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EFFECT OF SIZE-SELECTIVE PREDATION BY MUSKRATS
(*ONDATRA ZEBITHICUS*) ON A POPULATION OF UNIONID
CLAMS (*ANODONTA GRANDIS SIMPSONIANA*)

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SUMMARY

(1) The effect of size-selective predation by muskrats on the population size, size-structure, and growth of clams was evaluated in a small lake in central Alberta. Clam shells were collected at regular intervals over 1 year from muskrat middens found along the shoreline of the lake. The number, biomass, size distribution, and age distribution of clams eaten were compared with the number, biomass, and age and size distributions of clams in the lake.

(2) Muskrats ate almost 37000 clams, or 3% of the population in the study area in 1 year. When expressed as biomass, muskrats ate 677 kg of clams, which was equivalent to 5.8% of the biomass and 31% of the annual production of clams in the study area.

(3) Muskrat predation was highly size-selective—86% of the clams eaten were > 55 mm long compared to 37% for clams in the lake—and had a strong effect on the size structure of the clam population. When all age-classes were combined, the biomass of clams > 70 mm eaten exceeded the annual production by an amount equivalent to 9.5% of the estimated biomass in the lake. Muskrats ate the fastest growing clams between 3 and 9 years old. Mean length at annulus did not increase for clams older than age-8 in the lake. The biomass of large clams in the lake will therefore decline if the observed predation continues.

(4) Muskrats ate a large fraction of the reproductive output (glochidia) of the largest clams. Only 6% of the glochidia of clams < 70 mm long was eaten whereas 21% of the glochidia of clams > 70 mm long was eaten. Genetic selection for slow growth has not occurred.

INTRODUCTION

Many studies document the existence of size-selective predation in aquatic ecosystems. With the exception of fish preying on zooplankton, however, the consequences of size-selective predation on the prey populations are poorly understood. It is relatively simple to measure the abundance and species make-up of zooplankton populations and it is well established that fish can eliminate the larger zooplankton species from lakes by selective predation on the largest size-classes (Brooks & Dodson 1965; Wells 1970; Vanni 1986). However, the consumption rates needed to eliminate large zooplankton from any given lake are unknown. The consequences of size-selective predation on large aquatic animals (e.g. fish and unionid clams) are much less understood.

The results of studies of fish predation on zooplankton cannot be generalized to predation in long-lived animals which show indeterminate growth because of fundamental differences in life histories. Zooplankton generally are short-lived, show determinate

growth, and have relatively low individual fecundity. Fish and clams are generally long-lived, show indeterminate growth, reproduce over many age-classes, and have relatively high, size-dependent, individual fecundity. Consequently, the effect of selectively removing larger individuals from a population of fish or clams depends on the numbers taken, the sizes taken, and whether the target population is food-limited. Initially, exploitation of food-limited fish populations results in increased growth and fecundity of the survivors (Healey 1980; Hanson, Belanger & Schoenicke 1983; Hanson & Leggett 1985; Langeland 1986). However, overexploitation of the larger size-classes of any fish population eventually leads to the loss of the most fecund individuals and to a decline in the abundance of that species (Favro, Kuo & McDonald, 1979; Goodyear, Cohen & Christensen 1985; Francis 1986). Unlike zooplankton, it is usually possible to estimate the number of individuals removed from a population but it is very difficult to estimate the size of the fish population being exploited (Francis 1986; Getz, Francis & Swartzman 1987). Hence, even relatively low levels of exploitation can result in the gradual loss of larger individuals from a population over a period of decades and could even result in genetic selection for slow growth (Handford, Bell & Reimchen 1977; Favro, Kuo & McDonald 1979; Beacham 1983).

