

# Invariant size selection of blue mussels by roach despite variable prey size distributions

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**ABSTRACT:** Predation is a key trophic component with a potentially large influence on rocky shore community organization. We studied prey size selection by roach *Rutilus rutilus*, feeding on blue mussels *Mytilus edulis* in the northeastern Baltic Sea. In this region, roach feed extensively on abundant populations of blue mussels living at the very edge of their range primarily set by low salinity conditions. The study area is characterised by a marked decline in mean mussel size from the saltier west to the less salty east. We predicted that average prey size of roach would decrease with decreasing availability of larger prey but increase with increasing size of the predator. The size of mussels ingested by roach ranged from 2 to 28 mm, largely covering the size distribution of blue mussels in the area. In accordance with our prediction, body size of the predator was the foremost factor determining patterns of prey selection and mean prey size increased steadily with increasing size of the predator. Roach were size selective, preferring median and large mussels in proportions different from their accessibility in the habitat. Contrary to our expectations, no differences between the areas were seen regarding prey size selection. These results contrast with optimal foraging theory predicting that predators under higher prey densities decrease the proportion of less profitable prey. Our results suggest that roach have the potential to significantly affect the blue mussel dynamics in areas with poor prey availability and we predict that ongoing environmental change in the Baltic will likely increase its impact.

**KEY WORDS:** Prey size selection · Predator–prey · *Mytilus* · Edge species · Optimal foraging · Body size · Rocky shores · Top-down effects

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## INTRODUCTION

Climate and environment change is expected to have significant effects on the composition and structure of marine communities (Sagarin et al. 1999) with, e.g., changes in distributional ranges of species (Schiel et al. 2004). In the Baltic Sea, 3 predominant large-scale processes—(1) increased eutrophication, (2) sea warming and (3) decreased salinity—have raised concern about the future state of the sea. These processes are per se considerable direct threats to the coastal ecosystems, but also impose threats to the ecosystem indirectly by alterations in species distribution and the

strength of species interactions (e.g. Berlow et al. 2002). Understanding the origin, extent and scales of these processes is essential. It is equally important to predict how the biota will interact in response to these processes. Despite the long-recognized increase of freshwater roach *Rutilus rutilus* in the Baltic Sea, very little is known about how this species is interacting with brackish water organisms, especially those inhabiting rocky sublittoral habitats. In this paper, we report some outcomes of the ongoing changes in the sea that benefit freshwater roach (e.g. Lappalainen 2002) but are unfavourable for its marine prey (Westerbom 2002, Westerbom & Jattu 2006).

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Prey size selection is a common feature of the feeding behaviour of cyprinid fish (Scott 1987, Prejs et al. 1990, Nagelkerke & Sibbing 1996) and size-dependent predation has been shown to substantially affect the structure and dynamics of a wide variety of natural prey populations (Navarrete & Menge 1996, Persson et al. 1996, Hamilton 2000, Magoulick & Lewis 2002). Optimal foraging theory has been used to explain prey size selection in various species of fish (Werner & Mittlebach 1981, Bence & Murdoch 1986, Prejs et al. 1990, Mikheev & Wanzenböck 1999). The theories predict that predators select prey types or prey sizes that maximize the net rate of energetic return. Several studies on the feeding behaviour of fish have shown that fish often have a preference for large prey (Prejs et al. 1990, Rutkowski 1994). This behaviour has been explained by optimal foraging theory: larger prey usually maximize net energy intake. When prey density is high, an optimal feeder should consume prey that provide the highest net energy intake, and reduce the intake of less profitable prey (Werner & Mittlebach 1981). If prey density is low, however, and predators are food limited, the body size range of selected prey should increase (Stephens & Krebs 1986, Blumenshine et al. 2000). The theory predicts that the optimal diet depends only on the abundance of high profitability prey, whereas the abundance of low profitability prey, even if highly abundant, should not influence diet selection (Hughes 1997).

The optimal size depends greatly on the size of the predator, since larger predators can generally handle and consume larger prey. Larger predators are also capable of handling a greater range of prey types (Hughes 1997, Scharf et al. 2000). Therefore, the risk of an individual prey being consumed by a predator depends not only on the size structure of the prey population, but also on the size structure of the predator population (Scharf et al. 1998). In addition, minimal sizes of prey may be coupled with predator size since large predators may experience problems in handling small prey (Sousa 1993).

As one of the dominant species on the sublittoral hard bottoms, blue mussels have great importance for the coastal ecosystems in the northern Baltic Sea. Blue mussels are key species in terms of production and consumption of nearshore nutrients; they stabilise nearshore communities and provide a food source for many fish and benthivorous seabirds (Seed & Suchanek 1992). While predation is recognized as one of the primary factors structuring intertidal rocky shore mussel assemblages, comparatively few studies have examined the effects of fish predation on sublittoral marine mussel assemblages.

