

# Effect of size-dependent muskrat (*Ondatra zibethica*) predation on the spatial distribution of a freshwater clam, *Anodonta piscinalis* Nilsson (Unionidae, Bivalvia)

Jukka Jokela and Pia Mutikainen

**Abstract:** We studied the effect of central-place foraging by muskrats on the spatial distribution of freshwater clam *Anodonta piscinalis*. We also analysed the prey-size preference of muskrats. We collected *A. piscinalis* shells from four muskrat middens representing different prey populations and sampled the clam populations quantitatively. Muskrats had clear effects on the spatial distribution of the clams. At all study sites the area close to shore had no clams. The width of the empty area was correlated with the number of shells found in the muskrat midden. The density of clams decreased and their mean size increased with the distance from muskrat midden at two of the sites. Muskrats did not prey on clams smaller than 50 mm. Muskrats preferred 60- to 70-mm clams at three of the sites and 85- to 90-mm clams at the fourth. In an analysis conducted using ages, a selection gradient on the growth rate of clams was found for three of the study populations. However, spatial refuge from predation and inconsistency of selection may slow down or counterbalance the evolutionary response to predation.

**Résumé :** Nous avons étudié les effets de la concentration des efforts de quête de nourriture du Rat-musqué commun sur la répartition spatiale de la moule d'eau douce *Anodonta piscinalis*. Nous avons également étudié les préférences de proies quant à la taille chez ce rat-musqué. Nous avons examiné quatre zones de défécation de rats-musqués et y avons recueilli les coquilles de moules représentant des populations différentes de proies et nous avons également procédé à une analyse quantitative des populations de moules. Les rats-musqués avaient une influence bien définie sur la répartition spatiale des moules. À tous les sites, la zone près des rives était dépourvue de moules. La largeur de la zone vide était en corrélation avec le nombre de coquilles trouvées dans les zones de défécation. À deux endroits, la densité des moules était moins élevée et leur taille moyenne, plus élevée, au fur et à mesure qu'augmentait la distance de la zone de défécation la plus proche. Les rats-musqués ne consommaient pas les moules plus petites que 50 mm; ils ont montré une préférence pour les moules de 60–70 mm à trois des sites et pour les moules de 85–90 mm au quatrième. Une analyse en fonction de l'âge a démontré l'existence d'un gradient de sélection sur le taux de croissance des moules chez trois des populations. Cependant, le refuge à l'abri des prédateurs et l'action aléatoire de la sélection peuvent ralentir ou contre-balancer la réponse évolutive à la prédation.  
[Traduit par la Rédaction]

## Introduction

Predation may have both ecological and evolutionary effects on the prey population. It is well known that predation may have an effect on the prey population dynamics (Hansson and Henttonen 1985, 1988; Steen et al. 1990) and on the spatial

distribution of prey (Zaret 1980; Ramcharan et al. 1992). In foraging theory, optimal prey is defined as prey that returns the highest amount of energy per unit time spent searching, transporting, and handling the prey (Stephens and Krebs 1986). Several studies have shown that in the case of hard-shelled molluscs, the handling time of prey increases as a function of mollusc size (Prejs et al. 1990; Robles et al. 1990; Ward 1991). As a consequence, most of the predators of molluscs are expected to select their prey according to size, preferring a size that is optimal in terms of used and gained energy. One outcome of size-selective predation is a difference in size distribution between prey individuals available and prey individuals consumed. In addition, size-selective predators that forage from a certain fixed location (nest site, feeding stone, etc.) and return to this location to handle and consume captured prey (central-place foraging; Orians and Pearson 1979) may change both the spatial and

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**Table 1.** Sampling sites, numbers of clams sampled, and numbers of shells collected from muskrat middens.

	Site A	Site B	Site C	Site D
No. of 1-m <sup>2</sup> plots	180	30	55	30
No. of clams	212	444	252	525
No. of clams eaten	60	257	90	101
Distance from shore <sup>a</sup> (m)	30–92	20–29	15–34	3–18
No. of clams per 1-m <sup>2</sup> plot	1.18 (1.49)	14.80 (13.01)	4.58 (6.16)	17.50 (17.12)
Depth (DPTH; m)	2.15 (0.30)	6.01 (0.76)	1.96 (0.36)	1.02 (0.28)
Current speed (CRVL; m/s)	0.11 (0.04)	0.14 (0.03)	0.09 (0.03)	0.23 (0.07)
Percentage of vegetation	18.28 (25.30)	0.67 (2.17)	64.00 (32.48)	18.83 (17.80)
Percentage of rock (PCST)	22.41 (18.84)	5.00 (10.67)	6.93 (12.11)	37.33 (27.50)
Sediment coarseness (SECO)	5.73 (0.61)	4.20 (0.55)	3.91 (1.07)	6.75 (1.74)
Percentage of organic sediment (ORG)	1.26 (1.57)	0.68 (0.34)	4.65 (3.50)	1.05 (0.71)

Note: Values in parentheses are standard deviations of the mean.

<sup>a</sup>Distance of the sampled transects from the muskrat midden. The starting point of the transect indicates the distance from the midden to the first clams offshore.

size distributions of their prey. One prediction of the central-place-foraging models is that larger prey are transported from a greater distance than small prey.

Predation may also induce evolutionary changes in the life-history traits of the prey. For example, preference for the largest prey individuals may function as a selective pressure favouring earlier reproduction (Reznick et al. 1990; Luning 1992; Stibor 1992) or evolution of defensive structures that decrease the risk of predation (Luning 1992; Spitz 1992).