Clams share the life-history traits of fish. However, from the point of view of examining the effects of predation on a population, clams offer a major advantage to researchers because of their sedentary nature. Therefore, the population size and size structure is more readily determined for clam populations than for fish populations. Furthermore, freshwater clams have few natural predators due to their large size and thick shells. However, muskrats (*Ondatra zibethicus* Linnaeus) prey on bivalves (Headlee 1906; Van Cleave 1940; Triplet 1983) and have been accused of destroying entire clam beds (based on the observation of clam shells on muskrat feeding platforms). Muskrats consume the largest individuals in the clam population (L. E. Convey, personal communication). Thus, muskrat predation could have an effect on the age and size structure of clam populations. The present study examines the effects of size-selective predation by muskrats on the clam population in a small lake in Alberta. The goals of the present study were to determine: (i) the fraction of the clam population in the lake eaten by muskrats in 1 year; (ii) the effects of predation by muskrats on the age and size structure of the clam population; (iii) whether muskrats consumed significant quantities of the fastest growing clams; and (iv) the fraction of the reproductive output of various size-classes of clams eaten by muskrats.

MATERIALS AND METHODS

Study area

This study was done in Narrow Lake (54°35'N, 113°37'W), a small (surface area 1.14 km²), deep (mean depth 14.4 m), moderately productive (mean summer total phosphorus 12.9 mg m⁻³) lake in the Boreal forest zone of central Alberta. The lake has three basins. Unionid clams are found throughout the littoral zone (0–6 m) of the lake with the exception of that part of the south basin where the littoral zone is dominated by beds of the macroalgae *Chara* (> 10 cm tall). Unionid clams are absent from these *Chara* beds (Hanson, Mackay & Prepas 1988a). The morphometry and water chemistry of Narrow Lake have been described by Prepas & Trew (1983) and Prepas & Vickery (1984). *Andonta grandis simpsoniana* Lea is the only unionid clam in Narrow Lake and dominates the

biomass of the benthic fauna (Hanson, Mackay & Prepas 1988a). Very few clams are found deeper than the edge of the littoral zone (6 m) in Narrow Lake. Muskrats are the only known vertebrate predator on unionid clams in Narrow Lake.

Sampling the natural clam population

Clam abundance was estimated from collections made biweekly from 28 May to 9 August 1986 and from 9 May to 19 August 1987 in the north basin of the lake. Clams were collected by taking twelve bottom samples with a $23 \times 23 \times 23$ cm Ekman dredge from each of 1, 2, 3, 4 and 5-m depths on each sampling site. There were seventeen randomly chosen sampling sites in the north basin of the lake. A total of 54 m^2 of substrate was sampled in this study. Sediments were sieved through a 6-mm screen which retained all clams $> 8\text{--}10$ mm long. This size corresponded to *c.* 50% of age-1 clams and 100% of clams age-2 and older (Hanson, Mackay & Prepas 1988b). Only clams age-2 and older were used in this study. The population means and 95% C.L. were based on \log_{10} -transformed data for biomass estimates and on square-root transformed data $((x+1)^{0.5})$ for density estimates.

All clams were taken, alive, to the laboratory where the debris encrusting the shell was removed and live weight, total length, age, and total length at each annulus were recorded. Throughout this paper live weight refers to the biomass of the living animal with shell shut and includes the water inside the shell. The use of annuli to age clams is generally accepted for the genus *Anodonta* because they show clear growth rings and false annuli are usually easy to differentiate from true annuli (Ghent, Singer & Johnson-Singer 1978; Haukioja & Hakala 1978; McCuaig & Green 1983). The age and length–frequency histograms were based on age and length at the 1986 annulus. This avoided variation due to seasonal growth. Annual production for 1986 was calculated from clams collected in 1987 by the methods described by Lewandowski & Stanczykowska (1975) and Hanson, Mackay & Prepas (1988a). A Walford plot (Ricker 1975) was done to determine whether there was any evidence of size-selective mortality within year-classes.

Fecundity estimates

To determine clam fecundity as a function of size, we collected 102 clams (10–85 mm long) from Narrow Lake and twenty-three clams (75–94 mm long) from nearby Long Lake in September 1987. The clams were transported alive to the laboratory and quickly frozen and stored (-40°C) until glochidia could be counted. We counted glochidia rather than eggs as a measure of reproductive output because glochidia are much larger and easier to count. We did not observe any clams still carrying eggs during September 1987. To count glochidia, clams were partially thawed, total length measured (to 0.1 mm), and the shell opened by severing the two adductor muscles. The partially frozen marsupia were removed with a scalpel, cut into small (0.5×0.5 cm) pieces, placed in 100 ml of water in a calibrated beaker, and agitated vigorously with a blunt probe. This agitation released the glochidia and broke the remaining tissue into very small fragments. The volume of water and glochidia was brought up to 200 ml (or 400 ml for large samples), mixed thoroughly and a 1-ml subsample was removed with a Hensen–Stempel pipette and placed in a zooplankton counting chamber where the entire subsample was counted. Three replicates were done for each clam and the mean value was calculated. The total number of glochidia per clam was determined by multiplying the mean number of glochidia ml^{-1} by the appropriate dilution factor (200 or 400). Size-specific fecundity was determined by linear regression (least-squares method) of glochidia number (\log_{10} -