Freshwater roach are of major importance in temperate lakes and ponds, where they play an important role

as consumers of detritus, macrophytes, algae, bottom dwelling invertebrates and zooplankton. Their omnivorous feeding behaviour together with their ability to prosper in deprived environments has rendered roach dominant in mesotrophic and eutrophic temperate lakes (Brabrand 1985). Roach have also become increasingly abundant in the brackish northern Baltic Sea during the last 2 decades (Lappalainen 2002), with 10-fold increases in catch per unit efforts (CPUE) in an adjacent monitoring area (Ådjers et al. 2006). The progressive eutrophication of coastal waters (Lappalainen 2002), seawater warming (Seinä et al. 1996, 2001) and declining seawater salinity (Rönkkönen et al. 2004) have favoured roach, which has successfully invaded the entire archipelago and is now the most abundant species in test-fishing catches in the Gulf of Finland (Lappalainen 2002). Successful reproduction among roach is dependent on low salinities (Jäger et al. 1981), and eutrophication increases macrophyte coverage, which provides shelter for larvae and juveniles. During the 1990s, the annual period of ice cover shortened (Seinä et al. 1996, 2001) and warm and early springs may further favour roach reproduction as the species is favoured by warm water (Mann 1991). As an increasingly abundant species in the outermost archipelago, roach may exert considerable predation pressure on populations of blue mussels since they feed extensively on mussels (Rask 1989, Lappalainen et al. 2004). Roach have shown size-selective feeding behaviour when foraging on zebra mussels *Dreissena polymorpha* in lake ecosystems, and studies indicate that size-selective behaviour may structure remaining mussel populations (Prejs et al. 1990, Rutkowski 1994). The foraging behaviour of this predator is therefore likely to influence the dynamics of blue mussels in the north-eastern Baltic Sea. This contrasts with previous assessments, which assumed that predation pressure on blue mussels in the northern Baltic is insignificant (e.g. Kautsky 1981, Reimer & Harms-Ringdahl 2001).

We studied size-selective predation by freshwater roach feeding on blue mussels at 3 regions in the western and central Gulf of Finland, northeastern Baltic Sea. The aim of the study was to determine whether (1) size-selective predation occurs, and (2) roach adjust their foraging behaviour to prey availability at 3 areas characterised by different availability of different sized blue mussels. This variation in size distribution is due to a strong salinity gradient across which the proportion of large mussels in the population decreases towards the east, where low salinity terminates the range of the mussel (Westerbom et al. 2002). The area therefore provides an opportunity to study the foraging behaviour of roach under natural conditions where their main prey item varies in size and abundance. Although predation is considered to be an important

determinant of abundance, distribution and size structure of rocky shore mussel populations (e.g. Paine 1974, Seed & Suchanek 1992), considerably less is known about how diets of predators relate to changes in the abundance of their prey (Trenkel et al. 2005). In line with theory (e.g. Hughes 1997), we predicted that consumed mussels at the easternmost area would be markedly smaller than consumed mussels at the 2 western study areas where mussel beds are composed of considerably larger mussels. Lappalainen et al. (2004) addressed the question of species composition in the diet of roach in the same areas and showed that shelled molluscs formed over 95% of the diet, with blue mussels being the dominant species in the diet at all areas.

## MATERIALS AND METHODS

**Study area.** The study was conducted on exposed rocky shores at 3 study areas, Hanko Western (hereafter referred to as A1; 59° 55' N, 22° 50' E), Tvärminne (A2; 59° 55' N, 23° 15' E) and Söderskär (A3; 60° 07' N, 25° 25' E), in the western and the central Gulf of Finland, northern Baltic Sea (Fig. 1). Wave exposure and ice scouring shape the shallow seabeds in these areas (Westerbom & Jattu 2006), where bottoms typically consist of rock and boulders. Mussel density and biomass at A2 and A3 fluctuate widely on a 3 to 5 yr basis, whereas populations at A1 are comparatively stable in structure and density (Westerbom et al. 2002).

**Mussel sampling.** Benthic samples were collected using SCUBA in July 2000. In 2001, additional samples were collected at A1 and A3 to achieve accurate measures of the standing blue mussel populations. Using a metal frame with one side ending in a net bag, standard areas of 400 cm<sup>2</sup> were randomly selected from mussel beds at approximately 6 to 8 m depth, representing the optimal depth of blue mussels in the areas (Westerbom et al. 2002, Westerbom & Jattu 2006). In each area, 12 samples were collected from 3 sites ( $\Sigma$  36 samples per area). To count the mussels, samples were sieved through nested sieves (1, 2, 4 and 9.5 mm). Subsequently, 100 mussels from each mesh per sampling site were selected at random and measured using calipers (to 0.1 mm accuracy). Data from all stations within an area were pooled, as the actual feeding locations of the fish were unknown (Persson & Greenberg 1990, Mitchell et al. 1999). The differences in blue mussel distribution were consistent and non-overlapping between areas during the study, i.e. the size distribution at A1 could not be found at A2 or A3, and vice versa.

**Fish sampling.** Fish sampling was carried out during the warm water period June–September in 2000 using

multimesh gill nets to estimate the size structure of roach populations and ordinary 25 to 35 mm gill nets to specifically catch large specimens of roach. Additional samples were collected at A1 and A3 in 2001, at the same locations and approximately the same depths where bottom samples had been collected. Nets were set in the sea in early evening and hauled up next morning. Fish length was measured and fish were weighed, the intestines were removed and deep-frozen or preserved in ethanol for diet analysis. In all, 360 roach of 14 to 31 cm standard length (SL) contained shell fragments and were used in the analysis of size selection.

