

## Differences in feeding selectivity and efficiency between young-of-the-year European perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*) – field observations and laboratory experiments on the importance of prey movement apparency vs. evasiveness

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**Abstract:** Feeding selectivity and efficiency of young-of-the-year European perch and roach were compared under field and laboratory conditions. In laboratory experiments, the importance of prey evasiveness versus prey movement conspicuousness for fish selectivity was evaluated with respect to changing Cladocera/Copepoda prey ratio. Feeding efficiency was additionally investigated in relation to feeding time (5, 10, 20 min) and prey density (approx. 50, 200, 700 ind. L<sup>-1</sup>). In Řimov Reservoir, the diet of both fish species was nearly exclusively composed of crustacean zooplankton. In roach, diet shifted from rotifers and bosminids in May, towards *Daphnia* sp. and *Leptodora kindtii* in June and July. *Daphnia* contributed almost exclusively to the roach diet since June, composing on average more than 94% of total prey. Cyclopoid copepods, occurred in the roach's diet only on the first sampling date; later on both cyclopoid and calanoid copepods were completely absent. On the other hand, copepods played an important role in the diet of perch. In early and mid-June when their share in the zooplankton was particularly high, copepods contributed by more than 50% to the diet of perch. Although their contribution dropped with their decline in zooplankton in June/July, by the end of July they again comprised about one third of perch's diet. In both fish species, the increase in numbers of cladocerans in their diet was related to increase in SL. In roach, the numbers of consumed prey were doubled every twenty days during the investigated period. In perch the increase was not so consistent, but significantly higher efficiency of perch was reported on three out of six sampling dates. In laboratory experiments, roach showed a distinct avoidance for copepods and a preference for cladocerans. Both prey categories were only fed non-selectively when they dominated the prey mixture. Perch selectivity was more diversified. Contrary to roach, perch were fed copepods non-selectively on a balanced prey ratio. Further, with an increasing share of Cladocera, a situation resembling that of roach and Copepoda was avoided. However, when the share of copepods in the prey mixture dropped below ten percent, they were consumed non-selectively and with their ongoing decline in the prey mixture their preference even increased. Feeding efficiency differed significantly between perch and roach when foraging on copepods exclusively or on a prey mixture where copepods predominated. In the short time feeding experiment (5 min) with copepods, perch consumed on average 5.9 times more prey than roach. Although roach increased their success with increasing time it was still 1.7 times greater than for perch in the long time feeding experiment (20 min). Total numbers of prey consumed were positively affected by prey density and feeding time. With increasing feeding time, the consumption rate generally declined. With a fourfold increase in feeding time, the numbers of consumed prey increased on average only two times. Only in roach feeding on copepods did the numbers of prey consumed per minute of feeding increase with increasing feeding time. However, the overall numbers were low. Differences in feeding selectivity and efficiency between perch and roach juveniles were found to be significant both in the field and laboratory experiments. In roach, selectivity was determined solely by prey evasiveness. By contrast, perch's selectivity was influenced by prey movement conspicuousness; prey escape abilities did not play an important role. Perch were more efficient foragers on evasive prey, but its feeding efficiency for non-evasive prey was not lower than that of roach. According to our observations, we suggest feeding behaviour to be responsible for the roach's inefficiency in capturing evasive copepods.

**Key words:** juvenile fish; foraging ecology; *Daphnia*; Cyclopidae; Diaptomidae; movement pattern apparency

### Introduction

European perch *Perca fluviatilis* L., 1758 and roach *Rutilus rutilus* (L., 1758) belong to the most common fish species in meso- to eutrophic temperate water bodies in Europe (Persson et al. 1991; Kubečka 1993). As a consequence, young-of-the-year perch and

roach dominate the 0+ fish communities of these aquatic ecosystems. A general succession from the dominance of perch to roach with increasing ecosystem productivity has been documented for lakes of different trophic status (Persson et al. 1991; Jeppesen et al. 2000; Olin et al. 2002), and when comparing fish community structure within reservoirs

with pronounced longitudinal gradients (Vašek et al. 2006).

Better competitive abilities of juvenile roach for *Daphnia* sp. (Persson 1987) resulting in a shift in feeding- and subsequently habitat-preference of young-of-the-year perch and thereafter increased competition with older perch and additionally decreased growth and recruitment to piscivorous stage from which pressure could be put backwards on the abundance of roach, have been suggested as responsible for these changes in fish community structure (Persson & Greenberg 1990).

The basic presumption in Persson's and Greenberg's "perch – roach juvenile competitive bottleneck" is that roach is a superior forager on at least *Daphnia* or rather superior zooplanktivore in general. On contrary, other studies (Matěna 1995; Macháček & Matěna 1997; Peterka & Matěna 1998) do not report such important differences between perch and roach in feeding efficiency for *Daphnia*. Some have even found perch to be a more efficient forager, particularly when foraging on cyclopoid and calanoid copepods for which distinct avoidance of roach is well-documented repeatedly (Hammer 1985; Bergman 1990; Matěna 1995; Macháček & Matěna 1997; Vašek et al. 2006).