transformed) on total length (mm). This regression was used to estimate the number of glochidia produced by the various size-classes of clams in the lake and collected from middens. In this analysis, clams were assumed to be hermaphroditic because 94% ($n = 65$) of the mature clams (> 50 mm) collected during September 1987 contained glochidia. The effect of muskrat predation on the reproductive output of various size-classes of clams was determined by comparing the estimates of reproductive output of various size-classes of clams in the lake with estimates of the numbers of glochidia which would have been in the clams of the same size which were eaten by muskrats.

Clams eaten by muskrats

Muskrats dived for clams in the littoral zone of the lake, carried the clams ashore, and bit through one valve of the shell. The muskrats ate the visceral mass and discarded the remains, usually with one valve intact, in discrete piles (or middens) on shore or in shallow water beside logs. We surveyed the entire shoreline of Narrow Lake for middens on 3–4 May 1986. This survey indicated there was substantial predation by muskrats in the central basin of the lake and light predation on clams in the north basin. The central basin was chosen as the study site and searched weekly for fresh shells. No freshly eaten clams were found in the central basin during May–June 1986, whereas fresh shells were found in the north basin at the end of June. Consequently, the central basin sampling site was abandoned.

The shoreline of the north basin was intensively searched in early July 1986 and all active middens were marked with coloured surveyor's tape in an area representing 68.6% of the basin. All old shells were removed from the study area by 21 July 1986 and quantitative sampling was begun. Shells were collected from middens at 3- or 4-day intervals from 22 July until 2 September 1986 and then biweekly until 26 October. The lake froze on 7 November 1986. Collection of shells resumed when ice receded from the shore area on 21 April 1987 and continued at 1- or 2-day intervals until the lake was ice free on 28 April. Sampling was biweekly from 29 April until 23 July 1987.

All shells were returned to the laboratory where encrusting debris, remains of viscera, and the broken valves were removed. The total length and age of the shells were determined for 24 861 shells. The length at the annulus formed in June 1986 was determined either for all of the shells collected in a sample period or, if the number of shells collected was large, for a randomly chosen subsample of 500 shells (a total of 6488 shells were measured). All lengths were measured to the nearest 0.1 mm. Estimates of total length of the shell were conservative because the muskrats frequently broke off part of the new shell growth. The age of a shell was determined by counting annuli. Live weights were estimated from the live weight–total length relationship calculated for the live clams collected in the study area:

$$\log_{10} W = 3.022 \log_{10} TL - 4.184$$

$$r^2 = 0.99, n = 1101$$

Predicted weights were corrected for the effects of back-transformation (Baskerville 1972; Sprugel 1983).

Size- and age-frequency distributions were determined for all samples combined. The size-frequency distributions were based on the length and age at the 1986 annulus to remove the bias of seasonal growth and having data collected over parts of 2 years (1986–87). The age- and size-frequency distributions of shells collected from middens were

compared by means of contingency tables (*G*-test) to the age- and size-frequency distributions of clams collected from the lake.

The effect of muskrat predation on the natural clam population was determined by comparing the estimates of the numbers and biomass of clams eaten with the estimates of total numbers, biomass, and annual production (for 1986) of clams in the study area of the lake. The effect of muskrat predation on the age and size structure of the clam population was determined by comparing the biomass of clams eaten in various age- and size-classes with estimates of the biomass and annual production of clams of the corresponding age- and size-classes in the lake. To determine whether muskrats ate faster growing clams, we compared the size-frequency distributions of clams of a given age collected from middens with the size-frequency distributions of clams of the same age in the lake. In addition, the biomass of clams eaten which were > 70 mm long for each age-class was compared with the biomass and annual production of clams > 70 mm long for the same age-class of clams in the lake to determine whether muskrats ate a significant fraction of the fastest growing clams in the various age groups.

