Effect of size-dependent muskrat (Ondatra zibethica) predation on spatial distribution of a freshwater clam, Anodonta piscinalis Nilss. (Unionidae, Bivalvia)

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Abstract

We studied the effect of central-place-foraging by muskrat on the spatial distribution of freshwater clam, Anodonta piscinalis. We also analysed the prey size preference of muskrats. We collected Anodonta 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 correlated with the number of shells found in the muskrat midden. Clam density decreased and their mean size increased with the distance from muskrat midden at two of the sites. Muskrats chose their prey according to size, not preying on clams smaller than 50 mm. In three of the sites muskrats preferred 60-70 mm clams, and at one 85-90 mm clams. These results indicate that muskrat predation may considerably decrease clam population densities. However, the most intense foraging is limited to the areas close to shore. In an analysis conducted by age, a selection gradient on the growth rate of clams was found at three of the study populations. However, spatial refugee from predation and inconsistency of selection may slow down or counterbalance the evolutionary response to predation.

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 time unit 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 which is optimal in terms of used and gained energy. One expected outcome of size-selective predation is a difference in the size-distribution between prey individuals available and prey individuals consumed. In addition, size-selective predators that forage from certain fixed location (nest-site, feeding stone, etc.) and return this location to handle and consume captured prey (central-place-foraging, (Orians and Pearson 1979), may change both the spatial and size-distribution of their prey. One prediction of the central-place-foraging models is that larger prey is transported from further 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, Spitze 1992).

We studied the prey preference of muskrat (Ondatra zibethica) in four populations of a freshwater clam, Anodonta piscinalis Nilss. (= Anodonta anatina L.). The interaction between muskrat and clam is suitable for studies of size-selective predation for several reasons. First, in Scandinavia, muskrat (Ondatra zibethica) is the main predator foraging on adult freshwater clams. Muskrat was introduced to Finnish fauna in the 1920's from North America, where clams are a part of muskrats 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 the size and growth rate of clam individuals of the same age both within and among clam populations (Haukioja and Hakala 1978b). According to Reichholf (1975) and Hanson 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 opposite to what is the favourable trait composition without predation.

In addition, the system is easy to handle methodologically. Muskrats are territorial (Messier et al. 1990, Hjälten 1991) and use particular feeding sites where the shells of preyed clams accumulate (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 measure the size and growth of the preyed clam reliably (Hanson et al. 1989). Similarly, it is possible to collect quantitative samples of 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: 1) Does the muskrat predation affect the population density or spatial distribution of clams? 2) Is the predation size-selective? 3) Does the prey size preferences of muskrats differ among the populations? 4) If 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 and 26° 15-20' E). Site A is an oligotrophic slowly 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 meters downstream from site A. The bottom is sorted sand with practically no vegetation. Site C is a more eutrophic, slowly 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 stream-like part of the water course, about 200 m below site C. There is a riffle between sites C and D. Near the shore of 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 muskrat from each of the four sites at the end of May - beginning of June 1986 (Table 1). Since clam shells decay considerably in three months (Jokela, unpublished), the shells collected were those of clams consumed during the previous winter. At any of the sites we did not find remains of newly eaten clams during the summer, suggesting that the muskrats did not prey upon clams during the summer.

We sampled the clam population at each site in May, July and September. Samples were collected from 1 m^2 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 off-shore. 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^2) to ensure exact sampling. All the plots were searched twice by the diver. The diver searched clams also by hand thus being able to find the clams burrowed in the sediment (mainly young clams). The minimum length of the transect was 10

meters. However, if we found fewer than 60 clams within these 10 meters, 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 container (volume 1 litre) into the sediment to the depth of 5 cm, then pulling a shovel under the container and sealing it underwater. Current velocity was measured at every fifth plot as the time taken by a water-filled plastic bag (volume 2 l) to travel 5 meters. Where necessary due to abrupt changes in turbidity or bottom material, the current velocity was measured from 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).

