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THE FOOD OF ROACH, *RUTILUS RUTILUS* (ACTINOPTERYGII: CYPRINIFORMES: CYPRINIDAE), IN A BIOMANIPULATED WATER SUPPLY RESERVOIR

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Background. Roach, *Rutilus rutilus* (Linnaeus, 1758), is an omnivorous fish species that is able to utilise a range of food resources. Both juvenile and older roach can negatively affect zooplankton abundance in freshwater bodies of water; hence populations are often reduced (biomanipulated) in order to increase zooplankton populations. The aim of this study was to assess the roach diet after large-scale removal of cyprinids (bream, roach) from a reservoir. The study was done to clarify the roach diet after three years of intensive reduction of cyprinid fish and also to find out how the roach feeding behaviour impacts the quantity of filtering zooplankton. As such, this study may help to explain more general relations within the aquatic food web and specify the roach diet during the vegetative season (from spring to autumn).

Materials and methods. This study was undertaken at the Hamry water supply reservoir in the Czech Republic. Samples of macrozoobenthos, periphyton, and zooplankton were collected as representative food resources. Fish were caught using a 100-m littoral beach seine during the April to October growing season in 2011. Supplementary fish were caught using a pelagic Nordic gillnet in August and September 2012 and a 15-m beach seine in June and August 2012. Gut contents were preserved in 4% formaldehyde for later laboratory analysis (frequency of occurrence, index of preponderance, index of gut fullness).

Results. 'Detritus' was the major component found in roach guts, with no difference observed in age category or locality (littoral vs. open water areas). Significant differences were observed, however, between younger (0+ and 1+, 36–92 mm) and older (>3 years, >92 mm) fish. The 0+ and 1+ age groups also fed on zooplankton ($P < 0.008$), accompanied by Chironomidae (1+), while diet of older roach (3–4+; 6–8+) included macrophytes and periphyton, together with Cladocera (fish from open water; $P < 0.008$).

Conclusion. The results demonstrate that detritus was the main 'dietary' component of roach during the growing season, with macrophytes and periphyton as complementary dietary items. Zooplankton was an important dietary component of mainly younger roach age classes. Roach appear to be an important component in ichthyo-eutrophication of the Hamry Reservoir, mainly through transfer of phosphorous from plants to water.

Keywords: diet analysis, gut, biomanipulation, age groups

INTRODUCTION

Roach, *Rutilus rutilus* (Linnaeus, 1758); bream, *Abramis brama* (Linnaeus, 1758); and European perch, *Perca fluviatilis* Linnaeus, 1758 typically dominate fish stocks in water supply reservoirs (drinking water reservoir) of the Czech Republic (Pivnička 1992). Roach are feeding generalists, usually utilising the most available food resource (Hellawell 1972, Prejs and Jackowska 1978, Prejs 1984, Horppila and Nurminen 2009). Such dietary plasticity allows it to find food in habitats offering less than ideal conditions for other species, whose feeding demands may be greater (Baruš and Oliva 1995).

Planktonic crustacean such as Cladocera and Copepoda tend to dominate in the food of younger age classes; Tarvainen et al. (2002), for example, found 0+ roach (71–90 mm) to be exclusively zooplanktivorous (*Bosmina*, *Chydorus*), while Hammer (1985) observed the same cladoceran species dominating roach fry diet in Lake Lankau (Germany). Similarly, Vašek et al. (2006) as well as Peterka and Matěna (2009) have both described

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zooplankton as the main food of 0+ roach in Czech reservoirs. The proportion of zooplankton in roach diet changes, however, according to ontogenetic stage, with the proportion of macrophytes and detritus increasing as the fish gets older (Matěna 1995, 1998).