RESULTS

Abundance and growth of clams in the lake

The mean abundance of clams in the littoral zone of the north basin of Narrow Lake (28 May 1986–19 August 1987) was 18.4 clams m^{-2} (95% C.L. = 15.8–21.1 clams m^{-2}) or 175.1 g m^{-2} (live weight; 95% C.L. = 138–221 g m^{-2}). This represented 1.23 million or 11.7 tonnes of clams in the study area. The Walford plot was not linear (Fig. 1) and a linear fit was not obtained until the data representing clams older than age-8 were omitted. The asymptotic length derived from the Walford plot for clams age-8 and younger was 150 mm; much larger than the largest clam (83.6 mm) collected from the lake or from muskrat middens. The close proximity of the last four data points to each other and the 1:1 line indicates mean length increased very little after age-8 and that size-selective mortality was occurring.

Predation rate

Muskrats ate fewer than fifty clams per day from ice-out until mid-summer but ate an average of 350 clams per day during autumn (Fig. 2) and an average of 120 clams per day from the time open water appeared near shore on 21 April 1987 until the ice disappeared on 28 April 1987. Muskrats ate 36 771 clams over a 1-year period, which represented 3% of the number of clams age-2 and older in the study area. In terms of biomass, muskrats consumed 677 kg of clams or 5.8% of the biomass in the study area. Annual production by clams in 1986 was equivalent to 19% of the biomass of clams > age-1 in the lake. Thus, the biomass eaten by muskrats was equivalent to 31% of the annual production of clams age-2 and older.

Age distributions

The age distribution of clams eaten by muskrats differed markedly (*G*-test, $\chi^2_{10} = 809.5$, $P < 0.001$) from that of clams in the lake (Fig. 3). No age-2 and very few age-3 and age-4 clams were eaten. Only clams of age-9 comprised similar fractions of the clams eaten (5%) and the clams present (4%) in the lake. The age distribution for clams in the lake indicates there was wide variation in year-class strength, e.g. ages 2 and 5 were strong year-classes

Muskrat predation on clams

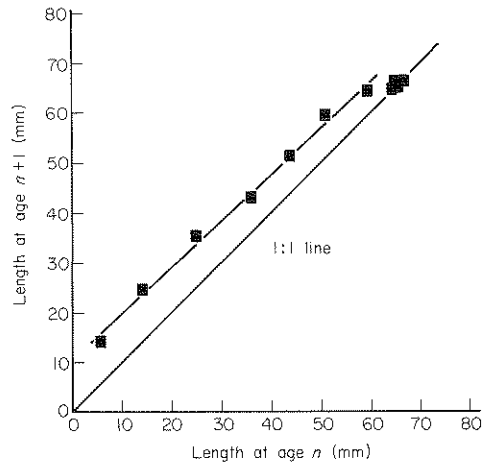


FIG. 1. Walford plot (Ricker 1975) based on mean length at annulus for clams 1–12 years old in the north basin of Narrow Lake during 1986. The regression was $Y = 10.8 + 0.93X$, $r^2 = 0.99$, $n = 7$, S.E. of slope = 0.0194, $\bar{X} = 33.49$, $\Sigma x^2 = 10173$, $MSE = 39.5$, $P < 0.001$. The regression equation only applies to clams 2–8 years old.

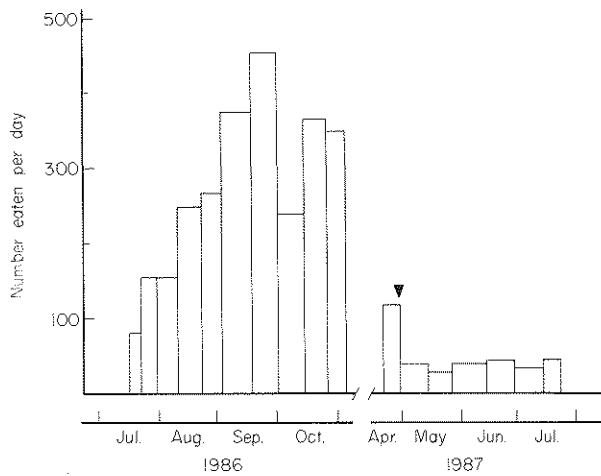


FIG. 2. Number of clams eaten per day by muskrats in the north basin of Narrow Lake from 22 July 1986 to 23 July 1987. The solid arrow indicates the day the ice disappeared from lake 28 April 1987.