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

We calculated index for sediment coarseness (SECO) using equation

$$\mathrm{SECO} = \sum_{i=1}^{n} [p_i * (n - i + 1) / n]$$

where n= total number of sediment fractions sieved (10) and p_i = relative mass of fraction i in a sample. Index is assigned 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 spot on the shore line (midden). We analysed the spatial effects of predation using three analyses. First, to estimate the area where clams were removed from, we converted the number of clams in the muskrat midden to spatial units. This was done by calculating how many square meters the number of clams in the midden corresponds to (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 muskrat midden. We repeated the analysis by using the average density of clams in the calculation of the index of foraged area. However, since muskrat predation may decrease the density of clams, maximum density may be more reliable estimate of original density of clam population. Prediction is that, if muskrats remove clams in a systematic fashion, then as the index of foraged area increases the distance of first clams from the shore also increases. Second, 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. Third, to detect 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.

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 density of clams using information about the habitat. Analysis was conducted at each site. The dependent variable was the number of clams per plot. Current velocity (CRVL), depth (DPTH), percentage of stony surface (PCST), organic content of sediment (ORG), and sediment coarseness (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 clam (divided into 5 mm categories according to the length the previous year) to explain the probability of being chosen as prey by muskrat using LOGIT-models. In the LOGIT-analysis, binomial dependent variable (in this case preyed/living) can be explained with either categorical or continuous independent variables. We used the length as a categorical independent variable to be able to fit non-linear 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 the predation was independent of the 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 proportions 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 Anodonta clams, the length at three 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 the preyed and the 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 less 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 and SPSSx 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 three meters at site D to thirty meters at site A (Table 1). The distance of the nearest clams correlated positively with the index of foraged area (Pearson $r = 0.998$, $N = 4$ $P = 0.002$)(Fig. 1). When the analysis was conducted using the average density of clams in calculating the index, the results did not change (Pearson $r = 0.914$, $N = 4$, $P = 0.086$, one-way $P = 0.043$). At three of the sites clam density increased with distance from the shore (Pearson $r = 0.29$, $P < 0.001$; $r = 0.65$, $P < 0.001$, and $r = 0.67$, $P < 0.001$, sites A, C and D, respectively)(Fig. 2). The correlation was strongest at sites C and D, where the first clams were closest 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 $r = 0.50$, $P = 0.008$, and $r = 0.557$, $P = 0.002$, respectively), indicating that foraging may have an effect on size-distribution of clams at some sites. However, the

correlation was weak at sites A and B (Pearson $\underline{r} = 0.054$, $\underline{P} = 0.806$, and $\underline{r} = -0.210$, $\underline{P} = 0.275$, respectively) .

Regression analyses of the density of clams and the environmental variables showed that the density was not related to 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 (Table 2), whereas at sites B, C and D they explained more than 50% of the variation (Table 2). At two of the four sites (sites A, B), the density of clams decreased, and in two of the sites increased with depth (sites C, D)(Table 2). At the sites B and D the density of clams was higher, where the percentage of stony surface was high, indicating that boulders had a positive effect on the clam abundance. At the site C, the density of clams increased as the current velocity increased.

Prey selection by size

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

At three of the sites (A, B and 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 data. However, the most preferred size classes

were distinct in these populations too (Fig. 4). At site C, the linear (preference for bigger clams) and at site D the quadratic (preference for certain size-classes) models fitted the data best (Table 3). However, at all sites except C the observed preference profile was more or less dome shaped (Fig. 4).

Prey selection by growth rate

The growth rates of preyed and living clams were compared by age at each of the study populations using two-way analysis of variance. At three of the four sites (B, C, D) the AGE*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). The slower growing clams were preferred at older age classes; however, the difference is not as clear as among the young clams (Fig. 5). At site D the results may be of suspect because the assumption of homogenous 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 interaction between age and predation were statistically significant.