**Reconstructing mussel size from shell fragments.** As cyprinids have strong pharyngeal teeth that effectively crush the shells of mussels, the mussel size has to be reconstructed from shell fragments found in the intestine of the fish. The thickness of the umbo has been used to estimate the original size of mussels (Prejs et al. 1990, Hamilton 1992, Öst & Kilpi 1998, Mitchell et al. 1999). To estimate the size of ingested mussels a regression between known mussel length and umbo thickness was used. Due to the proximity of A1 and A2 (20 km), the length of mussels eaten by roach at A1 was approximated from the equation based on mussels collected at A2. For A3, we used a separate regression. Using a fine-grained nail-file, umbos were sequentially ground to uncover their thickest part. Several measurements were taken for each umbo and the

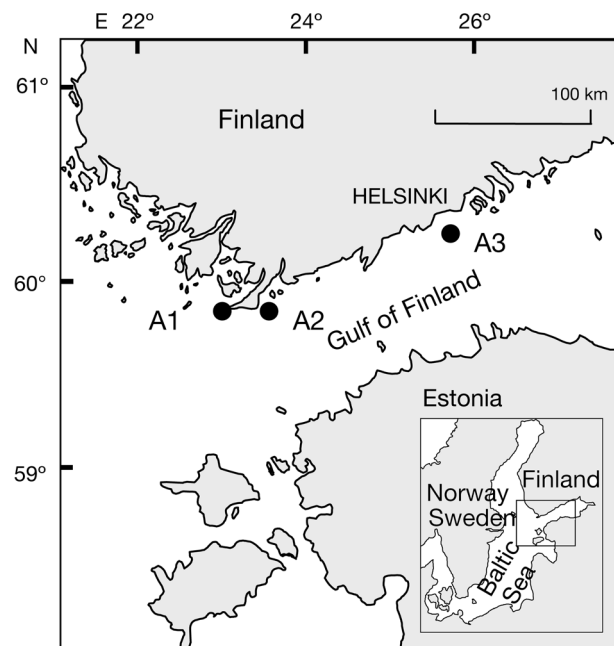


Fig. 1. Study areas Hanko Western (A1), Tvärminne (A2) and Söderskär (A3), in the western and central Gulf of Finland, northern Baltic Sea

thickest part was used in further analyses. For measurements, we used a microscope with an accuracy of 20 µm (20 µm divisions). Both umbo thickness and mussel length were log-transformed making the data fully homoscedastic. No distinction was made between left and right umbo.

**Shell fragments in roach intestines.** As the number of umbos found in the alimentary canal varied considerably in individual roach, and as both the samples (umbos) and the units (fish) were unbalanced (i.e. complicating nested designs), we used the mean umbo size in each intestine when analysing and describing the data (Sokal & Rohlf 1995). Grinding was usually impossible among the smallest mussels (<3 mm). In these cases, we used the un-ground measures. The error induced by this procedure was trivial, as the difference

between ground and un-ground umbos among the smallest mussels was minute. Medium- and large-sized mussels were always ground, and rejected if the thickest part of the umbo could not be reliably determined and measured. Besides shell fragments, intestines also contained small intact mussels. These mussels (4% of all umbos) were considerably smaller than the bulk of crushed mussels and therefore likely do not represent items actively chosen by the fish. Consequently, we excluded these mussels from further analyses. On average,  $3.7 \pm 0.15$  (SE, range 1 to 16) umbos per fish were analysed. This corresponds to approximately half of all umbos that were found in the intestines. Rejected umbos were often split centrally over the umbo and could not reliably be used. These rejected umbos originated from both large and small mussels in visually equal proportions.

To analyse the preference of different fish sizes for different mussel classes we calculated Chesson's selectivity index ( $\alpha$ ) according to the formula:  $\alpha = (r_i/n_i) / [\sum(r_j/n_j)]$ , where  $r$  is the proportion of consumed mussels belonging to a particular size class and  $n$  is the proportion of that size class in the natural population. The index varies between 0 and 1 and weights the roach preference for one mussel size class  $i$  against the average preference for the alternative size class  $j$  (see Krebs 1999). The index was calculated on the whole data set on all ingested mussels.

**Data analysis.** We used parametric tests whenever the data fulfilled the assumptions of the tests (checked with the Wilk-Shapiro test and Levene's test), and pairwise comparisons of means were done with post hoc Tukey tests ( $p < 0.05$ ). If necessary, data were  $\log(x+1)$ -transformed and re-checked. In weighted ANCOVA, we further checked parallelism of slopes of  $y$  on  $x$  for all groups. All statistical tests were made using individual roach as the sampling unit. Statistical analyses were performed using the SPSS (11 for Windows) statistical package. Mean values are given with standard errors (SE) unless otherwise noted.

## RESULTS

### Prey abundance and description of the mussel populations

There was a marked difference in *Mytilus edulis* size distribution between the areas (Fig. 2), with consistently larger mussels towards the west (Kolmogorov-Smirnov test;  $D = 0.37$ ,  $n_{A3} = 9116$ ,  $n_{A2} = 22\,260$ ,  $p < 0.0001$  and  $D = 0.15$ ,  $n_{A2} = 22\,260$ ,  $n_{A1} = 14\,618$ ,  $p < 0.0001$ ). Densities of mussels differed between the areas (Scheirer-Ray-Hare test;  $H_2 = 43.7$ ,  $p < 0.0001$ ) with most mussels at A2 ( $22\,260 \pm 2082\text{ m}^{-2}$ ) and fewest