In deep valley reservoirs lacking shallow vegetated shorelines, zooplankton also represents a major dietary element in older roach age classes (Kubečka et al. 1998, Vašek and Kubečka 2004). Linfield (1980), when studying roach diet in lakes of northern Britain, found that diet changed with fish length, with roach < 100 mm consuming mostly Cladocera (23%–29%), phytoplankton (7%–23%), Diptera (5%–17%), and macrophytes (6%–13%). The quantity of Cladocera and macrophytes decreased to 9%–13% and 10%–12%, respectively, and the quantity of Diptera, algae, and Trichoptera increased up to 8%–28%, 6%–10%, and 2%–10%, respectively, in roach longer than 100 mm.

In analysing gut contents of adult roach (120–240 mm) from the Włocławek Reservoir in Poland, Szczyglińska (1987) found that roach ate mainly plants and aquatic macroinvertebrates (mostly *Pisidium* sp. and *Viviparus viviparus*), with 'detritus' and sand also occurring in each alimentary tract. Brabrand (1985) noted that lower macroinvertebrate availability resulted in greater proportion of macrophytes in roach diet in a mesotrophic lake in north-eastern Norway. Similarly, during a period of low zooplankton abundance in a eutrophic lake in Finland, larger roach were observed to concentrate on plants and detritus as food items (Horppila and Peltonen 1997). Martyniak et al. (1991), who analysed the diet of 145–420 mm roach in the Pierzchały Reservoir in Poland, found that the most frequently and regularly eaten items were dreissenids (50%), larvae of Chironomidae and macrophyte material.

In a number of reservoirs, large numbers of cyprinids (e.g., bream, roach) have been removed in an attempt to affect the reservoir's food cascade, a process commonly termed biomanipulation. Excessive consumption of zooplankton by planktivorous fish can lead to algal blooms, which can seriously affect drinking water quality (Dokulil and Teubner 2000, Walker et al. 2007). Removal of large numbers of roach and bream (ca. 100 kg per hectare), along with large-scale stocking of predatory fish is expected to result in an increase in zooplankton density and an improvement in water quality (Prejs et al. 1994).

Between 2009 and 2011, 10 438 adult cyprinid fish weighing 3774 kg were removed from the Hamry Reservoir, including 8685 bream (>200 mm) and 1753 roach (>160 mm). The fish were removed from the reservoir early in the spawning season each year between April and May, the fish lengths taken corresponding to fish of four years and older (i.e., capable of spawning). Simultaneously, each May and June (2009–2011), 285 000 bream larvae/juveniles and 395 000 roach larvae/juveniles were also removed. Alongside removal of cyprinids, zooplankton quantities were also determined. Overall, the species composition of cladoceran zooplankton showed no change.

The aim of this study was to assess the diet of roach following the large-scale removal of cyprinids (bream, roach) from the reservoir. We hypothesise that the large-scale removal of roach from the reservoir will help improve zooplankton development. Such a result would add support to fish removal from water supply reservoirs with the aim of improving long-term water quality and lowering treatment costs.

MATERIAL AND METHODS

Study site. This study was carried out at the Hamry water supply reservoir (49º43′52″N, 15º55′1″E), near the town of Hlinsko in the Bohemian-Moravian highlands of the Czech Republic. Built between 1907 and 1912, the reservoir is fed by the River Chrudimka and was originally intended as a single-purpose structure for protecting Hlinsko and its surroundings against flooding. The dam is 17.4 m high with its crest at an elevation of 602.86 m. The reservoir is 42.3 ha in size and has a catchment area of 56.8 km^2; average depth is 2 m, with a maximum depth by the dam of 7.5 m. The reservoir presently serves as a drinking water source for Hlinsko and its surroundings. About half of the shoreline is associated with bankside meadows with a gentle slope and shore macrophytes that are flooded during higher water levels. The reminder of the shoreline has steep banks covered by a coniferous forest and its littoral zone featuring limited macrophyte vegetation. The inlet area is shallow with soft sediment and a thick layer of detritus from decaying meadow grass beds.
Methods. Littoral macrozoobenthos and periphyton were monitored monthly from April to August and in October of 2011 and 2012. At the same time, zooplankton samples were taken from three points of different depth (Fig. 1).