As a main factor responsible for fish preference for *Daphnia* and avoidance for copepods, the escape abilities of the prey have been pronounced (Drenner et al. 1978; Bohl 1982; Kerfoot et al. 1980; Winfield et al. 1983). However, field observations and laboratory experiments with perch, both European *Perca fluviatilis* (Furnass 1979; Rajasilta & Vuorinen 1983) and its close relative North American *P. flavescens* (Mitchill, 1814) (Mills et al. 1987; Confer & O'Bryan 1989), have shown that under specific circumstances these fish have behaved differently from the general scheme of *Daphnia* preference and contrastingly have selected the evasive cyclopoid and even more evasive calanoid copepods. Perch have done so particularly in long time feeding experiments or at high prey densities, i.e. under conditions when have been able to reach satiation quickly. Changes in preference in animals when satiated have been already suggested by Emlen (1966) and for 0+ fish this has been experimentally confirmed (Hart & Gill 1993; Wanzenböck 1996; Mikheev & Wanzenböck 1999). Hence, selection in satiated fish is most probably driven by other mechanisms than those generally responsible for *Daphnia* preference.

In particulate feeders, as young-of-the-year fish are, vision is the most important sense for prey detection (Lazzaro 1987). Therefore not surprisingly, prey visibility (Zaret & Kerfoot 1975) or apparent size (O'Brien et al. 1976) determines fish selection more significantly than actual prey size (Brooks & Dodson 1965). Moreover, recent experiments with virtual plankton images (Brewer & Coughlin 1996) show that fish select accordingly to the moving pattern of the prey and so prey motion can increase prey conspicuousness to fish predators as has been suggested by Zaret (1980).

The aims of this study were 1) to compare feeding selectivity and efficiency of young-of-the-year perch

and roach under field and laboratory conditions and 2) to investigate the importance of prey escape abilities versus prey movement conspicuousness as factors determining prey selection.

## Material and methods

### Field study

Juveniles of perch and roach were collected from the epipelagic habitat of a mesotrophic canyon-shaped Římov Reservoir, Southern Bohemia (Kubečka 1990). Surface tows (0–2 m) were performed using ichthyoplankton tow-net 3.5 m long, 2 m in diameter, with a mesh size of 1.5 mm. Sampling was done in the part of the reservoir near the dam (48°50'53" N, 14°29'12" E) during night hours (22:00–24:00) from the end of May up to the second third of July 1993. Collected fish were immediately killed with an overdose of tricaine (MS 222) and preserved in 10% formaldehyde solution. Concurrently with fish, quantitative zooplankton samples were taken by vertical hauls (5–7 m) with 140 µm plankton net and preserved in 4% formaldehyde solution. In the laboratory, at least three sub-samples were counted and individuals were identified to at least the family level. Standard lengths of fish were measured to the nearest 0.5 mm and digestive tract contents of 10 individuals of perch and roach on each sampling occasion were identified and counted. Diets were evaluated using the numerical method (Hyslop 1980).

### Laboratory experiments

Perch and roach juveniles were seined with 10 m ichthyoplankton beach seine from near the shore of the Římov Reservoir and transferred to the laboratory. In the laboratory, fish were kept in two 210 L holding aquaria at 23 ± 2°C and 16-h light period. Feeding was performed ad libitum with pond zooplankton of the same quality as that used later on in experiments. Prior to the experiments fish were kept at least three weeks under laboratory conditions to ensure habituation.

Low evasive cladocerans, moving in a slow hop-and-sink manner versus high evasive copepods, moving in quick jumps (Dodson 1996), were used as prey. Zooplankton samples were collected from fishponds with almost exclusively either cladocerans or copepods in the early morning of each experimental day. In the laboratory, two similarly sized stock samples of cladocerans (predominantly *Daphnia* sp., Table 1) and copepods (Cyclopidae and Diaptomidae, Table 1) were produced by sequential sieving through a set of sieves. Individuals which passed through 850 µm, but were retained on a 610 µm sieve were used. Zooplankton densities in the samples were analyzed and a prey mixture of required Cladocera/Copepoda ratio was prepared by mixing defined volumes of stock samples of both prey categories. Finally, the prey density of the experimental mixture was analyzed to determine the volume added to the experimental aquarium to obtain the required final prey density.

Feeding experiments were performed in a large aquarium 120 × 50 × 45 cm (l × w × h) filled according to the experimental set up with 180 or 210 L of water (30 or 35 cm water column, respectively). Except for the front wall, the aquarium was covered with black paper to isolate fish from external disturbances. Illumination was provided from above by a 36 W fluorescent tube. Light intensities were measured (BEHA DIGITAL LUX METER 93408) at the water surface and bottom as 2200 ± 200 and 800 ± 100 lux, respectively. The water temperature was within the same

Table 1. Selected biotic and abiotic characteristics of the feeding experiments; A, B denote the two experimental setups as described in Materials and methods, 5', 10', 20' indicate duration of feeding trials in minutes.