Discussion

Our results suggest that predation decreases the density of clams at the foraging area and changes the spatial distribution of prey considerably. Consistent results of three different analysis support this conclusion. First, an increase in the distance of the first clams from the shore coincide with an increase in the area that the number of shells in the muskrat midden corresponds

to (Fig. 1). Second, the density of clams increased with increasing distance from the shore at sites where the first clams were closest to the shore (Fig. 2), and thirdly, the mean clam size increased with the distance from the shore at those same sites. The lack of large clams in the near shore areas is difficult to explain with any other factor than predation. In sites where there are no muskrats, clams may be found from very shallow water (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 the 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, but 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 inadequate (Strayer and Ralley 1993). The inconsistency of our results of 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 emphasise that the occurrence of predators should be taken into account in such studies.

According to our results, muskrats select clams that are larger than 50 mm as their prey (Fig. 3). Hanson et al. (1989) found 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 are burrowed in the sediment, thus not being visible to muskrats. We do not have detailed data on the burrowing depths of Anodonta clams, but when collecting the clams, this behaviour was noted by the divers. When going through the plot, small individuals were found only when the sediment was searched by hand. If only clams that were visible had been collected, most of small individuals would have been missed, as noted also by Amyot and Downing (1991).

Clearly, muskrats had prey size preferences in all of the four study sites. At three of the sites muskrats preferred 60-70 mm clams. At site C the largest clams (>85 mm) were most preferred. This inconsistency in prey size preference may be due to, for example, different sizes of the foraging muskrats. Although the quadratic preference profile fit the data only at 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 and D), especially the increase in the mean size of clams with distance from the shore, our results suggest that the large clams may not have been foraged as intensively from longer distances as the small ones. The lack of clams observed in the near shore areas suggest that from close distances the size of the clam may not be that important, as long as it is big enough to be detected. This interpretation is contrary to the prediction of central-place-foraging models, which predict that larger prey is foraged from longer distances (Stephens and Krebs 1986).

Alternative explanation would be that muskrats have been foraging only within the near-shore area, where there were no clams left. Then, differences in age- and size-distributions of preyed and living clams could be due to differences between the near-shore 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, Hanson et al. 1988, Huebner et al. 1990), suggesting that also age- and size-distributions may change by depth. It is most probable that the growth rate differences in lakes are caused by temperature and resource gradients, not by depth per se. At our study sites turbid currents are mixing the water and thus there are no steep gradients in temperature or resources. Furthermore, at three of our study sites the maximum depth is below three meters, which is relatively

shallow compared to depth distribution of clams in lakes. Therefore, it is not likely that differences in age- and size-distributions of preyed and living clams would be due to some environmental gradient between near- and off-shore habitats. Another alternative explanation for the observed spatial distribution of clams would be that clams do not live in near-shore areas in the first place. This is not supported by our observations of clam populations where muskrats are not present, nor by studies where spatial distribution of clams Anodonta along a depth gradient has been studied (Haukioja and Hakala 1974, Ghent et al. 1978, Hanson et al. 1988, Huebner et al. 1990).

If an intermediate size of prey is preferred, faster growing individuals are selected as prey below the preferred size and slower growing individuals above the preferred size. In our analysis by age, this may be observed as a decrease in the growth rate of preyed clams by age. Theoretically, if predation is intense enough, this kind of selection may favour genotypes that either grow slowly, and avoid predation by being small, or grow fast to large size thus minimising the time 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 clams. These clams live in calcium poor soft water, where substantial increase in the growth rate is physiologically demanding task. A decrease in the growth rate would also lead to a lifetime reproductive output considerably, if not occurring simultaneously with an increase in longevity.