We studied the prey preference of muskrats (*Ondatra zibethica*) in four populations of a freshwater clam, *Anodonta piscinalis* Nilsson (= *Anodonta anatina* L.). The interaction between muskrat and clam is suitable for studies of size-selective predation for several reasons. First, muskrats are the main predators foraging on adult freshwater clams in Scandinavia. Muskrats were introduced into the Finnish fauna in the 1920s from North America, where clams are a part of their normal diet (Van Cleave 1940; Hanson et al. 1989; Neves and Odom 1989). Clams are the primary food for muskrats during the winter, and in areas of scarce macrophyte vegetation in other seasons as well (Reichholf 1975; Hanson et al. 1989; Neves and Odom 1989). Secondly, there is considerable variation in size and growth rate of individual clams of the same age both within and among clam populations (Haukioja and Hakala 1978b). According to Reichholf (1975), Hanson et al. (1989), and Convey et al. (1989), muskrats prefer the largest and fastest growing clams. Since the fitness of a clam increases with its growth rate and longevity (Haukioja and Hakala 1978a), size-selective predation, if severe enough, may cause a selection gradient that is opposite to the favourable trait composition without predation.

In addition, the system is easy to handle methodologically. Muskrats are territorial (Messier et al. 1990; Hjalten 1991; Marinelli and Messier 1993) and use particular feeding sites, where the shells of predated clams accumulate (Convey et al. 1989; Hanson et al. 1989). Usually only one-half of the shell is broken while the other remains intact. From the intact half of the shell it is possible to reliably measure the size and growth of the predated clam (Convey et al. 1989; Hanson et al. 1989). Similarly, it is possible to collect quantitative

samples showing the density, age, and size structure of the living clam population. Finally, changes in the spatial distribution of the clams can be measured without continuous observation, since clams are rather sessile.

We addressed the following questions: (i) Does muskrat predation affect the population density or spatial distribution of the clams? (ii) Is the predation size selective? (iii) Do the prey-size preferences of muskrats differ among the populations? (iv) If it is size-selective, does predation generate selection on the growth rate of clams?

## Material and methods

### Description of the study sites

We sampled four sites along the Rautalampi water course in central Finland (62°32–37'N, 26°15–20'E). Site A is an oligotrophic, slow-flowing lake outlet. The bottom material consists of sand and boulders with scarce macrophytes (*Lobelia dortmanna*, *Isoetes* sp., and *Myriophyllum* sp.) (Table 1). Site B is a large pool below a riffle about 150 m downstream from site A. The bottom is sorted sand with practically no vegetation. Site C is a more eutrophic, slow-flowing part of the water course, about 20 km downstream from sites A and B. The bottom material is a mixture of fine sand and soft sediments covered by *Ranunculus peltatus* and the water moss *Fontinalis antipyretica*. Site D is a streamlike part of the water course, about 200 m below site C. There is a riffle between sites C and D. Near the shore at site D the bottom material is sorted sand; in the middle of the channel it is coarser, with some boulders and bigger stones. At site D the water current is faster than at the other sites, especially in the middle of the channel (Table 1).

### Collection of data

We collected one midden of clam shells eaten by muskrats from each of the four sites at the end of May and beginning of June 1986 (Table 1). Since clam shells decay considerably in 3 months (J. Jokela, unpublished data), the shells collected were those of clams consumed during the previous winter. We did not find remains of newly eaten clams at any of the sites during the summer.

We sampled the clam population at each site in May, July,

and September. Samples were collected from 1-m<sup>2</sup> plots arranged as three transect lines (one transect per month) perpendicular to the shore (Table 1). We began the transects from where a SCUBA diver starting from the location of the muskrat midden at the shore found the first clams offshore. The diver was experienced in detecting clams, and used only vision to locate the first clams. The plots of the transects were framed with a portable metal grid (area 1 m<sup>2</sup>) to ensure exact sampling. All the plots were searched twice by the diver. The diver also searched for clams by hand (in the top 10 cm of the sediment), and was thus able to find the clams (mainly young ones) burrowed in the sediment. The minimum length of the transect was 10 m; however, if we found fewer than 60 clams within 10 m, we extended the transect.

We measured several abiotic and biotic characteristics of the habitat (Table 1) to assess the microhabitat preferences, if any, of the clams. Before collecting the clams, the diver estimated the percentages of vegetation cover and rocky surface for each plot. The diver also measured water depth and took a sediment sample upstream from the plot by pressing a plastic 1-L container into the sediment to a depth of 5 cm, then pushing a shovel under the container and sealing it underwater. Current velocity was measured at every fifth plot as the time taken for a water-filled plastic bag with a volume of 2 L to travel 5 m. Where necessary because of abrupt changes in turbidity or bottom material, the current velocity was measured at every second plot.

#### Laboratory methods

In the laboratory, we determined the length and age of the clams, and the length at each year ring using Vernier calipers (Haukioja and Hakala 1978b). In this species annuli are easily distinguished from false rings, and age determination by annuli is reliable, as verified by Haukioja and Hakala (1978b) and Pekkarinen (1991).

We sieved dried (60°C, 40 h) sediment samples into 10 fractions with a Wentworth sieve series (Cummins 1966) in which each size category is twice the preceding one (from <0.063 to >16 mm). Before sieving, part of each sample was separated for analysis of the organic matter content, which was calculated as the percentage of mass lost during burning (700°C, 2 h).

We calculated the index of sediment coarseness (SECO) as

$$\text{SECO} = \sum_{i=1}^n \left[ \frac{p_i(n-i+1)}{n} \right]$$

where  $n$  is the total number of sediment fractions sieved (10), and  $p_i$  is the relative mass of fraction  $i$  in a sample. The index is assigned a value between 1 and 10; the higher the value, the coarser the sediment.