	Denoted and (actual) Cladocera/Copepoda ratio		<i>Daphnia</i> sp. <i>Diaphanosoma</i> <i>brachyurum</i>	<i>Ceriodaphnia</i> sp.	Cyclopoidae	Diaptomidae	Prey density (ind. L <sup>-1</sup> )			Perch (ind.)			Roach (ind.)			Starvation (h)	Water temp. (°C)
										5'	10'	20'	5'	10'	20'		
A	14/1	(13.7/1)	93.2		5.2	1.6	272	6		6		25.5		24			
	8/1	(8.4/1)	89.4		6.8	3.8	189	5		5		22.0		22			
	6/1	(5.9/1)	85.4		13.8	0.8	135	6		6		21.0		25			
	5/1	(4.5/1)	79.0		18.1		184	4		4		24.0		23			
	3/1	(3.1/1)	75.0	0.4	18.4	6.2	168	6		6		23.0		25			
	2/1	(2/1)	67.1		32.5	0.4	160	6		6		19.0		25			
	1/1	(1/1.3)	44.2		52.6	3.2	170	6		6		27.0		25			
	1/2	(1/1.6)	30.5	8.5		61.0	250	6		6		21.0		22			
	1/3	(1/2.6)	26.2	1.5		72.3	254	6		6		21.5		22			
	1/4	(1/3.5)	22.5		10.5	67.0	157	6		6		22.0		22			
	1/11	(1/11)	7.7	0.6		91.7	319	6		4		22.5		24			
B	Cladocera	(21.8/1)	95.6			4.4	166	4	4	4	3	4	4	21.0	22		
	Copepoda	(1/70.4)	1.4		0.5	98.1	155	4	4	4	4	3	3	21.5	21		
	More Clad.	(5.6/1)	84.0	0.8	12.4	2.8	43	4	4	4	3	3	4	23.0	22		
	More Clad.	(4.5/1)	79.0	2.9	18.1		184	4	4	4	4	4	4	24.0	23		
	More Clad.	(4.1/1)	80.4		18.6	1.0	720	4	4	4	3	3	3	22.0	22		
	More Cop.	(1/4.9)	14.7	2.2	5.5	77.6	64	4	4	4	3	4	4	20.0	22		
	More Cop.	(1/3.2)	19.7	4.4	34.4	41.5	231	3	4	4	4	4	3	22.0	24		
	More Cop.	(1/5.4)	14.2	1.4	18.6	65.8	660	4	4	4	3	4	4	22.0	23		

range as in the holding aquaria ( $23 \pm 2^\circ\text{C}$ ). The aquaria were stocked with fish  $23 \pm 4$  h prior to the experiments to standardize hunger level and ensure empty digestive tracts in the fish.

Two sets of experiments were performed that differed in experimental design. In the first experimental setup (Table 1A) fish selectivity was investigated with respect to changing Cladocera/Copepoda prey ratio solely. Groups of twelve fish, six perch and six roach, were used in each of eleven experiments conducted in 180 L of water. Fish were allowed to feed for 10 min at a mean prey density of 205 ind. L<sup>-1</sup>, then removed, killed by an overdose of tricaine (MS 222) and preserved in 10% formaldehyde solution for later analyses.

In the second setup (Table 1B), additionally to the effect of prey ratio, the effect of feeding duration and prey density on fish selectivity and efficiency was evaluated. Eight experiments were conducted in which the experimental aquarium was vertically divided by two nets (mesh size 1.5 cm) into three equal compartments (70 L) with four perch and four roach in each. Compartmentalization allowed the conduction of three parallel experiments differing in duration, with feeding times of 5, 10 and 20 min. Two experiments were performed with almost exclusively Cladocera and Copepoda at mean density of 160 ind. L<sup>-1</sup>, respectively, the other six with higher ratios of either Cladocera or Copepoda at prey densities of approximately 50, 200 and 700 ind. L<sup>-1</sup>. As in the first set of experiments fish were killed with an overdose of tricaine (MS 222) and preserved in 10% formaldehyde solution. Thereafter, standard lengths were measured to the nearest 0.5 mm and numbers of prey consumed were confirmed by stomach content analyses. All experiments were carried out from late June to the end of July 1998 and 1999 daily in the afternoon hours.

#### Data analyses

Feeding selectivity was assessed using Ivlev's selectivity index (Ivlev 1961):

$$E_i = (r_i - n_i) \cdot (r_i + n_i)^{-1}$$

where  $r_i$  was the relative abundance of prey category  $i$  in the diet of fish and  $n_i$  was the relative abundance of prey category  $i$  in the environment. The index could achieve values ranging from  $-1$  to  $+1$ , where negative values indicated avoidance, whereas positive values indicated a preference for a particular prey category. Values between  $-0.3$  and  $+0.3$  were generally considered to be not significantly different from 0 and represented nonselective feeding (Lazzaro 1987). Constrained ordination analysis (Lepš & Šmilauer 2003) was applied for explanation of detrendence of diet composition on environmental data.

In our case RDA (redundancy analysis), a method based on linear species response, was chosen as the most appropriate. Scaling focused on inter-species correlations. For most of the statistical comparisons one-way ANOVA with fish species as a factor was used. Differences in standard lengths were compared by two-way ANOVA with fish species and sampling occasions or experimental trial as factors. Identified differences in SL between perch and roach were not significant neither in the fish from Římov Reservoir nor in the fish in the first or second experimental setup (two-way ANOVA,  $P = 0.107$ ,  $0.064$  and  $0.093$ , respectively). Therefore SL was not incorporated into statistical comparisons.