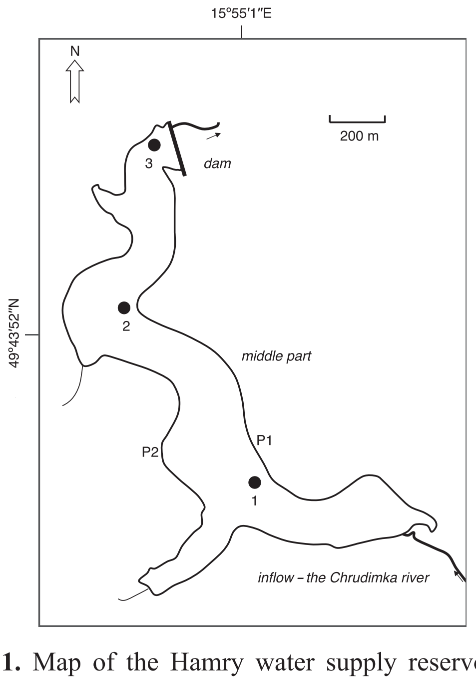

Fig. 1. Map of the Hamry water supply reservoir with sampling sites indicated (Sites 1, 2 and 3 indicate zooplankton sampling sites; P1 and P2 indicate macrozoobenthos and periphyton sampling sites)

Zooplankton samples from site 1 (depth 1.5 m) were taken using a standard 20 cm diameter zooplankton net towed horizontally for 6 m. Zooplankton samples from sites 2 (depth 4 m) and 3 (depth 7 m) were taken with the same equipment, but the net was pulled out vertically from depths of 4 and 6 m, respectively (see Přikryl 2006.

Submerged littoral vegetation was sampled manually at two littoral sites in order to examine overgrowing periphyton. Periphyton is expressed as percentage frequency between taxa.

Macrozoobenthos samples were taken simultaneously using a modified version of the PERLA method (Kokeš and Němejcová 2006), i.e., multi-habitat sampling with all habitats sampled proportionally. Samples were collected using a benthos net and kick-sampling for 3-min intervals. All zooplankton and macrozoobenthos samples were preserved in 4% formaldehyde. Macrozoobenthos samples were processed by removal of all organisms present in the sample or, if the sample was large, from a representative part (minimum 25%). Organisms were determined to the lowest possible taxonomic level and number of individuals per sample, and their relative abundance was calculated by dividing the number of individuals *n* in the sample (× 100) by the number of all individuals in the sample.

Depending on the volume of zooplankton, a subsample of 4, 5, or 6 mL was taken from a known volume of each plankton sample and placed into a counting chamber. Zooplankton organisms were identified in the laboratory of Povodí Labe, s.e., the authority responsible for managing the reservoir. Organisms present were determined, counted, and expressed as number of individuals per m^3. The organisms were then separated by size using a sieve, i.e., those 100–700 mm and those > 700, for future analysis.

Fish were sampled using a 100-m beach seine (maximum depth 4 m, mesh size 20 mm) along the shallow banks of the reservoir during the day in April, June, July, and October of 2011. During 2009, some fish were also sampled by electrofishing. Based on results from 2011, an additional sampling (September 2012) was completed using Nordic gillnets to collect fish from open water (overnight exposure). Only live fish were used for further analysis. Younger fish were sampled using a fry beach seine (15 m long, 2 m depth, 4 mm mesh size) in June and August 2012. On each occasion, ca. 20 individuals from the four dominant age (size) categories (0+ of 36–52 mm, 1+ of 55–92 mm, 3–4+ of 73–163 mm, and 6–8+ of 163–266 mm standard length; SL) were taken for diet analysis. The length frequency distribution of all roach sampled over 2011 and 2012 is displayed in Fig. 2.

Immediately after capture, fish were weighed (to the nearest 0.1 g), measured (SL; to the nearest 1 mm), then dissected and the gut contents separated. The gut contents were weighed (to the nearest 0.1 g) and preserved in 4% formaldehyde for later laboratory analysis.