Predation may also select for certain types of behaviour. If muskrats are not able to find individuals burrowed in the sediment, selection may favour clam

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

As noted above, discussion on the putative genetic change in the individual growth rates as a 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, two of which had statistically significant AGE*PREDATION interaction (Table 4, Fig. 5). Among the old individuals pattern was not that clear, although there was a slight tendency towards the predicted pattern (Fig. 5). The result was the same if clams size was used as an index of growth. It is not clear if the predation is strong enough to lead to selection which gives 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, were, as we are, reluctant to draw far reaching evolutionary conclusions about possible adaptive responses to predation.

To summarise, 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 clam population from predation risk. 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 spatial and demographic structure of the exploited clam population are worth further studies.

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Tables

TABLE 1. Description of sampling sites, number of clams sampled and number of shells collected from muskrat middens. Distance from the shore (DIST) refers to the distance of the sampled transects from the muskrat midden in meters. Starting point of the transect indicates the distance from the midden to the first clams offshore.

	Site A		Site B		Site C		Site D	
No of 1 m^2 plots	180		30		55		30	
No of clams	212		444		252		525	
No of eaten clams	60		257		90		101	
distance from the shore (DIST)	30 - 92		20 - 29		15 - 34		3 - 18	
	mean	± se	mean	± se	mean	± se	mean	± se
clams / 1 m^2 plot	1.18	1.49	14.80	13.01	8.58	6.16	19.25	6.61
depth (DPTH)	2.15	0.30	6.01	0.76	1.96	0.36	1.09	0.28
current speed (CRVL)	0.11	0.04	0.14	0.03	0.09	0.03	0.23	0.07
% of vegetation	18.28	25.30	0.67	2.17	64.00	32.48	19.85	18.09
% rock (PCST)	22.41	18.84	5.00	10.67	6.93	12.11	37.71	25.99
sediment coarseness (SECO)	5.73	0.61	4.20	0.55	3.91	1.07	6.84	1.68
% of organic sediment (ORG)	1.26	1.57	0.68	0.34	4.65	3.50	1.04	0.67

TABLE 2. Multiple regression models of relationship of clam density and abiotic environmental variables at the four study sites. See table 1 for abbreviations.

	Independent	Coeff.	se	std. coeff	t	P
Site A						
	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
		$R^2 = 0.10$	$F_{5,168} = 3.750$		$P = 0.0030$	
Site 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
		$R^2 = 0.54$	$F_{5,24} = 5.715$		$P = 0.0013$	
Site C						
	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
		$R^2 = 0.55$	$F_{5,47} = 11.655$		$P < 0.0001$	
Site D						
	DPTH	2.862	0.609	0.703	4.701	0.000
	PCST	0.018	0.005	0.410	3.683	0.001
	CRVL	-2.145	2.826	-0.124	-0.759	0.454
	SECO	0.091	0.092	0.133	0.996	0.328
	ORG	-0.038	0.176	-0.022	-0.217	0.830
	constant	-1.219	0.630		-1.934	0.063
		$R^2 = 0.72$	$F_{5,29} = 15.300$		$P < 0.0001$	

TABLE 3. Statistics of logit-models fitted to data. See text for description of models. χ^2 = likelihood ratio χ^2. High P-value indicates good fit to data.

	Model		χ^2	df	p
Site A					
	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
Site 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
Site C					
	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
Site D					
	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

TABLE 4. Analysis of variance of differences in growth rate of clams (length at three years of age) by age and predation (preyed/not-preyed) at the study sites. Age classes included in the test are the same as depicted in the Fig. 5.

		MS	df		F	P
Site A						
	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		0.284
Site 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		0.043
Site C						
	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		0.532
Site D						
	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		<0.001

Figure captions

FIG. 1. Distance of first clams found off-shore in relation to the index of foraged area. The index of foraged area is calculated by dividing number of shells collected from muskrat midden by maximum density of clams at each site. Sites from left to right are D, C, B, A, respectively.

FIG. 2. Number of clams per sample plot in four study sites shown against the distance of the plot from the shore at four study sites (A, B, C, D). Hatched bar on the x-axis depicts width of area where clams were not found. Stippled area separated by vertical line depicts area where censuses were not made. Note differences in scales of axes.