## Results

#### Field study

Juveniles of perch grew from initial  $13.7 \pm 1.5$  mm SL

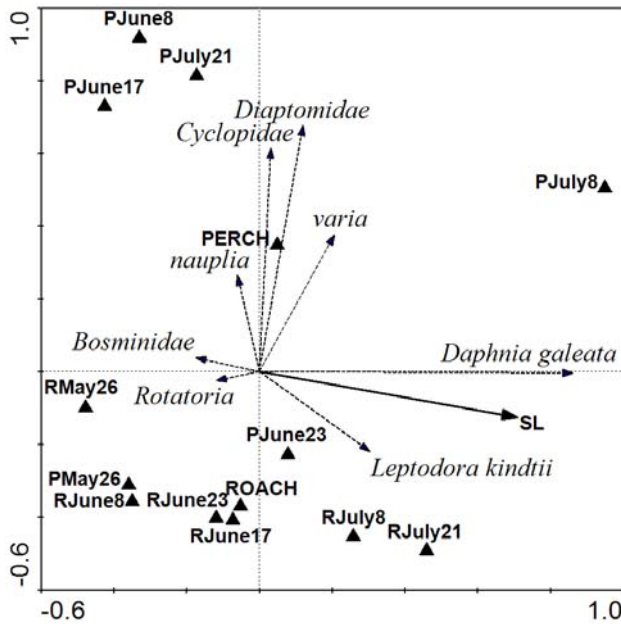


Fig. 1. Redundancy analysis (RDA) of the diet composition of pelagic perch ( $n = 60$ , 12–32 mm SL) and roach ( $n = 60$ , 12.5–35 mm SL) from the epilimnial of Řimov Reservoir from late May throughout second third of July. Consumed prey is indicated by dashed arrows, environmental (SL – standard lengths) and nominal environmental variables (sampling dates, with P or R discriminating between perch and roach samples) by bold arrows and triangles, respectively. Prey category *varia* includes *Diaphanosoma brachyurum*, *Polyphemus pediculus*, Chydoridae and chironomid larvae.

(mean  $\pm$  SD) at the end of May to final  $28.2 \pm 4.5$  mm SL in the second third of July. A similar increase in length (two-way ANOVA,  $P = 0.107$ ) was reported in roach, growing from  $13.0 \pm 0.4$  to  $30.6 \pm 2.9$  mm SL over the investigated period. The diet of both fish species was nearly exclusively composed of crustacean zooplankton. Rotifers played only a marginal role in the early diet of roach contributing a mean 0.8% to the total numbers of consumed prey in May. Similarly, chironomid larvae contributed to the perch diet in July when they composed an average of 1.3 and 0.6% of the total prey numbers, respectively. Ontogenetical changes in diet are summarized in Fig. 1.

The ordination analysis pointed out general differences between the two fish species. The roach diet shifted from rotifers and bosminids in May, towards *Daphnia galeata* G.O. Sars, 1864 and *Leptodora kindtii* (Focke, 1844) in June and July. Since June, *D. galeata* contributed almost exclusively to the diet of roach, composing on average more than 94% of the total prey. Copepods, namely cyclopoid copepods (Cyclopidae), occurred in the diet only on the first sampling date, but later on both cyclopoid and calanoid (Diaptomidae) copepods were completely absent.

On the other hand, copepods played an important role in perch's diet. Lower numbers of copepods were reported only in late June and early July, when their share declined from previous 57.6% in mid June to 6.5 and 13.5% in June/July, respectively. At the end of July

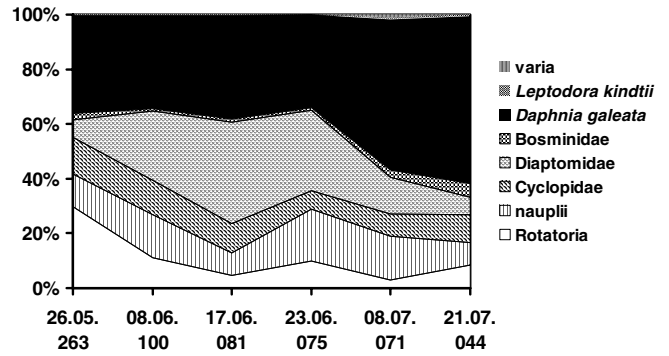


Fig. 2. Temporal variability in the zooplankton composition and abundance in the epilimnial of Řimov Reservoir. Prey category *varia* includes *Diaphanosoma brachyurum*, *Polyphemus pediculus*, Chydoridae and chironomid larvae.

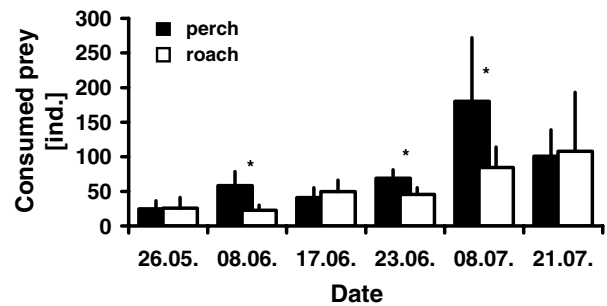


Fig. 3. Temporal variability in the numbers of zooplankton (mean  $\pm$  SD) consumed by individual perch ( $n = 10$  in each bar, 12–32 mm SL) and roach ( $n = 10$  in each bar, 12.5–35 mm SL) from the Řimov Reservoir, \* indicates significant difference between perch and roach (one-way ANOVA,  $P < 0.05$ ).

the share of copepods increased again to 34.1%. Contrary to previous sampling occasions cyclopoid copepods contributed more significantly than calanoid. During the period of decreased contribution of copepods, *D. galeata* composed on average more than 82% of the diet of perch.