A modification of the gravimetric method used by Hyslop (1980) was used to analyse food content in the laboratory. Mucus and mineral particles were separated from the sample and not included in further food analysis. The bulk of the sample, which consisted of macrophytes and detritus, was separated from determinable taxa under a binocular microscope; taxa were then examined under a magnification ranging from 40× to 450×. The proportion of total food intake (W_T) [%] represented by each category was evaluated using the indirect method of Hyslop (1980), using the following formula:

$$W_T = 100(W_i \cdot \Sigma W_i^{-1})$$

where: W_i is the weight of an individual food component i and ΣW_i is the weight of all food components combined.

Frequency of occurrence (FO) [%] of food items was calculated according to Pivnička (1981) using the formula:

$$\mathrm{FO} = 100(n \cdot \Sigma n^{-1})$$

where: n is the number of guts containing a particular dietary component and Σn_i is the number of all guts.

These two criteria are combined in order to express an index of preponderance (IP) using the following formula:

$$\mathrm{IP} = 100(W_i \cdot \mathrm{FO}_i) \cdot \Sigma(W_i \cdot \mathrm{FO}_i)^{-1}$$

where: W_i is the weight percentage of a particular food component i and FO_i is the frequency of occurrence of that food component. This provides a relevant measurable basis for sorting particular components and presents results that are a combination of frequency of occurrence and weight contribution of particular components (Natarajan and Jhingran 1961).

Food bulk weight was assessed to the nearest mg and presented as the index of gut fullness (IF) [$^{o}/_{ooo}$] using the formula:

$$\mathrm{IF} = 10^4 w \cdot W^{-1}$$

where: w = food weight, W = fish weight.

The percentage of each food item was compared separately using Mann–Whitney tests with Bonferroni correction of significance level to decrease the probability of committing a type I error in multiple testing (Sokal and Rohlf 1995). Bonferroni correction was applied in order to control familywise error rate in cases of multiple testing. For each food item, 6 cross-comparisons (0+ vs. 1+, 0+ vs. 3+–4+, 0+ vs. 6+–8+, 1+ vs. 3+–4+, 1+ vs. 6+–8+, 3+–4+ vs. 6+–8+) were conducted, thus correcting the significance level α from its original value of 0.05 to $0.05 \times 6^{-1} = 0.008$.

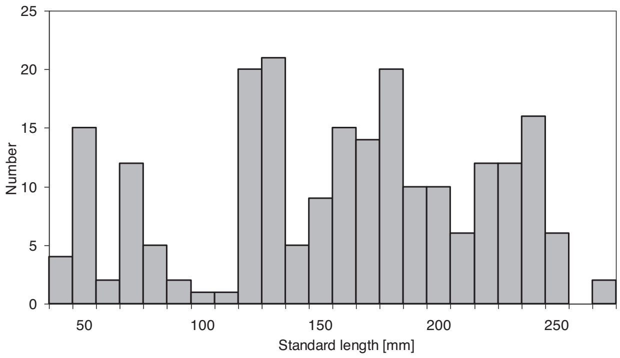

Fig. 2. Length-frequency distribution of roach, *Rutilus rutilus*, sampled from the Hamry Reservoir, Czech Republic, in 2011 and 2012

We declare that this study has been carried out in accordance with the valid legislation of the Czech Republic, particularly under laws No. 114/1992 Coll. No. 246/1992 Coll. and Instruction No. 554/77-34. No organism sampled in this study represented a species protected in the Czech Republic.

RESULTS

Food resources. From April through August, chironomid larvae were the dominant macrozoobenthic organisms, while Ephemeroptera and Mollusca dominated in October (Fig. 3). Bacillariophyceae were dominant in the periphyton assemblage throughout the year (Fig. 4). Cladocera > 700 µm were dominant in total volume of zooplankton over 2011–2012 (Fig. 5).