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

FIG. 4. Proportion (± 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. Broken horizontal line represents constant model. Constant model fits if preyed clams are not selected by size, but chosen in relation to abundance of each size-class. Solid line represents models with linear contrasts. Line is slightly curvilinear because the expected frequencies cannot have negative values. Linear model fits if either larger (positive slope) or smaller clams (negative slope) are preferred to others. Broken dome shaped curve represent models with quadratic contrasts. These contrasts were built around modal size-class to test for existence of preference

for a particular clam size. See text and Table 2 for statistics and choice between models.

FIG. 5. Length at three years of age of preyed (open circles) and living clams (black triangles) by age at the study sites (A, B, C, D). Values depict means ± one standard error for all age-classes that had more than three representatives in both groups. Circled age at x-axis refers to the most preferred size-class at that site.

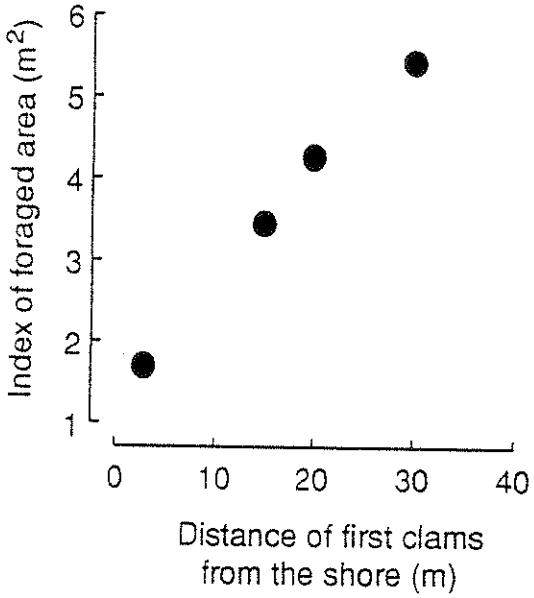


Fig. 1. Jokela & Mutikainen

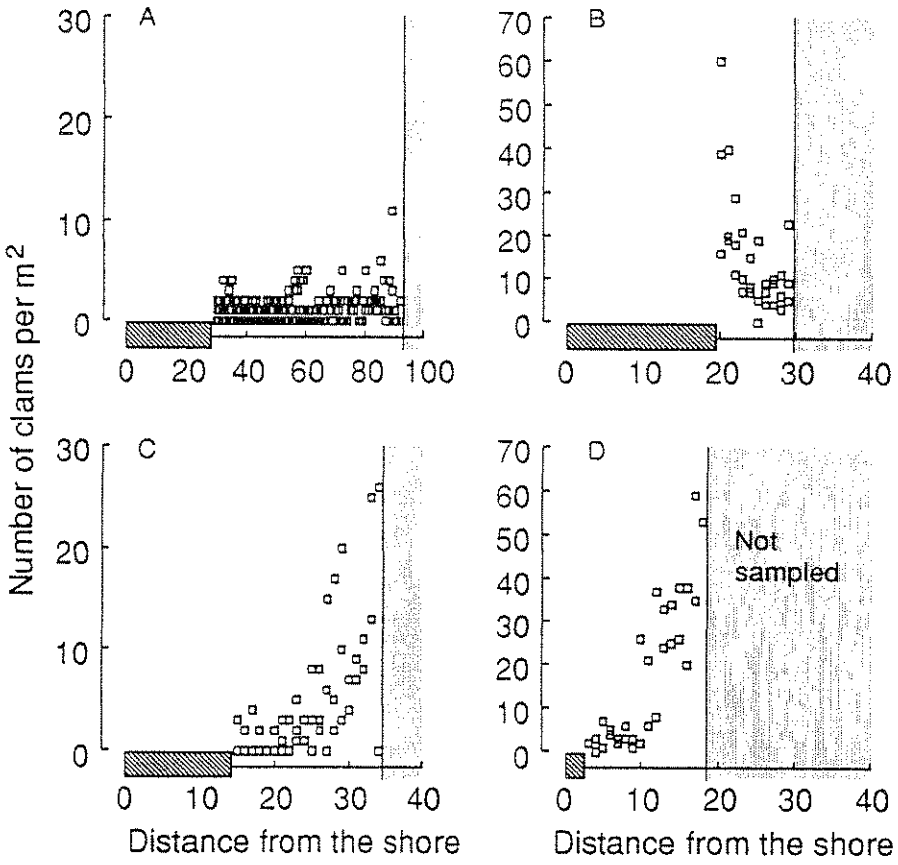


Fig. 2. Jokela & Mutikainen

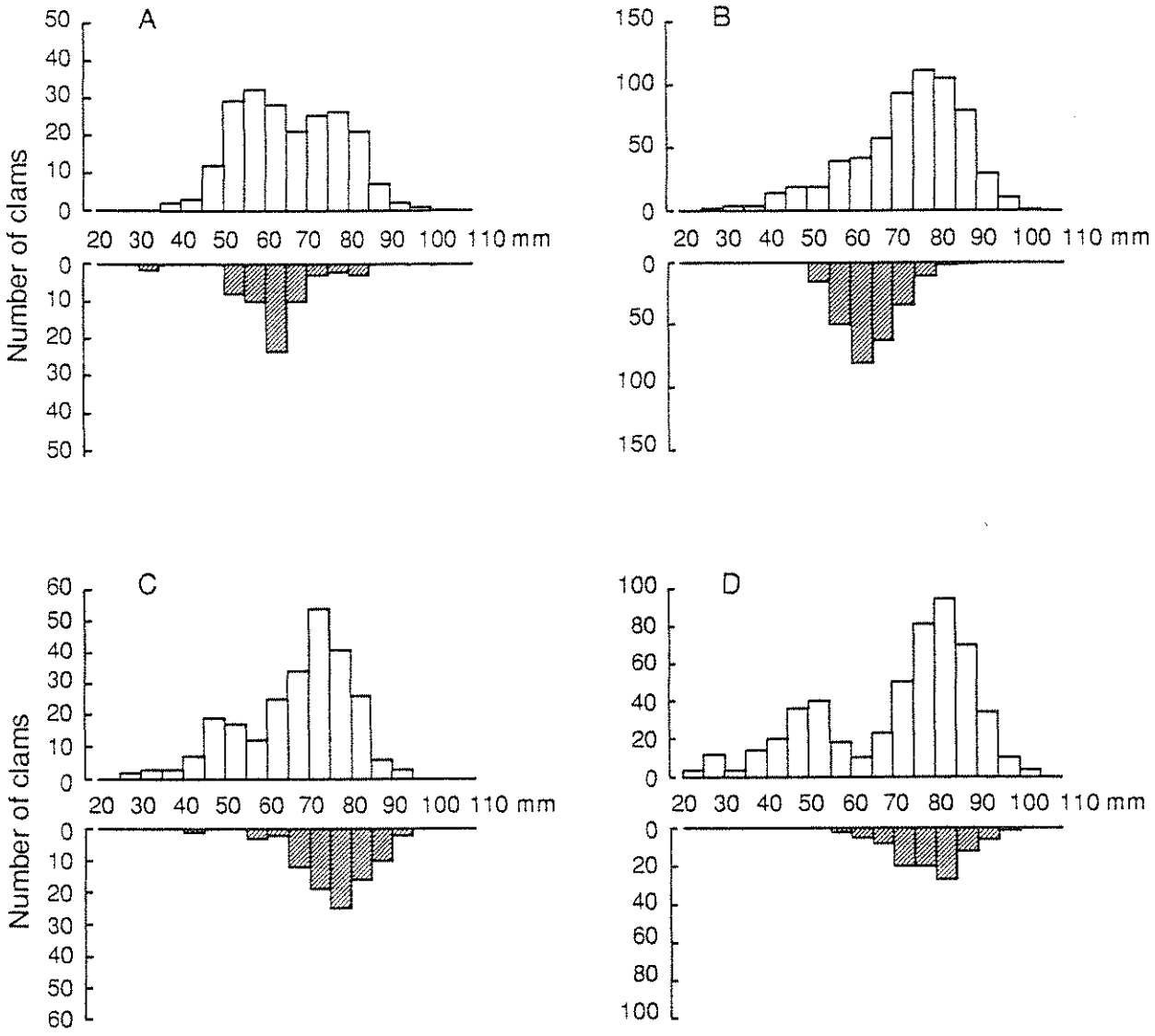
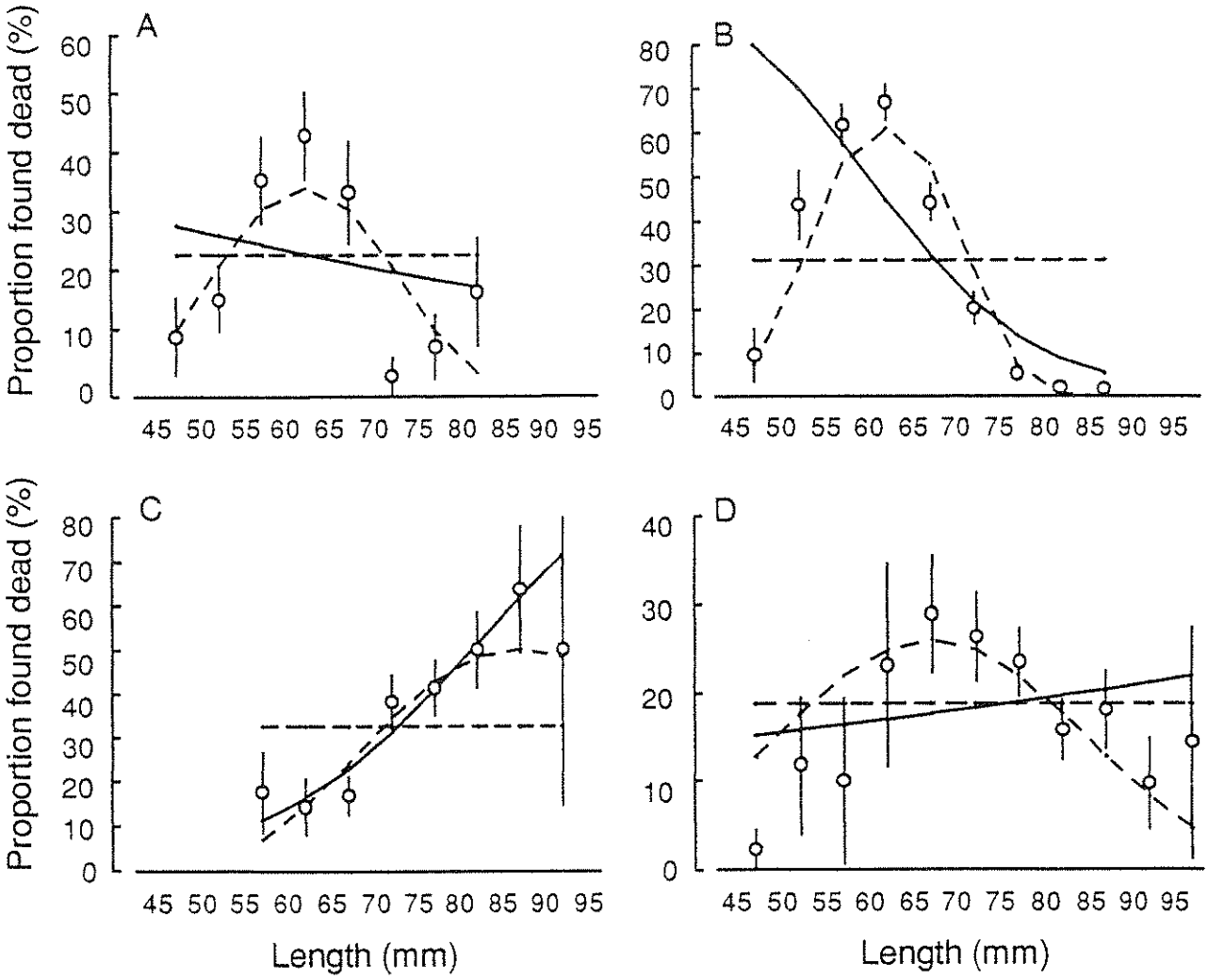