TABLE 1. Effect of muskrat predation on clams 3–12 years old from the north basin of Narrow Lake, 22 July 1986–23 July 1987

Age (y)	Clams in lake		Clams eaten			Decrease in biomass (%)
	Biomass (kg)	Production (kg y ⁻¹)	Biomass (kg)	Biomass (%)	Production (%)	
3	126	79	2	1.7	2.7	0
4	252	129	9	3.5	6.9	0
5	1963	687	110	5.6	15.9	0
6	1697	356	90	5.3	25.1	0
7	3153	504	170	5.4	33.9	0
8	1986	218	153	7.7	70.1	0
9	1166	93	44	3.8	47.0	0
10	909	64	52	5.7	81.6	0
11	349	21	21	5.9	100.0	0
12	64	3	14	22.0	440.6	17.0

and ages 3 and 4 were weak year-classes. The biomass of clams eaten in each age-class represented 3.5–7.7% of the biomass present in the lake, with the exception of age-12 where muskrats ate 22% of the biomass (Table 1). Annual production decreased with age, however, and the proportion of annual production eaten by muskrats increased until age-12 when the biomass of clams eaten exceeded the 1986 production by an amount equivalent to 17% of the biomass of clams age-12 and older in the lake.

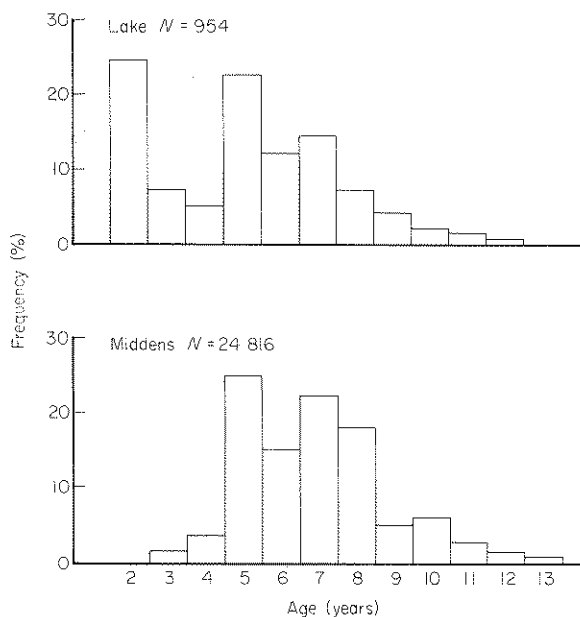


FIG. 3. Age-frequency distributions of clams collected from the lake and of clams collected from muskrat middens in the north basin of Narrow Lake. The data represent age based on the 1986 annulus.

Muskrat predation on clams

TABLE 2. Effect of muskrat predation on various size-classes of clams in the north basin of Narrow Lake, 22 July 1986–23 July 1987

Size (mm)	Clams in lake		Clams eaten		Decrease in biomass (%)	
	Biomass (kg)	Production (kg y ⁻¹)	Biomass (kg)	Production (%)		
40–85	11 217	1678	672	6.0	40.0	0
60–85	6543	658	537	8.2	81.6	0
65–85	3391	259	369	10.9	142.4	3.2
70–85	1016	41	137	13.5	334.1	9.5
75–85	87	5	25	28.3	492.4	22.6

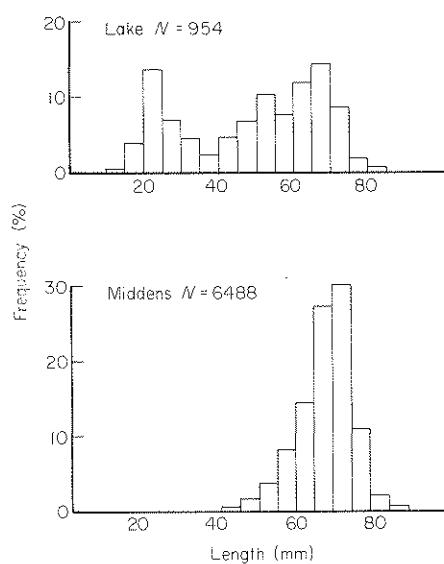


FIG. 4. Overall size-frequency distributions of clams collected from the north basin of Narrow Lake and of clams collected from muskrat middens during 1986–87. The lengths represent the total length at the 1986 annulus.