During our investigation relatively minor changes occurred in the zooplankton composition (Fig. 2). After the spring maximum of rotifers, the share of calanoid copepods increased gradually during June and declined in early July, followed by an increase in the share of *D. galeata*. This change in the relative share of calanoid copepods in the environment explains particularly well the observed changes in their relative importance in the perch diet. Contrary to zooplankton composition, zooplankton abundance decreased dramatically. After the peak of rotifers in May, zooplankton density declined from 263 ind.  $L^{-1}$  to 100 ind.  $L^{-1}$  in the early June and subsequently to 44 ind.  $L^{-1}$  in the end of July (Fig. 2).

In both fish species, the increase in numbers of largest cladocerans in the diet was related to the increase in SL (Fig. 1). The significance of this relationship was similar in both species. Total numbers of consumed prey increased consistently in roach. On average, numbers of consumed prey were doubled every twenty days during the investigated period (Fig. 3). In perch,

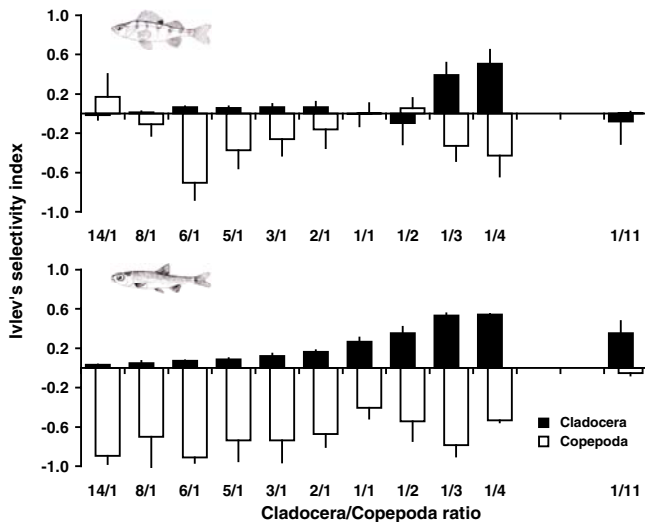


Fig. 4. Feeding selectivity (mean + SD) of perch (upper graph,  $n = 63$ , 41.7 mm SL) and roach (lower graph,  $n = 61$ , 39.5 mm SL) related to Cladocera/Copepoda prey ratios.

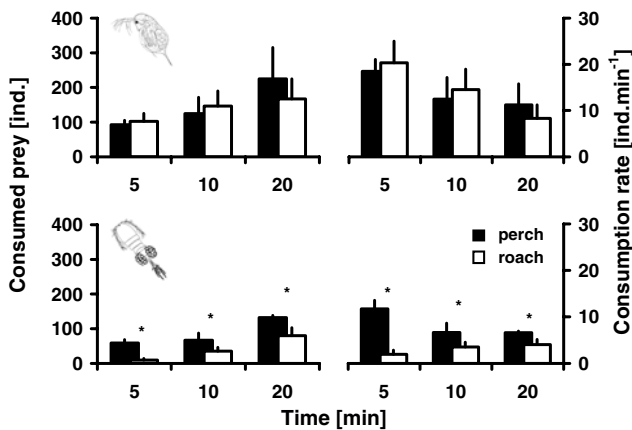


Fig. 5. Total number of prey consumed (mean + SD, left graphs) and consumption rate (mean + SD, right graphs) of perch ( $n = 24$ , 42.8 mm SL) and roach ( $n = 22$ , 42.1 mm SL) after 5, 10 and 20 min of feeding, Cladocera as prey in upper graphs, Copepoda in lower graphs, \* indicates significant difference (one-way ANOVA,  $P < 0.05$ ) between perch and roach.

this increase was not so consistent though higher feeding efficiency over roach was reported on three out of six sampling dates (one-way ANOVA,  $P < 0.041$ , Fig. 3).

#### Laboratory experiments – feeding selectivity

Fish were offered mixtures of prey ranging from a 14 fold higher share of cladocerans (predominantly *Daphnia* sp., Table 1) to an 11 fold higher share of copepods (predominantly Diaptomidae, Table 1). Roach showed high avoidance for copepods (Fig. 4). Copepods were only fed non-selectively when they dominated the prey mixture (92%). On the other hand, consumption of cladocerans increased from non-selective to positive preference with their decreasing share in the offered prey mixture, and even when they composed less than ten percent they were positively selected.

Perch preference was more diversified (Fig. 4).