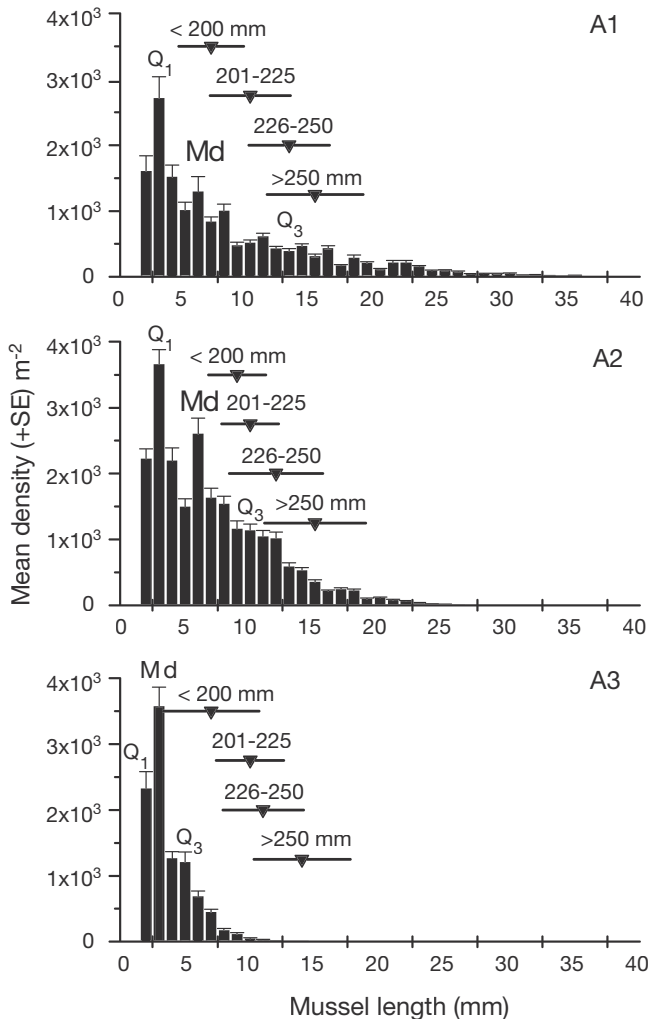


Fig. 2. *Mytilus edulis* *Rutilus rutilus*. Size distribution in the 3 study areas. Median (Md) length and quartiles ( $Q_{1,3}$ ) of mussels are given. Triangles and horizontal bars show mean ( $\pm$ SD) selected prey size for each roach size class

at A3 ( $9116 \pm 746 \text{ m}^{-2}$ ). Densities also differed between years ( $H_1 = 4.2$ ,  $p < 0.05$ ) but not within areas (Tukey's test). At A1, populations had a wide size distribution, with mussels ranging between 2 and 39 mm and mean abundance being  $14\,618 \pm 1020 \text{ m}^{-2}$ . Mussels in the size range 10 to 25 mm were extremely common at all sites, and even mussels 25 to 35 mm occurred regularly and abundantly in the sampling areas. Mussels at A2 varied in length between 2 and 30 mm, with an abundant representation of 2 to 9 mm long mussels followed by 10 to 15 mm long mussels, whereas mussels larger than 25 mm were comparatively few. At A3, populations were highly skewed towards small individuals; the range was from 2 to 17 mm. The occurrence of mussels larger than 10 mm was extremely low, although mussels up to approximately 20 to 25 mm could occasionally be found on the open rocky bottoms.

### Prey morphology

Umbo thickness was an accurate predictor of shell length. At A2, the non-linear regression equation between mussel length ( $L$ ) and umbo thickness ( $U$ ) was  $L = 35.11 \times U^{1.0761}$  ( $r^2 = 0.94$ ,  $n = 230$ ,  $p < 0.001$ ), and at A3 the relationship was very similar, following the equation:  $L = 34.07 \times U^{1.118}$  ( $r^2 = 0.90$ ,  $n = 230$ ,  $p < 0.001$ ). Among many species of fish, prey width or prey height may limit upper prey size instead of prey length, and prey width has commonly been used as a measure to characterise prey. To be able to compare results from earlier studies, we measured prey height and prey width from mussels at A2. There was a strong linear regression between both shell height and length ( $y = 0.51x + 0.59$ ,  $r^2 = 0.98$ ,  $n = 740$ ,  $p < 0.0001$ ) and shell width and length ( $y = 0.40x + 0.22$ ,  $r^2 = 0.94$ ,  $n = 740$ ,  $p < 0.0001$ ).

### Fish characteristics

Due to high numbers of small fish at A1 (Fig. 3), the average ( $\pm$ SD) size of all captured roach differed between the areas, being significantly smaller at A1 ( $20.1 \pm 4.3$  cm) than at A2 ( $22.5 \pm 3.0$  cm) and A3 ( $23.4 \pm 3.0$  cm) (Kruskal-Wallis,  $H_2 = 42.7$ ,  $p > 0.001$ ).