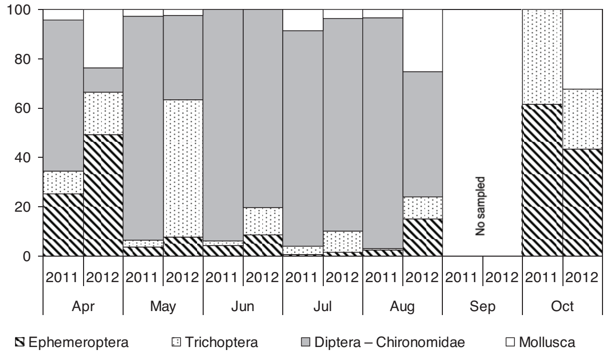

Fig. 3. Monthly macrozoobenthos composition at the Hamry Reservoir, Czech Republic, in 2011 and 2012

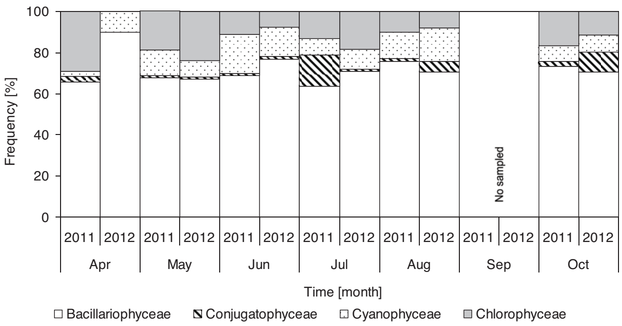

Fig. 4. Monthly periphyton composition at the Hamry Reservoir, Czech Republic, in 2011 and 2012

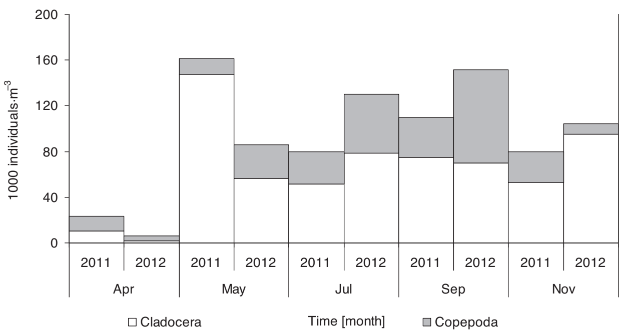

Fig. 5. Monthly zooplankton composition at the Hamry Reservoir, Czech Republic, in 2011 and 2012

Food of roach. The diet of 0+ roach consisted mainly of detritus (IP 63.8) and Cladocera (IP 33.8), with Copepoda (IP 2.4) being much less consumed (Table 1). Macrophytes remains were not recorded in the youngest age group. Roach fry consumed significantly more Cladocera and Copepoda than roach > 6–8+ ($P < 0.008$). No significant difference in detritus consumption was observed between 0+ and older groups ($P > 0.008$).

Detritus was dominant in 1+ roach diet (IP 82.6, Table 1), followed by Cladocera (IP 8.9) and Chironomidae (IP 7.0). Macrophytes (IP 1.0) and Copepoda (IP 0.5) were less important. 1+ roach consumed less zooplankton but more Chironomidae than 0+ roach (Fig. 6), and significantly more Cladocera and Chironomidae than older roach ($P < 0.008$).

The dominant food item of 3–4+ roach was detritus (IP 74.2 ± 5.0), with macrophytes (IP 16.1 ± 5.5) and periphyton (IP 7.5 ± 1.3) of secondary importance, both varying according to season. Cladocera, Chironomidae, Mollusca, Trichoptera, Copepoda, and Ephemeroptera were all marginal dietary components (Table 2). The average index of fullness in this group was 177.5$^{o}/_{ooo}$, with minimum values in April and maximum in June (Fig. 7).