With a balanced prey ratio perch fed on both prey categories non-selectively. Given an increased share of copepods in the prey mixture, perch revealed a negative preference for copepods and a positive preference for cladocerans. When the share of cladocerans dropped below ten percent both prey categories were consumed non-selectively. However, with an increasing share of cladocerans in the prey mixture cladocerans were consumed non-selectively. A negative preference for copepods increased up to a prey ratio of 6 fold higher share of cladocerans, from which copepods, the less abundant prey category, were again consumed proportionally to their share in the prey mixture. With their ongoing decline in the prey mixture (from 11.1 to 6.7%) perch's preference for them even increased.

#### Laboratory experiments – feeding efficiency

Feeding efficiency, expressed as numbers of consumed prey individuals, of perch and roach foraging on cladocerans (*Daphnia* sp. prevailed, Table 1) and copepods (Diaptomidae prevailed, Table 1) exclusively is shown in Fig. 5. For cladocerans, differences were not significant (one-way ANOVA,  $P > 0.388$ ) between both fish species.

On the other hand, roach consumed significantly fewer prey during short, medium and long time experiments when feeding on copepods (one-way ANOVA,  $P < 0.034$ ). The difference was most evident in the short time experiment, when perch consumed 5.9 times more copepods than roach. After 20 min of feeding the difference was not that obvious, but perch still consumed 1.7 times more prey than roach. In roach, the quantity of consumed copepods was lower than the numbers of consumed cladocerans irrespective of the feeding duration (one-way ANOVA,  $P < 0.039$ ). After 5 min of feeding, roach consumed on average 102 cladocerans, but only 10 copepods, and 167 cladocerans and 80 copepods after 20 min of feeding. In perch, the amount of consumed copepods was lower only when comparing the short time consumption (one-way ANOVA,  $P = 0.01$ ), but was not significantly different after 10 and 20 min of feeding (one-way ANOVA,  $P = 0.108$  and  $0.129$ ).

Perch consumed on average 93 cladocerans and 59 copepods in the short time experiment. This increased to 225 cladocerans and 132 copepods in the long time experiment. With increased feeding time the numbers of prey consumed per minute of feeding (i.e., consumption rate) generally declined. A fourfold increase in feeding time resulted in only a 2.4 times and a 1.6 times increase in the numbers of consumed cladocerans in perch and roach respectively, and in a 2.2 times increase in numbers of consumed copepods in perch. This corresponded to an approximately fifty per cent decline in the consumption rates of cladocerans, dropping from 19 to 11 and from 12 to 6.6 ind. min<sup>-1</sup> in perch and roach respectively, and for copepods declining from 20 to 8 ind. min<sup>-1</sup> in perch. In roach, the consumption rate for copepods was low but rose as feeding times were increased from 2 to 4 ind. min<sup>-1</sup>, which resulted in an 8 fold rise in the numbers of consumed copepod prey.

Table 2. Numbers (mean  $\pm$  SD) of prey consumed by perch ( $n = 71$ , 47.3 mm SL) and roach ( $n = 64$ , 43.1 mm SL) with respect to prey density, feeding duration (5', 10', 20') and higher share of Cladocera and Copepoda, bold faced values indicate significant difference between perch and roach (one-way ANOVA,  $P < 0.05$ ).

Clad/Cop ratio	Prey density (ind. L <sup>-1</sup> )	Consumed prey (ind.)					
		Perch			Roach		
		5'	10'	20'	5'	10'	20'
5.6/1	43	160 $\pm$ 14	229 $\pm$ 48	245 $\pm$ 54	118 $\pm$ 74	132 $\pm$ 68	231 $\pm$ 74
4.5/1	184	201 $\pm$ 49	446 $\pm$ 113	<b>628 <math>\pm</math> 60</b>	201 $\pm$ 83	357 $\pm$ 81	<b>340 <math>\pm</math> 171</b>
4.1/1	720	275 $\pm$ 164	435 $\pm$ 73	539 $\pm$ 193	221 $\pm$ 105	281 $\pm$ 161	411 $\pm$ 178
1/1	226	<b>285 <math>\pm</math> 12</b>	<b>521 <math>\pm</math> 69</b>	<b>764 <math>\pm</math> 46</b>	<b>158 <math>\pm</math> 88</b>	<b>249 <math>\pm</math> 109</b>	<b>398 <math>\pm</math> 112</b>
1/4.9	64	16 $\pm$ 18	<b>73 <math>\pm</math> 32</b>	156 $\pm$ 44	6 $\pm$ 7	<b>17 <math>\pm</math> 5</b>	105 $\pm$ 32
1/3.2	231	145 $\pm$ 83	<b>297 <math>\pm</math> 73</b>	<b>488 <math>\pm</math> 149</b>	48 $\pm$ 13	<b>161 <math>\pm</math> 65</b>	<b>292 <math>\pm</math> 131</b>
1/5.4	660	<b>235 <math>\pm</math> 35</b>	<b>399 <math>\pm</math> 60</b>	<b>551 <math>\pm</math> 57</b>	<b>106 <math>\pm</math> 59</b>	<b>167 <math>\pm</math> 27</b>	<b>338 <math>\pm</math> 87</b>