#### Data analysis

The foraging pattern of muskrats is spatially uneven, resembling central-place foraging (Orians and Pearson 1979). In this case the central place is a point on the shoreline (midden). We analysed the spatial effects of predation using three analyses. First, to estimate the area from which the clams were removed, we converted the number of clams in the muskrat midden to spatial units. This was done by calculating the number of square metres to which the number of

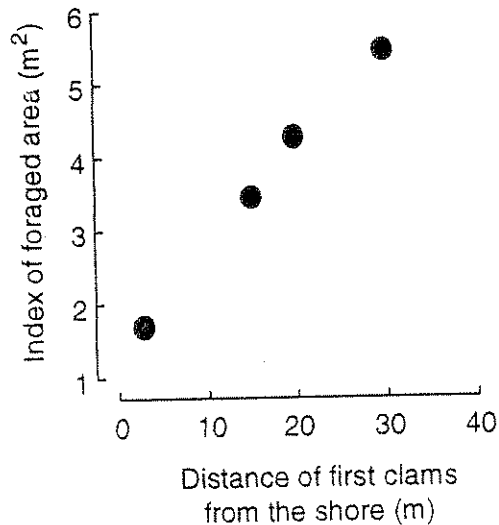
clams in the midden corresponds (number of clams in the midden/maximum density of living clams at the area). We calculated correlation coefficients between this index of foraged area and the distance of the closest clams to the muskrat midden. We repeated the analysis using the average density of clams in calculating the index of foraged area. However, since muskrat predation may decrease the density of clams, maximum density may be a more reliable estimate of the original density of the clam population. The prediction is that if muskrats remove clams in a systematic fashion, as the index of foraged area increases, the distance of the first clams from the shore also increases. Secondly, size-dependent predation may also affect the spatial size distribution of clams in the foraging area, as may be concluded from the predictions of central-place-foraging models. To estimate the spatial size distribution of clams, we calculated correlation coefficients between the distance of the plot from the shore and the mean length of the clams in the plot for all plots that had at least three clams. Thirdly, to detect a possible density gradient, we calculated correlation coefficients between clam density and distance from the shore. The two latter analyses were conducted separately for each of the study sites.

The density of clams may, of course, be independent of muskrat foraging and follow some environmental gradient. We used multiple regression to determine if it is possible to explain the density of clams using information about the habitat. Analysis was conducted for each site. The dependent variable was the number of clams per plot. Current velocity, depth, percentage of stony surface, organic content of the sediment, and SECO were used as independent variables. The number of clams per plot was log-transformed to reach normally distributed and homoscedastic residuals.

To discover if predation was size dependent, we used the length of the clams (divided into 5-mm categories according to the length in the previous year) in logit models to explain the probability of being chosen as prey by muskrats. In the logit analysis, the binomial dependent variable (in this case predated or living) can be explained with either categorical or continuous independent variables. We used length as a categorical independent variable to be able to fit nonlinear preference profiles to the data. In the modelling we used only those length categories for which we had data on both predated and living individuals. Suitable length ranges at sites A, B, C, and D were 46–85, 46–90, 56–95, and 46–100 mm, respectively, at 5-mm intervals. We first tested whether predation was independent of prey size (i.e., whether the proportion eaten was the same in all length categories). Secondly, we tested whether the predator preferred larger individuals to smaller ones, or certain size classes to others. For this purpose the proportion of preyed clams in each length category was fitted against linear (preference for larger clams) and quadratic (preference for a certain size class) profiles using contrasts (Fig. 4). Quadratic profiles were constructed around the modal size class (Fig. 4). See Murtaugh (1988), Salonen and Penttinen (1988), Festa-Bianchet (1989), Gotceitas and Colgan (1989), and Laurie and Brown (1990) for examples of the method and Norusis (1990) for details of the statistical procedure.

Size-selective predation may cause a selection gradient for growth rate, leading to a genetic change in the population. In

**Fig. 1.** Distance of first clams found offshore in relation to the index of foraged area. The index of foraged area is calculated by dividing the number of shells collected from the muskrat midden by the maximum density of clams at each site. From left to right, sites are D, C, B, and A, respectively.



clams of the genus *Anodonta*, the length at 3 years of age is the best estimate of the individual growth rate (Haukioja and Hakala 1978b). If a certain prey size class is preferred, we predict that below the age corresponding to the preferred size, the faster growing individuals of the age-class are preferred, whereas above the age corresponding to the preferred size the slower growing individuals are preferred as prey. We compared the growth rates of predated and living clams by age, using two-way analysis of variance. Analysis was performed separately for each site. In this analysis, interaction between age and predation suggests that selection on growth rate depends on age. Age-classes that had fewer than three individuals in either of the prey groups were excluded from the analysis. The assumptions of analysis of variance (normality of residuals and homogeneity of cell variances) were checked.

The statistical analyses were performed with the SYSTAT® (SYSTAT Inc., Evanston, Ill.) and SPSS® (SPSS Inc., Chicago, Ill.) statistical packages.

## Results

### Effect of muskrat foraging on the spatial distribution of clams

The distance from the shore to the point where the first clams were detected varied from 3 m at site D to 30 m at site A (Table 1). The distance of the nearest clams correlated positively with the index of foraged area (Pearson's  $r = 0.998$ ,  $N = 4$ ,  $P = 0.002$ ) (Fig. 1). When the average density of clams was used in calculating the index, the results did not change (Pearson's  $r = 0.914$ ,  $N = 4$ ,  $P = 0.086$ , one-way  $P = 0.043$ ). At three of the sites clam density increased with distance from the shore (Pearson's  $r = 0.29$ ,  $P < 0.001$ ;  $r = 0.65$ ,  $P < 0.001$ ; and  $r = 0.67$ ,  $P < 0.001$  for sites A, C, and D, respectively) (Fig. 2). The correlation was strongest at sites C and D, where the first clams were closest

**Table 2.** Multiple regression models of the relationship of clam density and abiotic environmental variables at the four study sites.