### Prey size selection

Of all sampled roach that contained food particles in their intestine, 67% at A1, 91% at A2 and 76% at A3 contained shell fragments of *Mytilus edulis*. Blue mussels constituted the single most important prey item

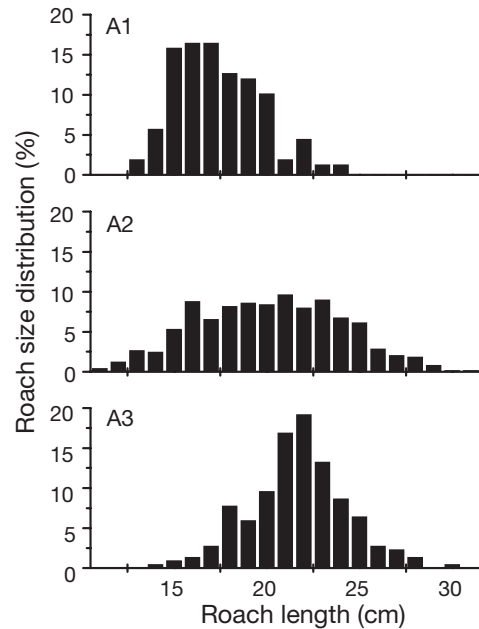


Fig. 3. *Rutilus rutilus*. Size structure of roach populations based on multimesh gill net catches. Note gradual increase in average roach size from the saltier west towards the less salty east.  $N = 158$  for A1, 489 for A2 and 219 for A3

among all roach size classes. The size of mussels ingested by roach ranged from 2 to 28 mm, largely covering the size distribution of blue mussels in the natural habitat. Only the biggest mussels at A1 and A2 were excluded from the roach diet. Roach that fed on blue mussels were size selective and even the smallest roach at A2 and A3 displayed high selectivity of specimens larger than, or equal to, the median of the area. Larger fish showed high selectivity toward bigger mussels (Figs. 2 & 4). There were no differences in the weighted mean size ( $\pm$ SE) of mussels consumed by roach in the 3 areas (A1 =  $11.1 \pm 0.3$  mm, A2 =  $10.3 \pm 0.2$  mm, A3 =  $10.4 \pm 0.3$  mm, ANCOVA,  $F_{2, 356} = 2.4$ ,  $p = 0.091$ ) whereas the covariate (fish length) significantly affected prey size ( $F_{1, 356} = 367.3$ ,  $p < 0.0001$ ). There were no differences in the amount of analysed umbos between the areas (ANOVA,  $F_{2, 357} = 0.596$ ,  $p = 0.55$ ).

Two-tailed Kolmogorov-Smirnov tests showed that there were significant differences between supply and mussels taken by fish in all areas (A1:  $D = 0.17$ ,  $n_1 = 14\,618$ ,  $n_2 = 349$ ,  $p < 0.001$ , A2:  $D = 0.41$ ,  $n_1 = 22\,260$ ,  $n_2 = 592$ ,  $p < 0.001$ , A3:  $D = 0.81$ ,  $n_1 = 9\,116$ ,  $n_2 = 391$ ,  $p < 0.001$ ). Chesson's index of selectivity (Fig. 4) showed that roach were selective towards the larger mussels in the habitat, and that preferences for larger individuals increased with the size of the predator. The smallest mussel size class (1 to 3 mm) was avoided by all roach size ranges in all areas and mussels of 4 to 6 mm were only preferred among the lower 2 roach size ranges at

