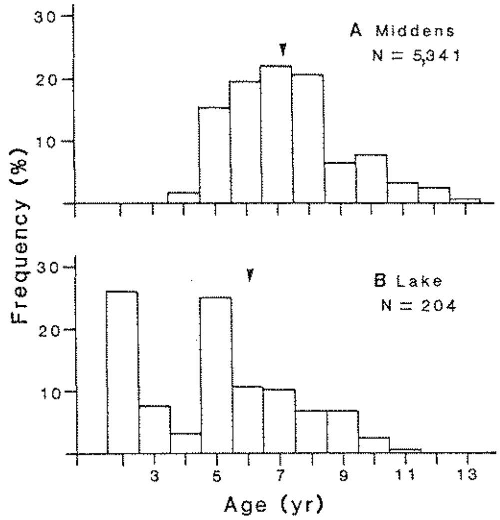

Fig. 1. Total length-frequency distributions of clams collected A) from muskrat middens, and B) from the north basin of Narrow Lake (>1 yr old). Arrows indicate the median length of each distribution.

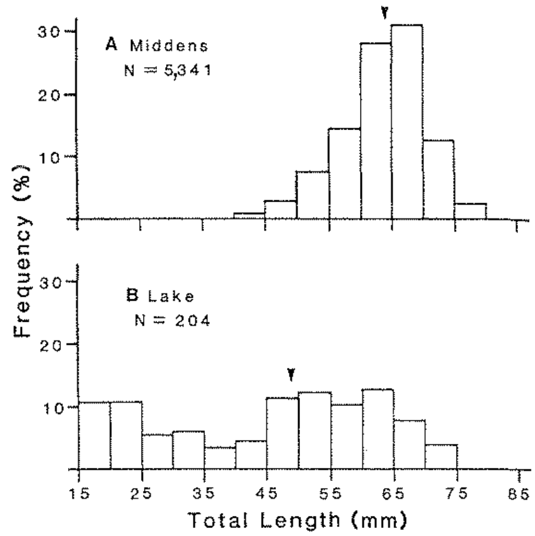

Fig. 2. Age-frequency distributions of clams collected A) from muskrat middens, and B) from the north basin of Narrow Lake (>1 yr old). Arrows indicate the median age of each distribution.

The length-frequency (Fig. 1) and age-frequency (Fig. 2) distributions indicate that the length and age of shells collected from muskrat middens clearly differed from the length and age of clams from the north basin of the lake. Shells <35 mm long and 3 years old were not collected from middens and clams >75 mm long and 11 years old were not collected from the lake. Hence, the lengths and ages of shells from middens were compared with those of clams in the lake only where the distributions overlapped (35.1–75.0 mm; 3–11 yr). The length and age distributions of clams consumed by muskrats still differed from the distributions of clams in the lake ($\chi^2 = 130.6$, 7 df, $P < 0.001$, and $\chi^2 = 101.4$, 8 df, $P < 0.001$, respectively). The median length and age of clams consumed by muskrats were 15.2 mm larger and 1.3 years older than those in the lake. Eighty-six percent of the clams eaten were between 55 and 75 mm long compared with only 36% for the clams in the lake.

DISCUSSION

The muskrat population consumed a minimum of 228 ± 23.6 clams/day or 1.4 ± 0.15 kg/day (wet wt) as soft body mass. If this consumption rate was constant, 38,640 clams, or 5.3% of the population of clams >2 years old in the north basin of Narrow Lake (Hanson et al. 1988) were consumed by muskrats during the ice-free season (184 days in 1986). This represents a small, but important, fraction of the clam population. Considering the low annual production rate of clams in Narrow Lake (production/biomass ratio = 0.25) (Hanson et al. 1988), muskrats could impose a strong selective pressure on the population if they selectively consume larger (and presumably fastest growing) clams over many years. However, we do not know whether the consumption rate remains constant over the entire ice-free season or the degree to which muskrats select fast growing individuals. The consumption rate appeared to increase through the summer (from 138 clams/day to 250 clams/day). Furthermore, muskrats may consume clams throughout the entire year. The proportion of the clam population eaten by muskrats could therefore be considerably higher and of greater importance to the population than estimated here.

The length and age distributions of clams from the middens differed from those in the north basin of Narrow Lake (Figs. 1 and 2); muskrats consumed larger and older clams. One consequence of this size selectivity is that muskrats consume faster growing clams. The size range most heavily preyed upon (55–75 mm long) includes clams 4–12 years old in Narrow Lake (Hanson et al. 1988), however, for clams 4–7 years old the lower limit selected (55 mm) is greater than the median length at age for clams

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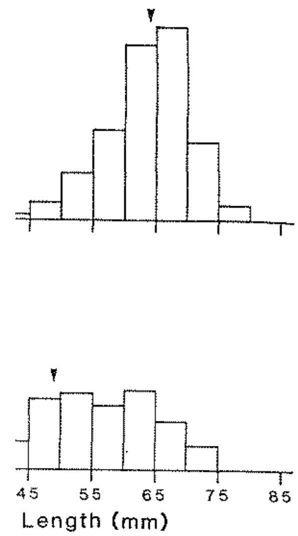

in the lake. This indicates muskrats were selectively preying on the faster growing clams in these 4 age groups. The apparent absence (or at least very low numbers) of clams >75 mm long in Narrow Lake (Hanson et al. 1988) may be indicative of this size selectivity.

The length and age distributions of shells from middens differed among dates, sites, and dates at a single site. The temporal and spatial variation in the length and age selectivity by muskrats for clams could result from a number of factors operating singly or in combination. These factors could include: (1) recruitment of young muskrats into the population who gradually increased the size of clams they eat because of improved handling ability with increased size and experience, (2) collection sites may overlap the range of several groups of muskrats; muskrats may move among sites and muskrats may alter their feeding sites over the season, (3) among site differences in availability of clams from the lake, and (4) variance in choice of clams by individual muskrats. These factors could also account for the slight increase in the median size of clams taken later in the sampling period (an increase from 63 to 64.2 mm long).

Stearns and Goodwin (1941) reported that animal matter comprised a substantial but undetermined amount of the muskrat's diet. When quantified, animal foods were estimated to comprise 5 (O'Neil 1949) and 7% (Ching and Chih-Tang 1965) of the diet. Muskrats are highly opportunistic in their feeding habits, hence, the consumption of animal foods may be far more important in lakes, such as Narrow Lake, than in marshes where clams are often absent.

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