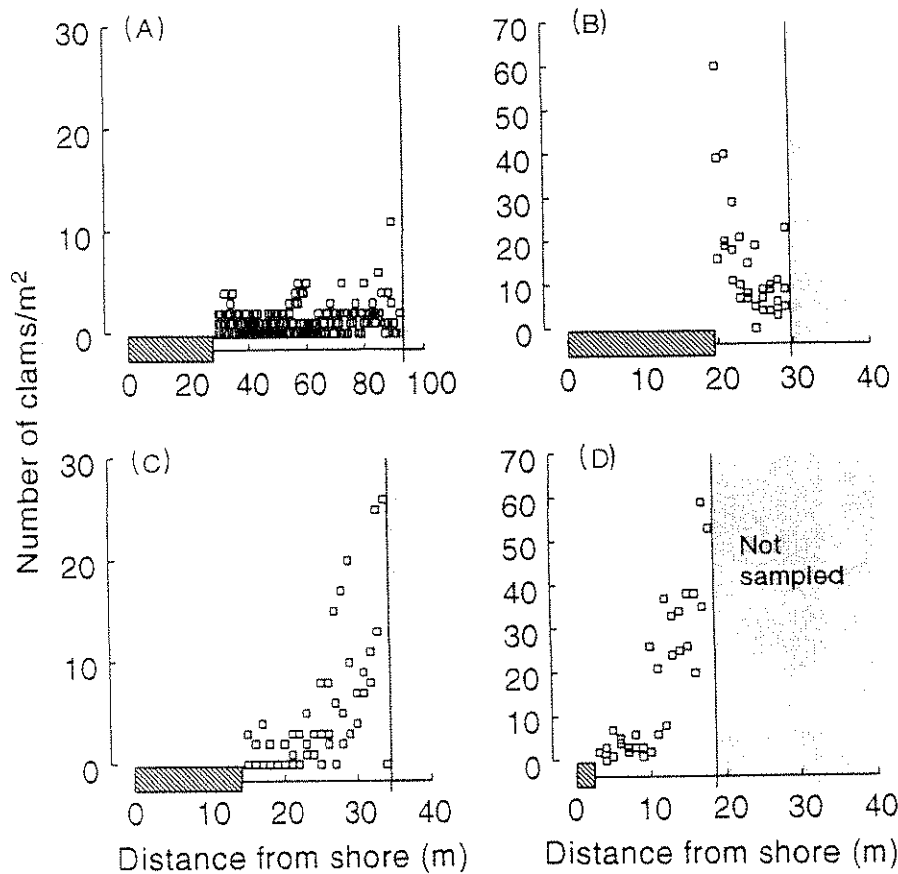
Independent variable	Coefficient	SE	Standardized coefficient	<i>t</i>	<i>P</i>
<b>Site A</b>					
DPTH	-0.411	0.154	-0.210	-2.670	0.008
PCST	-0.002	0.002	-0.050	-0.642	0.522
CRVL	1.742	1.195	0.115	1.458	0.147
SECO	0.114	0.072	0.120	1.574	0.117
ORG	0.040	0.028	0.106	1.426	0.156
Constant	0.616	0.564		1.091	0.277
$R^2 = 0.10$ , $F_{5,168} = 3.750$ , $P = 0.003$					
<b>Site B</b>					
DPTH	-0.345	0.162	-0.323	-2.137	0.043
PCST	0.041	0.011	0.530	3.672	0.001
CRVL	-4.654	5.027	-0.179	-0.926	0.364
SECO	0.383	0.264	0.258	1.451	0.160
ORG	1.025	0.512	0.422	2.003	0.057
Constant	2.698	1.326		2.035	0.053
$R^2 = 0.54$ , $F_{5,24} = 5.715$ , $P = 0.001$					
<b>Site C</b>					
DPTH	1.535	0.288	0.549	5.322	0.000
PCST	0.006	0.009	0.071	0.672	0.505
CRVL	-8.846	3.907	-0.228	-2.264	0.028
SECO	0.215	0.108	0.227	1.991	0.052
ORG	-0.029	0.031	-0.100	-0.936	0.354
Constant	-1.781	0.736		-2.419	0.020
$R^2 = 0.55$ , $F_{5,47} = 11.655$ , $P = 0.001$					
<b>Site D</b>					
DPTH	2.433	0.671	0.620	3.624	0.001
PCST	0.020	0.005	0.464	4.004	0.001
CRVL	0.884	3.236	0.053	0.273	0.787
SECO	0.017	0.099	0.025	0.173	0.864
ORG	-0.045	0.173	-0.027	-0.262	0.796
Constant	-1.132	0.622	0.000	-1.819	0.081
$R^2 = 0.87$ , $F_{5,24} = 15.130$ , $P < 0.001$					

Note: Independent variables are defined in Table 1.

to the shore (Table 1, Fig. 2). At site B the correlation was negative ( $r = -0.61$ ,  $P < 0.001$ ). Mean length of clams correlated positively with distance from the shore at sites C and D (Pearson's  $r = 0.50$ ,  $P = 0.008$  and  $r = 0.557$ ,  $P = 0.002$ , respectively), indicating that foraging may have an effect on the size distribution of clams at some sites. However, the correlation did not exist at sites A and B (Pearson's  $r = 0.054$ ,  $P = 0.806$  and  $r = -0.210$ ,  $P = 0.275$ , respectively).