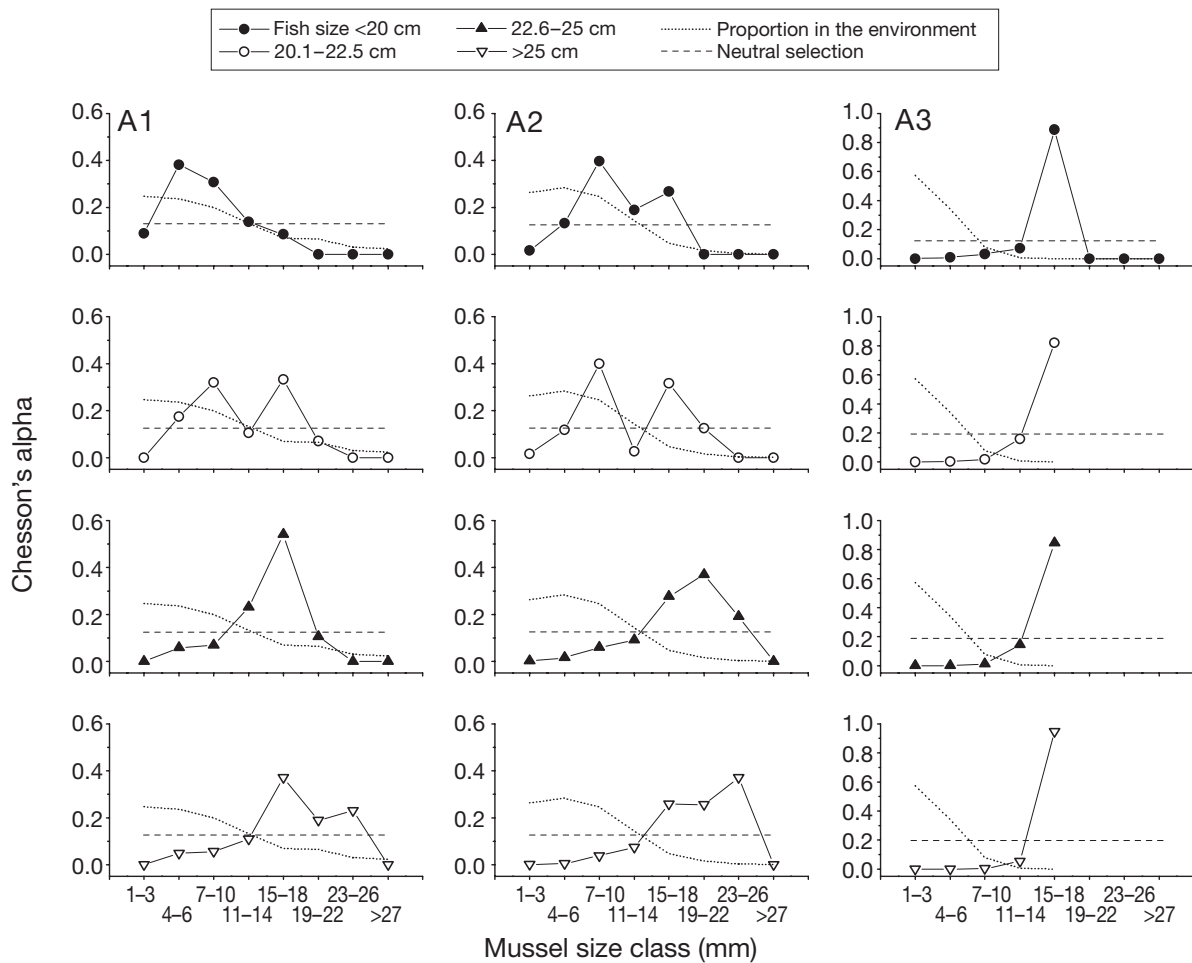


Fig. 4. *Mytilus edulis* and *Rutilus rutilus*. Size selection (Chesson's  $\alpha$ ) of mussels by different size ranges of roach (SL; mm) in the 3 study areas. Neutral selection (dashed line) is defined as  $\alpha = 1/m$ , where  $m$  = number of size classes;  $\alpha$ -values  $>1/m$  indicate selection for a size class and those  $<1/m$  a selection against. Since roach at A3 ate a much greater proportion of larger mussels than randomly found on rocky bottoms, the index for the upper 3 fish size ranges is only calculated for the lower 5 prey size classes

A1, and were neutrally selected or avoided by all other fish (Fig. 4). Roach generally preferred mussels larger than 10 mm but avoided the largest mussels in the habitats. The data further showed that the preference towards larger mussels generally increased from areas with high abundance of large mussels (A1) towards low abundance areas (A3).

As the areas did not significantly differ with respect to the selected prey size, the whole data set was pooled. Roach were also grouped to the nearest 1 cm. The pooled data showed a strong positive correlation between roach length and mean length of prey (Fig. 5). The maximum size of mussels taken showed that roach were capable of preying on all available mussels at A3. At A1 and A2, only small fractions of the entire population of mussels were outside the size range of potential prey for roach.

## DISCUSSION

### Comparisons with previous studies

Roach were size-selective when feeding on blue mussels, choosing larger mussels than proportionately available. With increasing size, the energy content of mussels increases as does their detectability. For the predator, the benefits of larger prey have to be balanced against their associated handling costs, which increase with mussel size (Prejs et al. 1990, Nagelkerke & Sibbing 1996). In areas of high abundance of prey, the net feeding efficiency (the ratio between costs and benefits) is largely determined by handling costs (Nagelkerke & Sibbing 1996). Baltic blue mussels have high flesh weights (Öst & Kilpi 1998), thin and weak shells (Reimer & Harms-Ringdahl 2001) and low

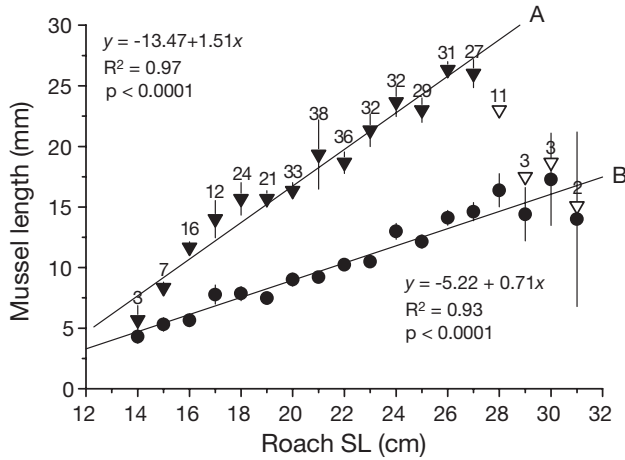


Fig. 5. *Mytilus edulis* and *Rutilus rutilus*. Lines representing (A, ▼) maximum size and (B, ●) mean size ± SE of selected prey against roach size. 'Maximum size' is the mean size (± SE) of largest mussels found in 3 different roach (if possible) within a size class (to reduce bias from isolated individuals). Regressions fitted to mean mussel size for each roach size class. Numbers above triangles indicate sample size. Due to the low amount of data in the 28 to 31 cm classes, line A is calculated only on size classes 14 to 27 cm. (▽) Maximum mussel size found in the 28 to 31 cm classes (no error bars shown because

they overlap the mean values)

byssus production, making them loosely attached to the bottom (Reimer & Harms-Ringdahl 2001). They therefore offer high net profitability due to their low crushing resistance and low detachment costs.