TABLE 3. Effect of muskrat predation on clams longer than 70 mm for clams 2–11 years old in the north basin of Narrow Lake, 22 July 1986–23 July 1987. Clams did not reach a length of 70 mm until age-6. Annual production was calculated from the production: biomass ratios specific to each age-class

Age (y)	Clams in lake		Clams eaten		Decrease in biomass (%)
	Biomass (kg)	Production (kg y ⁻¹)	Biomass (%)	Production (%)	
6	39.0	8.2	12.5	59.5	0
7	113.7	18.2	26.1	163.4	10.1
8	106.9	11.8	40.4	367.4	31.4
9	151.5	12.1	8.6	107.5	0.6
10	142.4	10.0	11.2	160.6	4.2
11	71.5	3.6	16.3	322.8	11.2

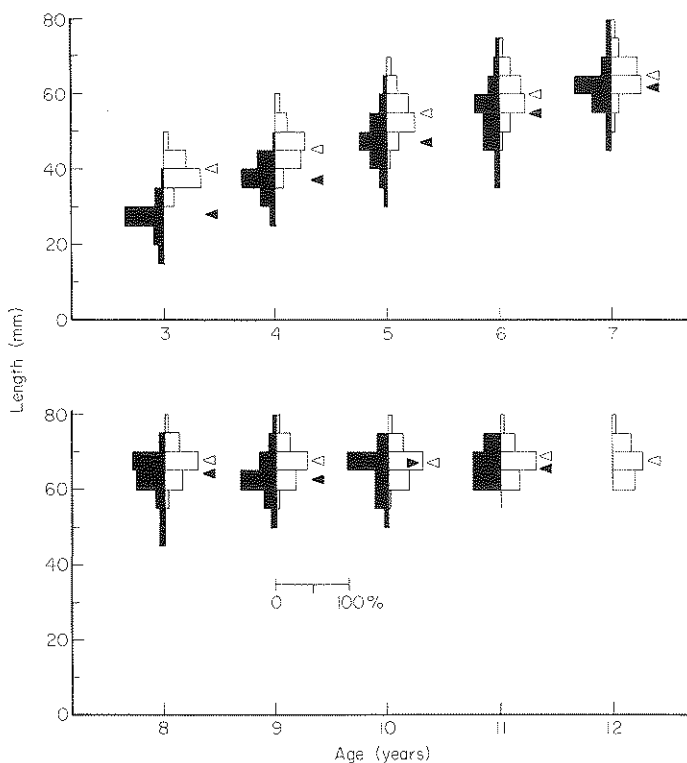


FIG. 5. Size-frequency distributions of clams 3-12 years old collected from the north basin of Narrow Lake (■) and from muskrat middens (□). The data represent length at the 1986 annulus. Too few clams 12 years old or older were collected from the lake to permit plotting a size-frequency histogram. The median length at age for clams collected from the lake is indicated by a solid arrow. The median length for clams collected from muskrat middens is indicated by an open arrow.

TABLE 4. Effect of muskrat predation on the number of glochidia produced by various size-classes of clams in Narrow Lake

Size (mm)	Number of glochidia ($\times 10^9$)	Glochidia eaten (%)
50-55	1.3	3.1
55-60	2.8	3.5
60-65	4.8	5.6
65-70	4.1	9.4
70-75	1.2	18.6
75-80	0.2	31.6
Total	14.4	7.5