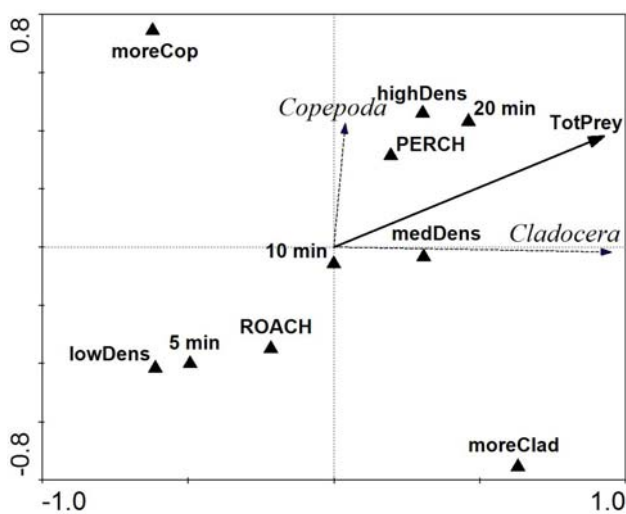


Fig. 6. Redundancy analysis (RDA) of the prey consumption by perch ( $n = 71$ , 47.3 mm SL) and roach ( $n = 64$ , 43.1 mm SL) individuals in feeding experiments with higher ratios of Cladocera (mainly *Daphnia* sp., 4–6/1) or Copepoda (Cyclopidae and Diaptomidae, 3–5.5/1) with respect to the duration of the experiments (5, 10 and 20 min) and prey density (low, medium and high – approx. 50, 200 and 700 ind. L<sup>-1</sup>). Feeding on Cladocera or Copepoda is indicated by dashed arrows, environmental (TotPrey – total number of prey consumed) and nominal environmental variables (prey density, prey ratio and duration of the experiments) by bold arrows and triangles, respectively.

When prey mixtures with a higher share (3–6 times higher, Table 1) of one prey category instead of exclusively either cladocerans or copepods were offered, observed patterns in feeding efficiency were the same as described above for cladocerans and copepods exclusively. Significant differences between perch and roach occurred generally when copepods prevailed in the prey mixture (Table 2), with perch having a higher feeding efficiency for copepods than roach. Total numbers of prey consumed were positively affected by prey density and feeding time (Fig. 6).

Although the effect of experimental duration was uniform, the increase in prey density was most affected from low (50 ind. L<sup>-1</sup>) to medium density (200 ind. L<sup>-1</sup>) (Fig. 6). For example, consumption of copepods in roach increased up to 9.5 times (Table 2).

The effect of increase from medium to high (700 ind. L<sup>-1</sup>) prey density was not that remarkable (Fig. 6), in some cases even lower total numbers of consumed prey were reported at high vs. medium density (Table 2). High density of prey and long feeding time positively affected particularly the perch foraging on copepods (Fig. 6).

## Discussion

In the epipelagic zone of Římov Reservoir, the diet of perch changed from nauplii towards copepodite stages and adults of both cyclopoid and calanoid copepods and finally to cladocerans *Daphnia galeata* and *Leptodora kindtii*, but with a persistent and considerable role of cyclopoid and particularly calanoid copepods.

On the other hand, the avoidance of roach by copepods was obvious. Aside from rotifers, small cladocerans of the Bosminidae family and early copepodite stages of copepods in May, *Daphnia* contributed almost exclusively to the diet of roach in June and July (on average > 94% of total prey) and copepods were completely absent in the diet at this time. Similar differences in feeding preference for planktonic crustaceans were confirmed by other field studies comparing the diets of juvenile perch and roach (Hammer 1985; Jachner 1991; Matěna 1995, 1998; Macháček & Matěna 1997). Most recently Vašek et al. (2006) evaluated the diet of 0+ perch and roach in offshore and inshore habitats of Římov Reservoir and similarly to our results found that copepods were an important prey of perch in both habitats, with a change from cyclopoid to calanoid copepods along the longitudinal profile of the reservoir as calanoid copepods replaced the cyclopoid towards the dam area.

In laboratory experiments, trends in selectivity were similar to those observed in the reservoir. Roach revealed a high negative selectivity for evasive copepods and preferred non-evasive *Daphnia*. Perch preference for *Daphnia* was not different from that observed in roach, but copepods were fed non-selectively both at a balanced prey ratio and contrastingly when their share in prey mixture dropped to approximately eleven percent. Preference even increased with the ongoing decline of copepods in the prey mixture. This sug-

gests that perch selectivity was not determined solely by prey evasiveness. If only prey escape abilities were the selective mechanism we would expect copepods, as prey with higher evasiveness, to be avoided particularly when *Daphnia* were dominant, as was observed in roach.

Therefore, we suggest prey movement conspicuousness is responsible for the change (from negative selection to non-selective consumption) in preference for copepods. This presumption is supported by the fact that change in preference occurred when copepods dropped in prey mixture i.e. after the movement-pattern became conspicuous. Given the general relevance of the "movement-pattern conspicuousness", *Daphnia* should be preferred when its share in prey mixture is low. However, this was particularly difficult to evaluate, because as *Daphnia* has low escape ability it is generally positively selected and whether movement conspicuousness plays role in increased selection for this prey cannot be decided with certainty. We can only speculate if this preference is based solely on the difference in movement-pattern or whether faster movement is by itself responsible for the increase in conspicuousness.