Our results appear largely to be consistent with those of Prejs et al. (1990) and Nagelkerke & Sibbing (1996), who studied size-selective predation of roach on zebra mussels *Dreissena polymorpha*. Prejs et al. (1990) showed that roach fed on mussels in proportions different from their availability in the habitat, and that prey size increased consistently with increasing size of the predator. This increase has been attributed to increase in gape size of the predator (Prejs et al. 1990, Nagelkerke & Sibbing 1996). At our western sites (A1 and A2), blue mussels were found in the food of all roach size classes, although the prevalence increased with increasing size of the predator (Lappalainen et al. 2004). However, at A3 the prevalence of ingested blue mussels was lower among large roach than among small roach (Lappalainen et al. 2004). This probably relates to the extreme shortage of large prey for larger roach at A3. Rather than selecting prey of less profitable size, larger roach decrease the proportion of blue mussels and increase the proportion of other food items such as gastropods and other bivalves (Lappalainen et al. 2004). Nonetheless, the common occurrence of blue mussels among large roach at A3 was unexpected; blue mussels constituted 39% of the whole diet, while the 2 next most common species

(*Cerastoderma glaucum* and *Macoma balthica*) together accounted for 33% (see Lappalainen et al. 2004). Even more surprising was the high prevalence of large mussels in the diet that were seldom found in the open habitat but that could be found in structural refuges (sensu Westerbom et al. 2002).

The maximum size of consumed mussels was very similar to the maximum observations of Prejs et al. (1990) and equalled observations of Nagelkerke & Sibbing (1996). Nagelkerke & Sibbing (1996) predicted that the maximum width of selected prey equals approximately 4.1% of SL, whereas in this study the corresponding value was 4.3% of SL (4.5% excluding the 2 largest roach size classes) (Fig. 6). Our results are therefore consistent with results of Prejs et al. (1990) and Nagelkerke & Sibbing (1996), showing that selected prey is on average considerably smaller than the size roach are capable of consuming (see also e.g. Schael et al. 1991, Bremigan & Stein 1994).

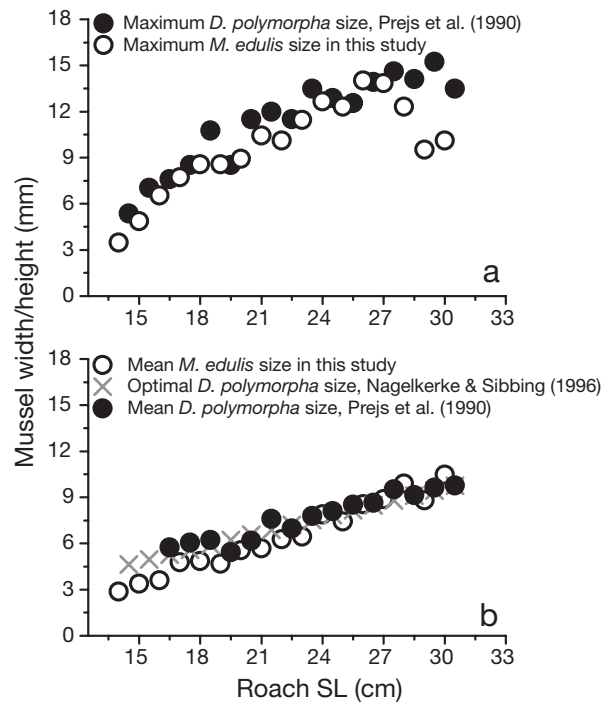


Fig. 6. *Mytilus edulis*, *Dreissena polymorpha* and *Rutilus rutilus*. (a) Maximum and (b) mean width/height of selected mussels including previous findings by Prejs et al. (1990) and Nagelkerke & Sibbing (1996). Width of *D. polymorpha* calculated from length using formula (from Prejs et al. 1990)  $y = 0.62x - 0.77$ , and optimum relationship between mussel width ( $W_{opt}$ ) and fish standard length estimated to be 3.2%, following Nagelkerke & Sibbing (1996). Since blue mussels in this area were greater in height than width, we used the mussel-height vs. fish-length relationship to compare the results of this study with the mussel-width vs. fish-length results of Prejs et al. (1990) and Nagelkerke & Sibbing (1996). Mean and maximum *D. polymorpha* sizes are derived from Prejs et al. (1990)

### Is foraging of roach consistent with theory?

Several hypotheses have been put forward to explain why molluscivorous predators select smaller mussels than at first sight would seem to be optimal. The main hypotheses include: (1) shell weight minimization (Bustness & Erikstad 1990), (2) risk-averse foraging behaviour due to large prey size (Draulans 1982) and (3) risk-averse foraging behaviour due to high variability in prey value (Draulans 1982). The (1) shell-weight minimization hypothesis states that a molluscivorous predator selects prey in order to minimize the intake of shell material. Prey with the highest ratio of tissue mass to shell mass is the most profitable. The proportion of shell mass among Baltic blue mussels increases more than the concurrent increase in meat content (Öst & Kilpi 1998). Hence, if accumulation of shell mass in the intestine reduces further intake of mussels, roach would do better consuming mussels with a high meat content relative to shell mass and therefore consuming intermediate sized prey would be rewarding. If shell mass minimization is important, the variability in tissue content within mussel size classes may also determine size selection (hypothesis 3). Variability of tissue mass of Baltic blue mussels is highest among the largest specimens, whereas tissue mass among the smallest mussels varies little within a year (Kautsky 1982). Large mussels therefore offer variable benefits but constantly high costs. Selecting intermediate mussels with less variance reduces this risk. Nagelkerke & Sibbing (1996) showed that roach sometimes make poor decisions, selecting mussels larger than can be handled (hypothesis 2). In environments with many mussels of various sizes, roach may do better taking mussels that are smaller and pose less risk in handling than those close to the maximum handling size. However, in low-density environments (e.g. A3) any mussel above some threshold size may be profitable, leading to a broad diet (Blumenshine et al. 2000) since in low density environments it may be energetically advantageous to maximize prey consumption per unit time rather than minimizing the costs of feeding. Interestingly, at A3, where the availability of optimally sized mussels is low, we did not find any indication that roach broaden their diet towards smaller prey. Instead, as shown by Lappalainen et al. (2004), large roach seem to decrease the proportion of blue mussels in their overall diet. Handling time may also vary with satiation so that the profitability of different sized prey may vary within a feeding bout. Mikheev & Wanzenböck (1999) showed that handling time among young-of-the-year roach increased over a feeding bout and roach gradually switched the size of selected prey from initially large individuals towards smaller prey as the feeding bout