Detritus was the main food item for 6–8+ roach caught in the littoral zone (IP 55.8 ± 19.5) throughout the monitored season, except for June when periphyton was dominant (IP 62.5). Macrophytes (IP 19.7 ± 15.4) were also frequently consumed, with highest consumption in April. Other items were consumed only occasionally (Table 2, Fig. 6). Average index of fullness for littoral zone 6–8+ roach was 197.3 $^{o}/_{ooo}$. Roach sampled in open water consumed primarily periphyton (IP 46.9), detritus (IP 27.4), and Cladocera (IP 15.8), with macrophytes (IP 8.7) also

Table 1

Index of preponderance of young (1+; 0+) and adult (6–8+) roach, *Rutilus rutilus*, in the Hamry Reservoir, Czech Republic, in 2012

		Date and age group		
		11 Jun (1+)	23 Aug (0+)	23 Aug–20 Sep (6–8+)
Food item	Cladocera	8.9	33.8	15.8
	Copepoda	0.5	2.4	1.2
	Chironomidae	7.0	0	0.7
	Macrophytes	1.0	0	8.7
	Periphyton	0	0	46.9
	Detritus	82.6	63.8	27.4
Parameter	n	20	20	20
	n_0	0	0	0
	TL [mm]	87.6 ± 9.6	54.8 ± 4.6	265.4 ± 34.6
	SL [mm]	70.1 ± 8.4	44.1 ± 4.0	219.1 ± 29.9
	SL range [mm]	55.0–92.0	36.0–52.0	150.0–266.0
	W [g]	6.8 ± 2.3	1.7 ± 0.4	234.1 ± 84.2

Length and weight values are mean ± standard deviation; n = number of fish, n_0 = number of fish without food, TL = total length of fish, SL = standard length, W = fish weight.

being taken. While roach in open water consumed more Cladocera than littoral roach, food from the littoral zone still dominated in the diet, indicating that these fish moved in-shore to feed over the dial period.

Changes in assemblage structure and quantity following the fish removal clearly indicate a decrease in predatory pressure on filtering zooplankton (Fig. 8).

DISCUSSION

Detritus was the dominant food item of roach in Hamry Reservoir, regardless of site, age, or date of capture supplemented with macrophytes, periphyton, and zooplankton. Zooplankton never formed a substantial part of the diet. The results indicate that roach periodically move between the littoral and open water zones, thereby utilising food over the whole reservoir. Studies in shallow lakes in Poland have also found that detritus, macrophytes, and periphyton formed significant components of roach diet (Klimczyk-Janikowska 1978, Tarkowska-Kukuryk 2008).

In the Mušovská Reservoir (mean depth 1.5 m), a shallow lake with a developed littoral zone in the Czech Republic, Adámek et al. (1985) observed that roach consumed mainly detritus and zooplankton at offshore sites, and detritus and periphyton at inshore sites, indicating that roach used all the food items accessible in its immediate vicinity. While it might be expected that results would be similar in shallow reservoirs, in a relatively shallow eutrophic lake in Denmark (mean depth 3.1 m), roach fed mainly on zooplankton (Michelsen et al. 1994). Zoobenthos were of minor importance and detritus appeared only in periods of low animal-food availability. In this case, it may be that roach displayed lower feeding efficiency on prey living in the sediment comparing to other species, e.g., sub-adult perch.

The most significant changes in roach food composition are found in steep-sided canyon-shaped valley reservoirs,

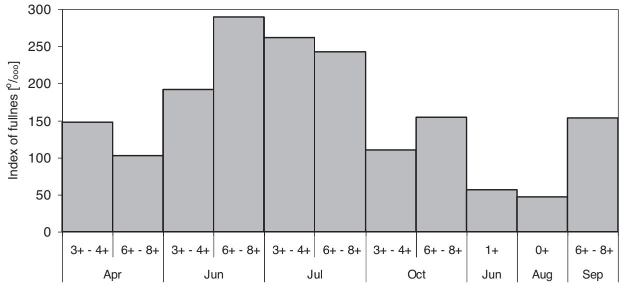

Fig. 6. Seasonal diet composition for roach at the Hamry Reservoir, Czech Republic, in 2011 and 2012