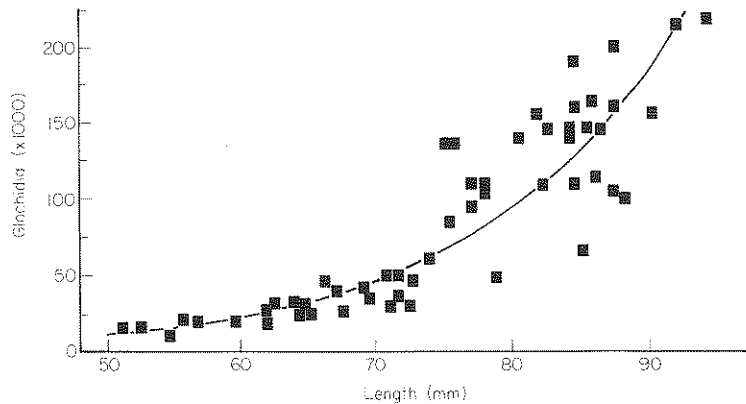


FIG. 6. Scatter plot of number of glochidia per clam vs. total length of *Anodonta grandis simpsoniana*. The regression was: $\log_{10} Y = 4.038 + 0.031 (TL - 50)$, $r^2 = 0.88$, $n = 63$, S.E. of slope = 0.0015, $\bar{X} = 23.51$, $\Sigma X^2 = 7978.5$, $MSE = 0.0167$, $P < 0.001$.

Size distributions

Muskrats clearly selected larger clams (Fig. 4). The median length of clam eaten was 63.4 mm compared to 47.1 mm for clams age-2 and older in the lake. Over 85% of the clams eaten were longer than 55 mm, whereas only 37% of the clams in the lake were longer than 55 mm. The difference between the two distributions, over the range where the data overlap (25–80 mm), was highly significant (G -test, $\chi^2_{10} = 470.6$, $P < 0.001$). Muskrats ate an amount equivalent to 6% of the biomass and 40% of the annual production of clams > 40 mm long in the lake (Table 2). The biomass of clams eaten which were > 65 mm long represented 11% of the biomass of clams > 65 mm long in the lake and exceeded the annual production by 42%. The biomass of clams eaten > 75 mm long exceeded annual production by an amount equivalent to 23% of the biomass of clams > 75 mm long in the lake.

Predation on fast growing clams

Muskrats preyed disproportionately upon the fastest growing clams from age-3 to age-9 (Fig. 5). The median length at a given age for clams recovered from middens exceeded the median length of clams of the same age in the lake, with the exception of age-10 where the medians were equal. A few clams in the lake exceeded 75 mm long by age-7 but the proportion did not increase in older age-classes. A threshold length of 70 mm was chosen to represent the fast growing clams (age 6–12) because the median length of clam in the lake did not exceed 70 mm for any age-class. Clams in the lake did not exceed a length of 70 mm until age-6 and muskrats ate 12.5% of this biomass (Table 3). From age-7 onwards, the biomass of clams > 70 mm long in each age-class which was eaten by muskrats exceeded the annual production for that age-class. For clams of age-8 in particular, the biomass of clams > 70 mm long which was eaten exceeded production by an amount equivalent to 30% of the estimated biomass in the lake. Muskrats appeared to deplete the biomass of clams > 70 mm long in the lake for clams age-7 and older.

Fecundity estimates

Clams in the study area did not mature until a length of 50 mm (4–5 years old). The number of glochidia produced per clam increased as a function of clam length (Fig. 6). Clams 60–65 mm long produced the greatest total number of glochidia (Table 4). Overall, muskrats ate 7.5% of the glochidia produced in the study area. Muskrats ate a proportionately larger fraction of the reproductive output of larger clams; 21% of the glochidia of clams > 70 mm long but only 6% of the glochidia of clams < 70 mm long.