progressed (see also e.g. Hughes 1997 for a discussion of the effects of memory, hunger state and packaging constraints). As this switch from large to small prey occurred much earlier in small than in large roach, it is possible that such switching behaviour explains the larger deviation from the optimum curve by small roach in this study (Fig. 6). This switching hypothesis also contradicts optimal foraging theory, since satiation should not influence selection (Mikheev & Wanzenböck 1999).

Our results show that roach use a wide spectrum of different-sized mussels, while simultaneously, the mean prey size is kept constant, irrespective of the availability of mussels. A mixed diet of different sized mussels was more a rule than an exception and therefore hypotheses 1 and 3 possibly explain our results, while hypothesis 2 is hardly relevant, especially at A3 where large mussels are extremely few.

### Consequences of roach predation on blue mussel populations

Depending on the size distribution of predators and prey, predation can selectively affect upper or lower ends of the prey size distribution (top-down effects). Our results clearly showed that roach in the study areas fed selectively on blue mussels in proportions different from their accessibility in the habitat. Especially at the easternmost area, A3, the proportionately high abundance of medium- to large-sized roach may severely impair the structure and dynamics of the mussel population (Figs. 2 & 3). As roach in the area feed mainly on large- and medium-sized mussels that are rarely encountered, they may during periods of low mussel recruitment skew the size structure of mussel populations towards smaller individuals. Since the A3 archipelago is very isolated and small, roach caught at A3 had also consumed their prey within the A3 archipelago. If roach switch feeding habitats away from the open rocky bottoms that dominate the seabeds in the area towards other habitats (stony bottoms or gravel bottoms where larger mussels were found 2 yr earlier, see Westerborn et al. 2002) as a response to declining availability of larger mussels on the rocky bottoms, they will rapidly extirpate the larger mussels from the alternative habitats also. Such a system is top-down controlled and any increase in mean mussel-size would depend on the abundance and feeding behaviour of its predators.

It has commonly been assumed that foraging predators are more susceptible to abiotic stress than sessile prey and that predator pressure will decline with increasing harshness of the environment (e.g. Menge & Sutherland 1987). This applies to environments



where both the predator and its prey are equally influenced by the stressor. Salinity is the foremost factor determining the abundance and distribution of species in the northern Baltic, especially that of blue mussels. Periods of long-term salinity decline have severe negative effects on the renewal of mussel beds, leading to declining populations (Westerbom et al. 2002). As a freshwater species, roach is unlikely to be detrimentally affected by salinity declines; on the contrary, roach numbers have continually been increasing during the last decades as contemporary ambient salinity in the sea has declined (Lappalainen 2002, Ådjers et al. 2006). Roach are therefore capable of eliminating large amounts of adult mussels, with proportionately larger effects during periods when mussel densities are declining for abiotic reasons. Even more importantly, we believe that omnivorous predators at the eastern rim of the distribution of blue mussels prevent any significant and long-lasting increase in the abundance of medium to large prey. In this region, sporadic recruitment success (Westerbom 2006) is incapable of sustaining a viable population composed of a wide size distribution, since any increase in individual mussel size will render it more susceptible to predation. At the same time, however, roach are unlikely to extirpate all mussels in the habitat since even the smallest roach showed no tendency to prefer the smallest mussels in the habitat. Nonetheless, by eliminating the biggest mussels that contribute most to gamete production and hence recruitment (Kautsky 1982), roach predation will have both direct and indirect effects on the viability of mussels in the area. In agreement with Westerbom et al. (2002) and Lappalainen et al. (2005), the present study strongly suggests that predation from vertebrate predators on Baltic blue mussels is by no means insignificant as has conventionally been assumed (Kautsky 1981, Reimer & Harms-Ringdahl 2001) but that predation may have a strong top-down effect on the population dynamics of northeastern Baltic blue mussels. In agreement with Lappalainen et al. (2005), this study also implies that predation effects of roach populations on mussel assemblages are expected to increase due to ongoing climate change and its attendant effects on increasing seawater temperature and declining salinity (Hänninen et al. 2000, Rönkkönen et al. 2004). Warmer sea temperatures increase the reproductive success of roach as well as their metabolic demands and consumption of mussels (Lappalainen et al. 2005). Lappalainen et al. (2005) calculated that an individual roach would consume 20 to 60 mussels  $d^{-1}$  and that the roach population at A2 can consume 15 to 30% of the total standing mussel populations. If sea temperatures continue to rise, seawater salinity will continue to decline, and if roach populations continue to increase, their effects on mussel pop-

ulations are expected to escalate. This topic, i.e. alterations in predator-prey interactions due to changes in the environment (i.e. consequences of anthropogenic climate change) has received little attention from sublittoral researchers, and deserves further investigation (Witman & Grange 1998).

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