Regression analyses of the density of clams and the environmental variables showed that density was not related to the same characteristic of the habitat at all sites (Table 2). At site A, independent variables explained only 10% of the variation in the density of clams, whereas at sites B, C, and D they explained more than 50% of the variation. At two of the four sites (A, B), the density of clams decreased with depth and in two (C, D), it increased with depth. The density of clams was higher at sites B and D, where the percentage

Fig. 2. Number of clams per sample plot in four study sites plotted against the distance of the plot from the shore (sites A–D). The hatched bar depicts the width of the area where clams were not found. The stippled area depicts the area where censuses were not taken. Note the differences in the scales of the axes.



of stony surface was high, indicating that boulders had a positive effect on clam abundance. At site C, the density of clams increased as the current velocity increased.

#### Prey selection by size

In general, the muskrats ate only a few individuals under 50 mm long (Fig. 3). This is especially evident at sites C and D, where plenty of small clams were available.

At three of the sites (A, B, D) the most preferred size class was between 60 and 70 mm (Fig. 4). At sites A and B, the size-independent logit model did not fit the data, and size dependence could not be reduced to either linear or quadratic profiles (i.e., the contrast models did not fit) (Table 3, Fig. 4). This indicates that the observed preference profiles were more complex than the profiles we fitted to the data. However, the most preferred size classes were distinct in these populations too (Fig. 4). For site C, the linear model (preference for bigger clams) fits the data best, and for site D the quadratic model (preference for certain size classes) fits the data best (Table 3). However, for all sites the observed preference profile is more or less dome-shaped (Fig. 4).

#### Prey selection by growth rate

The growth rates of predated and living clams were compared by age for each of the study populations using two-way analysis of variance. At three of the four sites (B, C, D)

the age  $\times$  predation interaction was statistically significant (Table 4). At sites B and C, the faster growing clams of the youngest age groups, 5 and 6, were chosen as prey (Fig. 5). For the slower growing clams, the older age-classes were preferred; however, the difference is not as clear as among the young clams (Fig. 5). At site D the results may be suspect because the assumption of homogeneous variances was not fulfilled (Cochran's  $C_{31,16} = 0.150$ ,  $P < 0.001$ ). At site A neither the effect of predation nor the effect of the interaction between age and predation was statistically significant.

## Discussion

Our results suggest that predation decreased the density of clams in the foraging area and changed the spatial distribution of prey considerably. Three different analyses supported this conclusion. First, an increase in the distance of the first clams from the shore coincided with an increase in the area to which the number of shells in the muskrat midden corresponds (Fig. 1). Secondly, the density of clams increased with distance from the shore at sites where the first clams were closest to the shore (Fig. 2). Thirdly, mean clam size increased with distance from the shore at the same sites. The lack of large clams in the nearshore areas is difficult to explain as being due to any factor other than predation. In sites where there are no muskrats, clams may be found in

**Table 3.** Statistics of logit models fitted to the data.

Model		$\chi^2$	df	P
<b>Site A</b>				
Linear	P + P × Le(1)	30.53	6	<0.001
Quadratic	P + P × Le(2)	19.50	6	0.003
Constant	P	29.19	7	<0.001
<b>Site B</b>				
Linear	P + P × Le(1)	123.30	7	<0.001
Quadratic	P + P × Le(2)	187.51	7	<0.001
Constant	P	249.13	8	<0.001
<b>Site C</b>				
Linear	P + P × Le(1)	4.05	6	0.669
Quadratic	P + P × Le(2)	24.34	6	<0.001
Constant	P	26.34	7	<0.001
<b>Site D</b>				
Linear	P + P × Le(1)	21.34	9	0.011
Quadratic	P + P × Le(2)	4.62	9	0.866
Constant	P	22.30	10	0.014

Note: See the text for a description of models. P is a constant term; Le(1) is the linear contrast for length; Le(2) is the quadratic contrast for length;  $\chi^2$  is the likelihood ratio  $\chi^2$ . A high P value indicates a good fit to the data.

very shallow water (J. Jokela, personal observation). Reichholf (1975) and Hanson et al. (1989) have reported similar patterns of clam distribution in the foraging areas of muskrats.

The results of the regression analysis indicate that clam density may be related to certain microhabitat characteristics (Table 2). Depth, the occurrence of boulders, and current velocity all seem to be of importance. However, the intensity of muskrat foraging may also depend on these same habitat characteristics. Our study sites represent very different foraging habitats for muskrats. The densities of clam populations vary considerably, one of the sites is deeper than the others, and the distances muskrats have to swim while foraging differ among sites (Table 1). The energetic costs of foraging may be expected to increase with depth and current velocity. Furthermore, when clams were collected, the diver noted that clams were concentrated in the crevices between the boulders. The clams in the crevices were not visible, and had to be pulled out by hand. These clams may have been out of reach of muskrats. In this type of study it is difficult to separate the direct effect of habitat on the density of clams from the indirect effect of habitat on the foraging efficiency of muskrats.

The traditional microhabitat approach used to study the abundance of unionacean clams has recently been criticised as being inadequate (Strayer and Ralley 1993). The inconsistency of our results from different sites supports the view that large-scale geomorphological processes may be more useful predictors of clam densities than microhabitat characteristics (Strayer and Ralley 1993). Our results also emphasize that the occurrence of predators should be taken into account in such studies.

According to our results, muskrats selected clams larger than 50 mm as their prey (Fig. 3). Hanson et al. (1989) found

**Table 4.** Analysis of variance of differences in growth rate of clams (length at 3 years of age) by age and predation (predated versus not predated) at the four study sites.