DISCUSSION

The largest clams in Narrow Lake were most strongly affected by muskrat predation. This differs from studies of decapod predation on bivalves in which the smaller size-classes of bivalves are most vulnerable to predators (Edwards & Huebner 1977; Elner & Jamieson 1979; Boulding & Hay 1984). The size-selective predation by muskrats on clams in this study could be used to model the effects of human exploitation of non-food limited fish populations in which the harvest removes the largest individuals. Clam growth in Narrow Lake is not food-limited (Hanson, Mackay & Prepas 1988b) and muskrats selectively removed the largest clams from the population in a manner similar to human harvest of many fish species. If the exploitation of a fish population is relatively low, the depletion of the population of larger individuals can remain undetected for many years and can even result in genetic selection for slow growth (Handford, Bell & Reimchen 1977; Favro, Kuo & McDonald 1979; Beacham 1983). The likelihood of detecting overharvest of fish or clams depends, however, on the size threshold used. In the present study, the harvest did not exceed the annual production of clams > 60 mm long whereas the harvest greatly exceeded production for clams > 75 mm long (Table 2). Depletion of the population of clams > 75 mm long could be detected after 1, or at most 2 years. The median length of clams eaten was 63.4 mm. If a threshold length of 65 mm were used, then it would take many years to detect a decline in the abundance of clams > 65 mm long (based on a decline of 3% per year). Variation in year-class strength and annual production could further mask any decline. The fact that muskrats ate the fastest growing individuals from nearly all age-classes and proportionately more of the reproductive output of the fast growing clams suggests that muskrat predation could select for slow growth in clams in Narrow Lake.

It is unlikely that muskrat predation has resulted in selection for slow growth of clams in Narrow Lake. Genetic selection for slow growing clams requires the whole population of clams in the lake be exposed to the same intensity of predation over a number of years. This is unlikely because muskrat populations fluctuate widely (Elton & Nicholson 1942; Errington 1954; Clay & Clark 1985). Furthermore, the intensity of muskrat predation varied between years and between basins in Narrow Lake (this study). Although the Walford plot (Fig. 1) indicated strong size-dependent mortality for clams > age-7, the data for clams 1–8 years old indicated there has been little or no selection for slow growth. Until age-8, the *Anodonta* in Narrow Lake had the same growth potential as *Anodonta* elsewhere. The theoretical maximum length (or L_{∞}) for clams in Narrow Lake was 150 mm, which compares favourably with estimates of 159 mm for *A. grandis* in Ontario (McCuaig & Green 1983) and 163 mm for *A. woodiana* in Hong Kong (Dudgeon & Morton 1983). Furthermore, clams became sexually mature at a length of 50 mm (4 or 5 years old) in Narrow Lake and do not reach a mean length of 65 mm until age-8. This

means that even the fastest growing clams would have a chance to reproduce several times before becoming vulnerable to muskrat predation. We hypothesize that genetic selection for slow growth could occur if muskrats change their size selectivity in response to declines in the abundance of large clams and maintain similar levels of exploitation.

The effect of muskrat predation on the age structure of the clam population was weak. Muskrat predation only exceeded annual production for clams 12 years old. Although *Anodonta grandis* live to > age-12 elsewhere (Green 1980; McCuaig & Green 1983), no clams > age-12 were collected from Narrow Lake. However, seventy-four (0.2%) of the shells collected from middens were 13–15 years old which shows there were clams > age-12 in Narrow Lake. The lack of clams > age-12 in our samples from the lake probably reflects the small likelihood of detecting such rare individuals with a sample size of 954 clams. It is also possible that the low number of clams > age-12 in the lake represents a number of poor year-classes and not the effects of muskrat predation.

A number of factors can influence the effect of muskrat predation on the clam population. The overall production: biomass ratio for clams in Narrow Lake during 1986 was low (0.19) compared with 1985 (0.25; Hanson, Mackay & Prepas 1988a), probably as a result of lower water temperatures. Differences in annual production could reduce the impact of muskrat predation on larger clams. However, the production: biomass ratio was low (<0.10) for large clams in both years. Unionid clam year-class strength is highly variable in Narrow Lake and elsewhere (Negus 1966; Tudorancea 1972; Hanson, Mackay & Prepas 1988a) and a series of strong year-classes would lessen the impact of muskrat predation on the clam population if the muskrat predation rate were relatively constant. However, muskrat predation rates will vary as a consequence of fluctuations in the muskrat population or due to variation in the availability of alternate foods. Thus, the effect of muskrat predation on the clam population will also vary.

The calculations in this study were based on the open-water season and if muskrats feed on clams in winter the effects of their predation would be greater. Muskrats in Narrow Lake live in bank burrows and it was impossible to determine whether they fed on clams in winter and left the shells in the burrows. Regardless, by having accurate estimates of the biomass, age structure, and size structure of the natural population, this study has shown that relatively little (but highly size-selective) exploitation was sufficient to exceed annual production and reduce the reproductive output of the largest size-classes of clams in the lake.

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