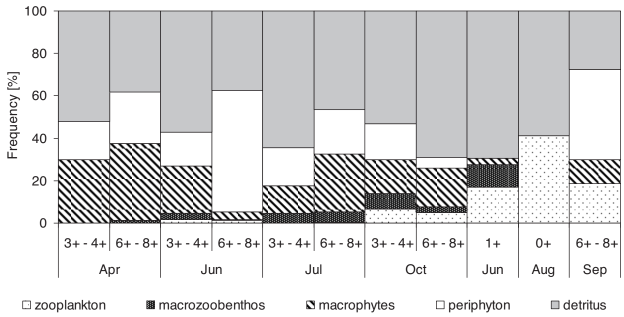

Fig. 7. Index of fullness dynamics for a range of age classes of roach, *Rutilus rutilus*, at the Hamry Reservoir, Czech Republic, in 2011 and 2012

Table 2

Index of preponderance for roach, *Rutilus rutilus*, in the Hamry Reservoir, Czech Republic, in 2011 Date and age group

		Date and age group							
		26–27 April		6 June		20 July		3 and 5 October	
		3–4+	6–8+	3–4+	6–8+	3–4+	6–8+	3–4+	6–8+
Food item	Cladocera	0	0	0.5	0.3	0	0.1	4.5	1.0
	Copepoda	0	0	0	0	0	0	0.3	0.1
	Ephemeroptera	0	0	0	0	0	0	0.2	0
	Trichoptera	0	0.4	0.1	0	0.3	0.2	0.3	0
	Chironomidae	0	0	0.5	0.1	0.7	2.5	0.1	0.2
	Mollusca	0	0	0	0	0	0	0.8	0.2
	Macrophytes	24.9	41.5	16.5	1.1	12.2	26.0	10.7	10.2
	Periphyton	7.5	14.9	9.6	62.5	5.9	13.8	7.1	1.3
	Detritus	67.6	43.2	72.8	36.0	80.9	57.4	75.9	86.9
Parameter	n	13	27	20	20	21	19	20	20
	n_0	3	9	0	0	0	0	0	0
	TL [mm]	184.1 ± 10.0	249.7 ± 30.1	171.7 ± 21.1	259.0 ± 28.6	148.6 ± 17.6	217.2 ± 8.2	155.5 ± 10.5	240.8 ± 30.3
	SL [mm]	151.1 ± 8.4	205.4 ± 26.2	141.3 ± 17.6	211.8 ± 24.2	118.7 ± 14.7	176.9 ± 7.6	125.2 ± 10.1	202.7 ± 25.9
	SL range [mm]	134.0–161.0	163.0–244.0	113.0–163.0	166.0–243.0	73.0–160.0	165.0–200.0	113.0–157.0	150.0–240.0
	W [g]	68.9 ± 12.7	189.4 ± 63.9	63.7 ± 24.6	222.2 ± 73.1	35.7 ± 13.2	122.1 ± 17.6	38.2 ± 11.4	185.1 ± 65.5

Length and weight values are mean ± standard deviation; n = number of fish, n_0 = number of fish without food, TL = total length of fish, SL = standard length, W = fish weight.

where macrophytes are generally absent. Hammer (1985), Ponton and Gerdeaux (1988), Giles et al. (1990), and Peterka and Matěna (2009) all found roach to specialise in feeding on crustacean zooplankton at such sites only Richeux et al. (1992) found, by contrast, in the deep lake of Pareloup (Massif Central, France) that smaller roach (10–21 cm) had a diet chiefly of detritus and zooplankton, whilst oldest individuals were detritivores. While roach typically select zooplankton in deep reservoirs, its ability to feed on detritus may also provide it with an energetic advantage, increasing the carrying capacity for this species in lakes where detritus occurs and is accessible. This may also be important in habitats where feeding competition occurs between roach and perch due to juvenile perch favouring macrozoobenthos (Okun and Mehner 2005). Adámek et al. (1987) sampled fish at two sites (middle and upper tributary) in a deep reservoir (maximum depth 85.5 m), and found that roach fed chiefly on detritus (49%) and zooplankton (40%) in the canyon-shaped middle section, and macrophytes (48%) together with detritus (36%) in the shallow upper section with a rich littoral zone. The high proportion of detritus indicated an offshore-inshore foraging movement, as also indicated in this study.