High susceptibility to predation for moving prey was suggested by Dodson (1996). Moreover, in their experiments with virtual plankton images Brewer & Coughlin (1996) reported rate at which fish chose a prey image moving half as fast as the other five surrounding images was not significantly different from the rate predicted by chance. In contrast, when two plankton images were offered, faster moving images were chosen significantly more often. This result suggested that rather than movement-pattern the faster movement of copepods increased the susceptibility to predation. That could particularly explain the result of Furnass (1979), who reported an increasing preference of juvenile perch for the small and evasive calanoid copepod *Eudiaptomus gracilis* (G.O. Sars, 1863) over *Daphnia galeata* with a declining share of *Eudiaptomus* in prey mixture.

Feeding efficiency differed significantly between perch and roach both in the field and in laboratory experiments. In Řimov Reservoir, the increase in numbers of consumed prey was consistent in roach, but not so consistent in perch. Nevertheless perch had a significantly higher feeding efficiency on half of the sampling occasions, while in the remaining samples feeding efficiency was not significantly lower. In laboratory experiments, numbers of consumed *Daphnia* were not different between perch and roach or were not higher for roach. But differences occurred when foraging on copepods exclusively or on prey mixture where copepods predominated. In these trials the feeding efficiency of perch was significantly higher than that of roach.

In roach increasing success in capturing copepods was observed with the increase in feeding time (from five to twenty minutes). However, even when the difference has declined threefold, perch still consumed nearly two times more prey after twenty minutes of feeding.

These results were in sharp contrast to the findings of Persson (1987), who found roach to be a more

efficient forager on both copepods (*Cyclops*) and cladocerans (*Daphnia*). Roach's handling times in his experiments were half that of perch on both *Daphnia* and *Cyclops*. Its attack coefficient was three times higher for *Daphnia* and even nine times higher when foraging on *Cyclops*. In our experiments handling times were not measured, but as handling times can be evaluated as a reciprocal of capture rates, comparisons of differences between both fish species can be drawn solely on them. Capture rates differed significantly only with respect to copepods and were lower in roach as was already described in the above paragraph.

The reason for the distinct differences observed in our study and the study performed by Persson (1987) can lie in the duration of conducted experiments. Our experiments took up to 20 min and reflected the effect of satiation. By contrast, Persson's experiments lasted from 10 s to 10 min, but the 10 min experiments were probably performed only with chironomids; it is not clear from the description of the experimental setup. Therefore, Persson's experiments may unduly emphasize a burst feeding of starved fish, which is not relevant to calculating a long time feeding average.

A sudden decrease in feeding rate after two to four minutes of feeding was documented by Wanzenböck (1995) in experiments with juvenile roach. He also reported nearly eight times higher handling times for *D. magna* Straus, 1820 (2.1 mm) than Persson (1987). Moreover, according to Wanzenböck (1995), the handling times in cyprinids should be principally higher than in percids, because cyprinids chew their prey with pharyngeal teeth, contrary to percids who swallow the prey whole.

In light of these findings we see the cause of the juvenile competitive bottleneck in perch and roach suggested by Persson & Greenberg (1990), resulting in increasing competitive success of roach over perch in temperate water bodies with increasing trophic status (Persson et al. 1991; Jeppesen et al. 2000; Olin et al. 2002), not to be directly related to higher feeding efficiency of roach for cladocerans or even copepods, but rather to the differences in the feeding plasticity of the two species. Roach, in contrast to perch, is able to forage on detritus and plant material (Horppila et al. 2000; Kahl et al. 2001; Persson 1983) and even cyanobacteria (Kamjunke et al. 2002) and therefore is able to more easily withstand periods of food deprivation, both of quantitative and/or qualitative character.

According to our opinion food deprivation affected perch and roach quite differently. By keeping our experimental fish, we observed perch to be highly susceptible to grow sick and die after relatively short periods of food deprivation or insufficiency in food of proper quality. Particularly bosminids were found to constitute a highly insufficient diet for perch (Peterka, unpubl. data). On the other hand food deprivation did not affect roach; they were even able to recycle indigested remains from their own excrements (Matěna, unpubl. data).

Comparing the feeding efficiency of young-of-the-year perch and roach we did not find perch to be less efficient foragers on planktonic crustaceans, both in the field and in laboratory experiments. The differences in numbers of consumed *Daphnia* were not significantly lower in perch. Contrary to roach, perch consumed significantly more copepods. Avoidance of cyclopoid and calanoid copepods was obvious in roach. Roach's inefficiency in consuming evasive copepods was most probably determined solely by prey escape abilities.

On the other hand, perch's selectivity seemed to be determined by other factors, particularly by prey movement conspicuousness or movement speed. In general, roach by its preference for *Daphnia* and obvious avoidance of copepods can be considered as zooplanktivore with a relatively predictable and constant impact on the zooplankton community structure. By contrast, perch's feeding preferences were much diverse and difficult to evaluate, particularly more factors contribute, that were not easily explainable by standard hypotheses. As an example for all, the preference for novel prey in prey-preconditioned yellow perch reported by Mills et al. (1987) can be mentioned. During the experimental trials we observed obvious differences in feeding behaviour between both fish species that could be attributed to perch's success in capturing evasive copepods. Therefore, we suggest paying further attention to factors affecting perch preference for cladocerans and particularly copepods.

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