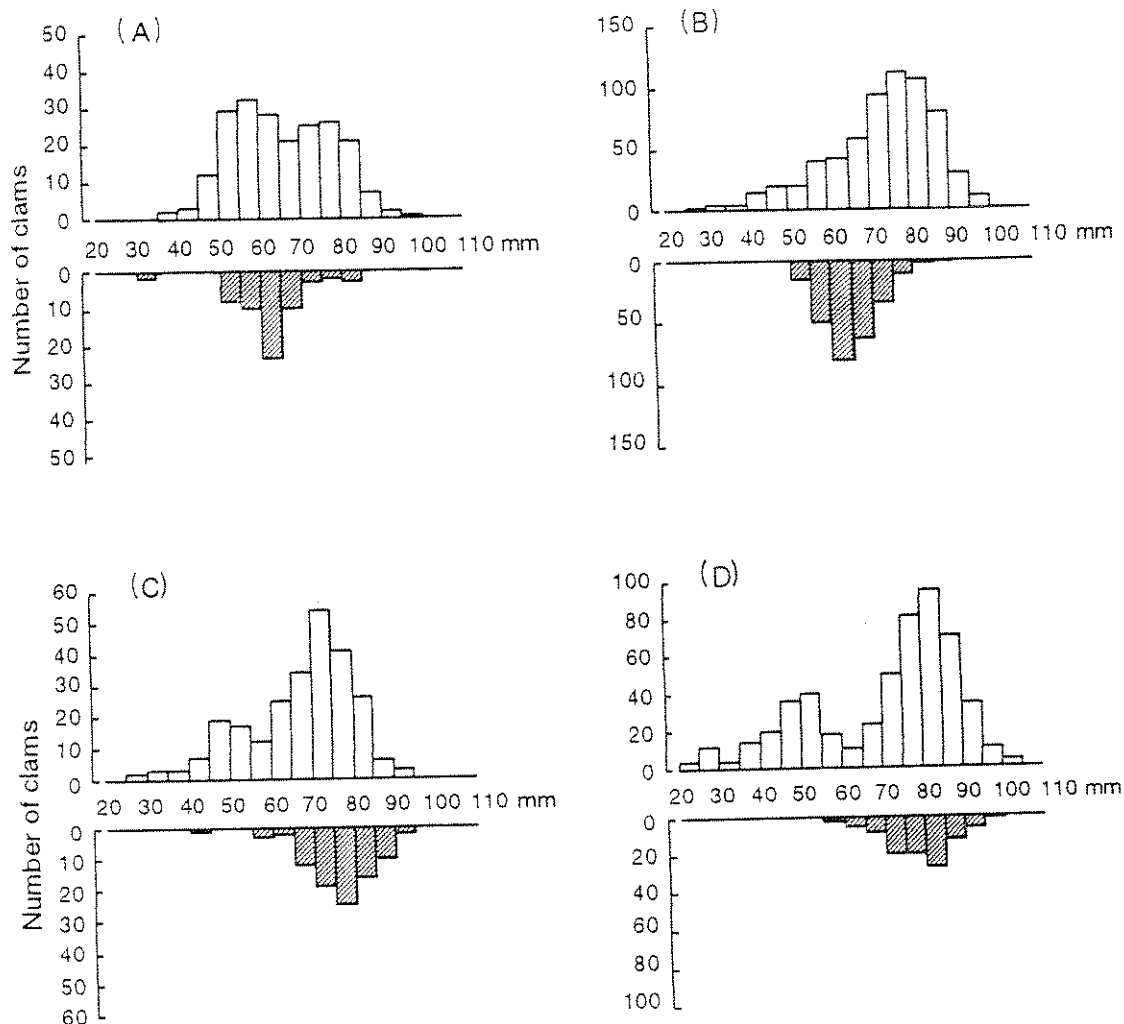
	MS	df	F	P
<b>Site A</b>				
Age	94.19	3	3.44	0.018
Predation	57.84	1	2.11	0.148
Age × predation	40.68	3	1.49	0.220
Error	27.37	165		
Cochran's $C_{21,8} = 0.20, P = 0.284$				
<b>Site B</b>				
Age	46.36	7	1.70	0.106
Predation	3.00	1	0.11	0.740
Age × predation	121.46	7	4.45	<0.001
Error	27.28	724		
Cochran's $C_{45,16} = 0.10, P = 0.043$				
<b>Site C</b>				
Age	174.23	8	5.11	<0.001
Predation	4.05	1	0.12	0.731
Age × predation	85.87	8	2.52	0.012
Error	34.07	263		
Cochran's $C_{15,18} = 0.10, P = 0.532$				
<b>Site D</b>				
Age	154.00	7	4.51	<0.001
Predation	126.23	1	3.70	0.055
Age × predation	106.64	7	3.13	0.003
Error	34.11	497		
Cochran's $C_{31,16} = 0.15, P < 0.001$				

Note: Age-classes included in the test are as depicted in Fig. 5.

the same threshold size in their study of muskrat predation on *Anodonta grandis simpsoniana* in Narrow Lake in southern Canada. This threshold may be due to the fact that young clams burrow in the sediment, and thus are not visible to muskrats. We do not have detailed data on the burrowing depths of *Anodonta* spp., but this behaviour was noted by the divers when they were collecting the clams. When they were going through the plot, they found small individuals only when searching the sediment by hand. If only clams that were visible had been collected, most small individuals would have been missed, as was noted also by Hanson et al. (1988) and Amyot and Downing (1991).

Clearly, muskrats had prey-size preferences in all of the four study sites. At three of the sites muskrats preferred 60- to 70-mm clams. At site C the largest clams (>85 mm) were the most preferred. This inconsistency in prey-size preference may be due to, for example, different sizes of the foraging muskrats (Convey et al. 1989). Although the quadratic preference profile fits the data only for site D, the preference by size at sites A, B, and D (Fig. 4) was surprisingly similar, considering the observed differences in the size distributions of clams that were available (Fig. 3). Our analyses do not yield information on the distance from which each clam was transported to the midden. Together with the results of the analysis of the spatial distribution of clams at two of the study sites (C, D), especially the increase in the mean size of clams

Fig. 3. Length distributions of clams grouped at 5-mm intervals at four study sites (A, B, C, D). Open bars indicate living clams and hatched bars predated clams.