Fig. 3. Jokela & Mutikainen



Flg. 4. Jokela & Mutikainen

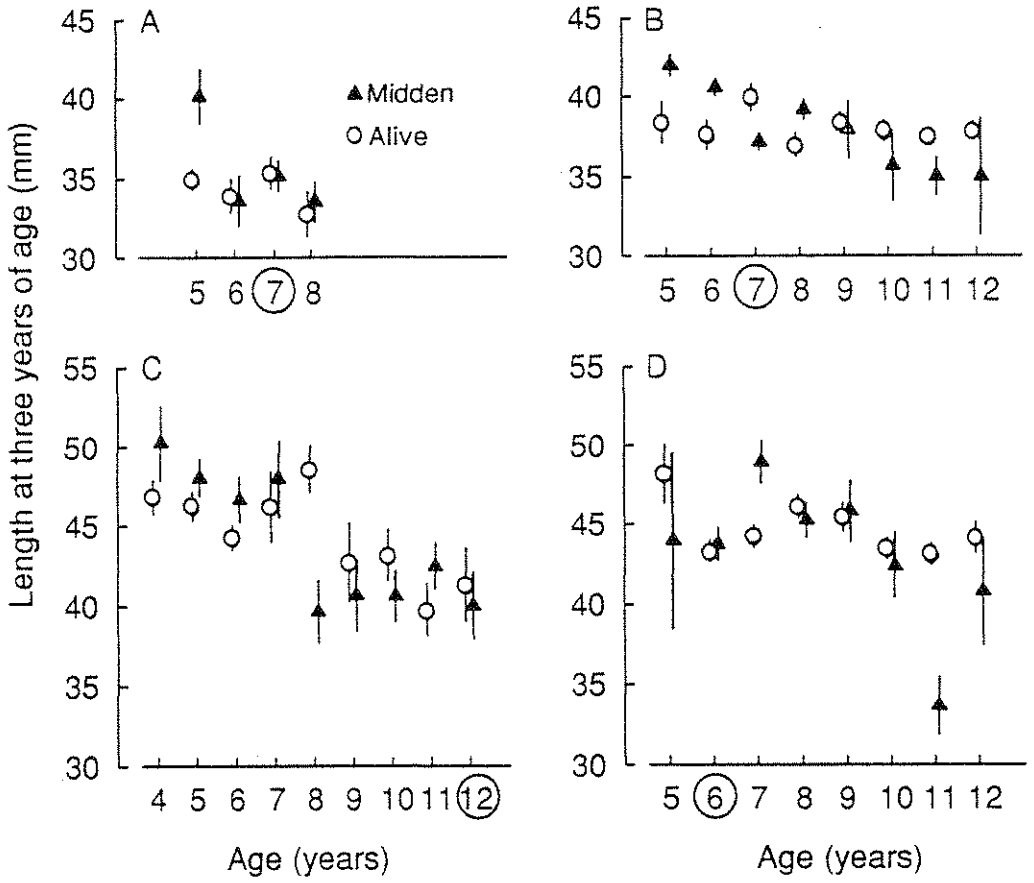


Fig. 5. Jokela & Mutikainen