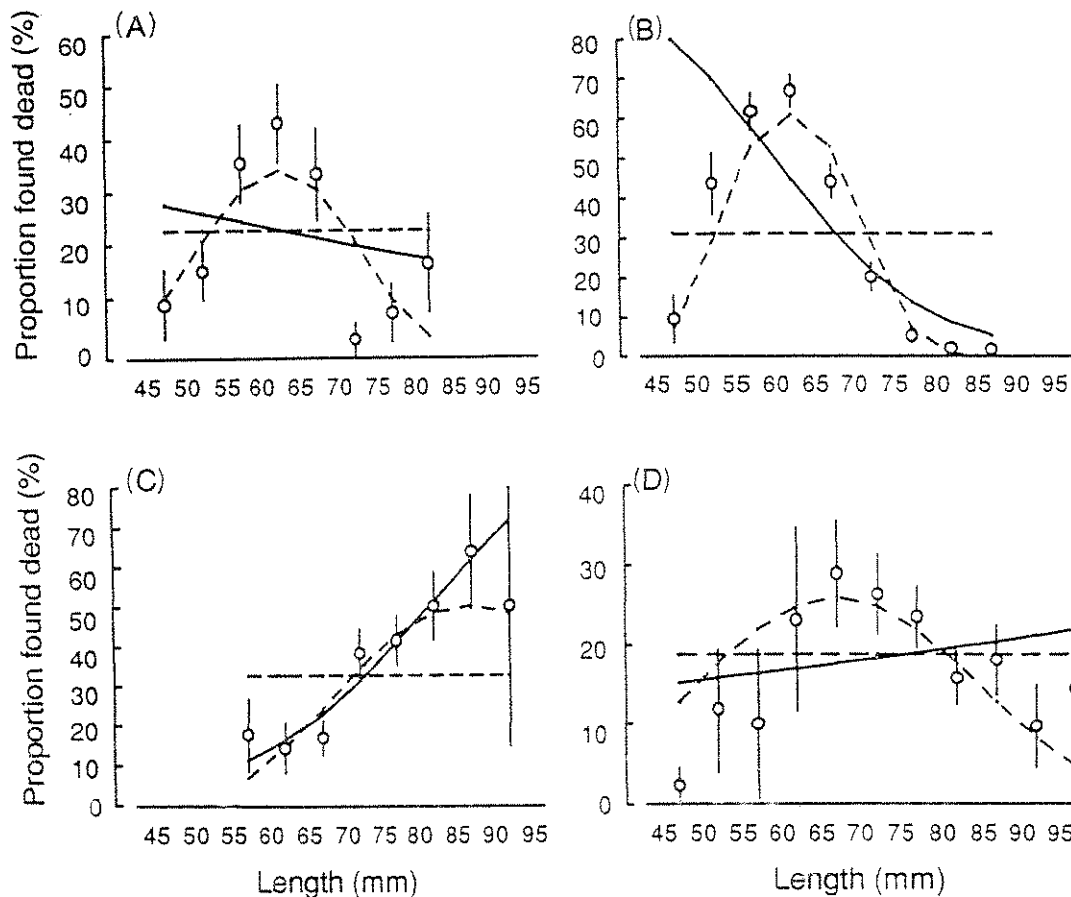
with distance from the shore, our results suggest that the large clams may not have been foraged as intensively from greater distances as the small ones. The lack of clams observed in the nearshore areas suggests that from shorter distances the size of the clam may not be that important, as long as it is large enough to be detected. Thus, optimal prey size could be modelled using a two-variable (clam size, distance from the shore) optimal foraging model, where transportation costs increase with prey size (Stephens and Krebs 1986; we thank J.M. Hanson for pointing this out to us).

An alternative explanation would be that muskrats had been foraging only within the nearshore area, where there were no clams left. Then, differences in the age and size distributions of predated and living clams could be due to differences between the near- and off-shore habitats. In lakes the growth rates of clams have been observed to change as a function of depth (Ghent et al. 1978; Huebner et al. 1990), suggesting also that age and size distributions may change with depth. It is most probable that the growth-rate differences in lakes are caused by temperature and resource gradients, not by depth per se (Hanson et al. 1988). At our study sites currents mix the water and thus there are no steep

gradients in temperature or resources. Furthermore, at three of our study sites the maximum depth is less than 3 m, so they are shallow compared with the depth distribution of clams in lakes. Therefore, it is not likely that differences in the age and size distributions of predated and living clams were due to some environmental gradient between near- and off-shore habitats. Another alternative explanation for the observed spatial distribution of clams is that clams do not live in nearshore areas in the first place. This is not supported by our observations of clam populations where muskrats are not present, nor by studies of the spatial distribution of *Anodonta* spp. along a depth gradient (Haukioja and Hakala 1974; Ghent et al. 1978; Hanson et al. 1988; Huebner et al. 1990). However, where ice is thick or the littoral zone is exposed to high waves, clams may be absent from shallow areas. In our study sites the ice cover during the winter is relatively thin (<30 cm) because of currents.

If prey of an intermediate size is preferred, faster growing individuals are selected below the preferred age and slower growing individuals above the preferred age. In our analysis by age, this may be observed as a decrease in the growth rate of predated clams by age. Theoretically, if predation is

**Fig. 4.** Proportion ( $\pm$  binomial SE) of clams predated in each size class at the four study sites (A, B, C, D). Lines depict expected frequencies of fitted LOGIT models and indicate the shape of the contrast used. The broken horizontal line represents the constant model: The constant model fits if predated clams are not selected by size but chosen in relation to abundance of each size class. The solid line represents models with linear contrasts. The line is slightly curvilinear because the expected frequencies cannot have negative values. The linear model fits if either larger (positive slope) or smaller clams (negative slope) are preferred to others. The broken curve represent models with quadratic contrasts. These contrasts were built around the modal size class to test for preference for a particular clam size. See the text and Table 2 for statistics and choice between models.



intense enough, this kind of selection may favour genotypes that either grow slowly, and avoid predation by being small, or grow fast to a large size, thus minimizing the time during which they are vulnerable to predation (Luning 1992; Black 1993). Both responses would require major alterations in the growth pattern and life-history traits of *Anodonta* spp. In Finland these clams live in calcium-poor soft water, where a substantial increase in growth rate is a physiologically demanding task. A decrease in growth rate would also lead to a considerable decrease in lifetime reproductive output if it does not occur simultaneously with an increase in longevity.

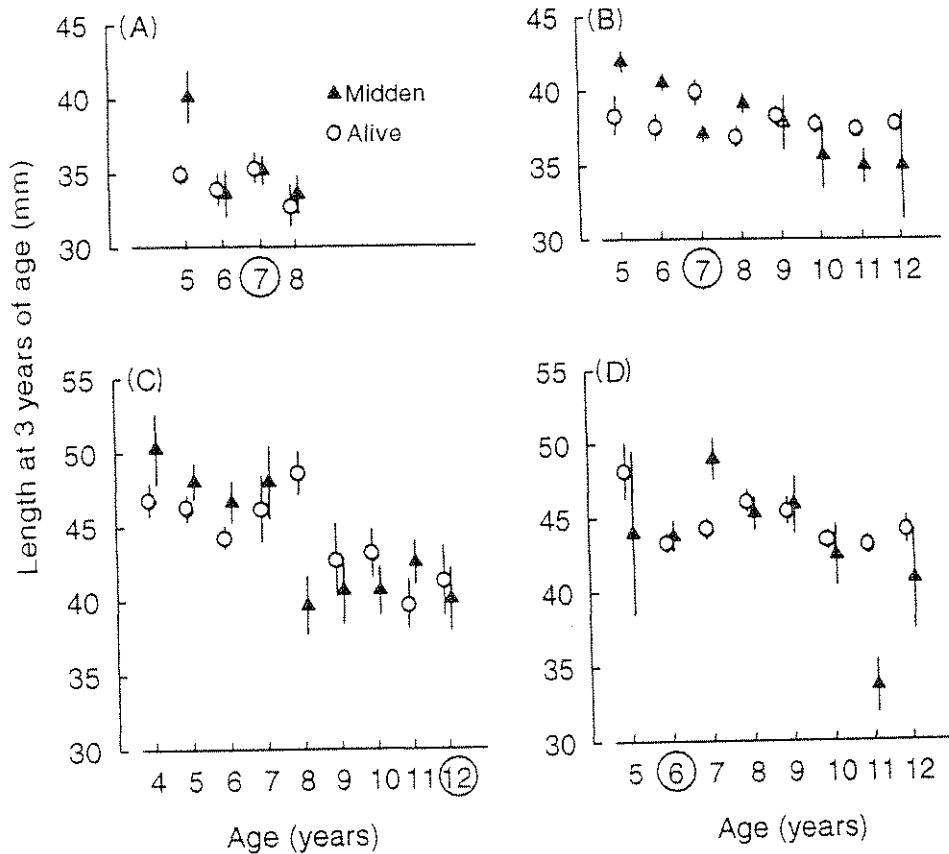
Predation may also select for certain types of behaviour. Small clams burrow in the sediment, so only the siphons are exposed when they are feeding. Recent studies have shown that clams filter actively during darkness and are more often closed in the morning (Englund and Heino 1994). Burrowed individuals that are not feeding may be difficult to detect visually. If muskrats are not able to find nonfeeding individuals burrowed in the sediment, selection may favour clam

genotypes feeding at night and tending to spend more time burrowed in the sediment. Unfortunately, studies of burrowing depths and feeding behaviour of clams are scarce (but see Amyot and Downing 1991; Englund and Heino 1994) and are usually not connected to the predation history of the population under study.

As noted above, discussion of a putative genetic change in individual growth rates in response to muskrat predation is relevant only if muskrat predation is intense enough, and if predation imposes a selection gradient on the growth rate of clams. However, the selection gradients we documented were not consistent or clear (Fig. 5). Muskrats chose fast-growing young individuals at three of the sites, for two of which there were statistically significant age  $\times$  predation interactions (Table 4, Fig. 5). Among old individuals there was no clear pattern, although there was a slight tendency towards the predicted pattern (Fig. 5). The result was the same if clam size was used as an index of growth. It is not clear if predation is strong enough to lead to selection, giving



Fig. 5. Length at 3 years of age of living ( $\circ$ ) and predated clams ( $\blacktriangle$ ) by age at the four study sites (A, B, C, D). Values depict means  $\pm$  1 standard error for all age-classes that had more than three representatives in both groups. The circled age on the x axis is the most preferred size class at that site.



an advantage to genotypes with a specific growth pattern. Hanson et al. (1989) approached this problem quantitatively. They documented a clear selection gradient for slower growth, but after measuring the intensity of predation they were, as we are, reluctant to draw far-reaching evolutionary conclusions about possible adaptive responses to predation.

To summarize, muskrats are efficient predators capable of changing the spatial distribution of their prey population. However, predation is most intense close to the shore, thus releasing part of the clam population from the risk of predation. Muskrats chose their prey by size, but not necessarily similarly at each site. Predation may cause selection on the growth rate of clams, but it is not clear whether predation is strong enough to lead to genetic changes in the prey population. Muskrat predation on clams would make an excellent study system for optimal foraging theory. The foraging behaviour, time budget, and energetics of muskrats in relation to the spatial and demographic structure of the exploited clam population are worth further studies.

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