The majority of the above-mentioned publications did not distinguish age categories in the fish studied. Our results, however, indicate that there are age differences, with one-year-old fish consuming mainly detritus and zooplankton and older fish showing a significant preference for detritus, macrophytes, and periphyton. Age differences have also been observed by Horppila (1994), who found that the importance of zooplankton decreased and that of benthos and plants increased, with increasing roach size. Similarly, Volta and Jepsen (2008) observed a clear age difference when comparing diet of in shallow and deep reservoirs, with young roach consuming mainly algae and older specimens consuming mainly zooplankton, detritus and macrozoobenthos.

While a number of authors have considered adult roach to be molluscivorous (Prejs 1976, Szczyglińska 1987, Specziár et al. 1997), we observed no preference for Mollusca, even in larger roach (>163 mm). Note, however, that representation of Mollusca in the macrozoobenthos assemblage did increase slightly in autumn.

Prior to the large-scale removal of cyprinids documented in this study, only Šampalík (unpublished*) had studied roach feeding activity in the Hamry Reservoir. His study, however, took place during the spawning period (April–June) in 2009 and 2010. He found that macrophytes were the dominant food component (50%–70%) of roach diet. In comparison with our results, therefore, there has been no obvious change in overall diet. Inshore roach samples, collected using the same method as Šampalík (unpublished), indicate that detritus and periphyton had slightly increased in roach diet in 2011, and macrophytes slightly decreased. In comparison, a dietary shift was observed at a lake in Finland following biomanipulation, when biomass of roach and bream was reduced to 33% and 10%, respectively. Roach of almost all size classes started to forage on macrozoobenthos. In this case, however, the lake in question had no submerged littoral zone available as an alternative food source (Persson and Hannson 1999).

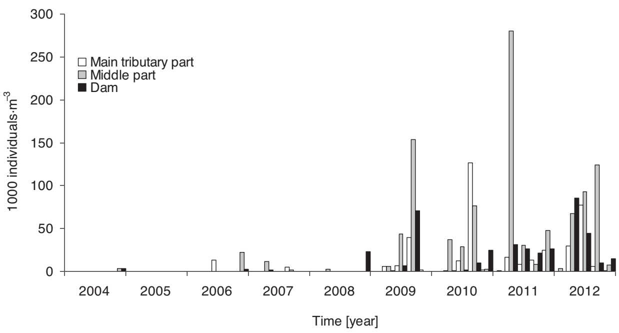

Fig. 8. Zooplankton abundance at the Hamry Reservoir, Czech Republic, during the five years before fish removal (2004–2008; data supplied by Povodí Labe) and from 2009 to 2012

Roach are able to utilise a wide range of available food resources due to their feeding plasticity. In deep canyon reservoirs with an absence of macrophytes, therefore, adult roach tend to consume cladocerans zooplankton; while in shallow reservoirs with flooded macrophytes, periphyton (e.g., diatoms) is used as easily accessible food source for both sub-adult and adult roach.

Younger roach age classes (i.e., 0+ and 1+) can play a negative role in water quality management when planktonic filtrators form the major part of food. On the other hand, older fish can also contribute to eutrophication when their feeding is primarily focused on detritus and macrophytes, through the transfer of phosphorus in plants back into the water. In this study, despite the dominant food item being detritus and Cladocera averaging only 21.35% (0+ and 1+ category) and 2.47% (3–4+ and 6–8+ category), this volume of Cladocera in roach diet proved important for the filtering ability of the whole community. Large-scale removals of cyprinid fish, therefore, can contribute significantly to the development of filtering zooplankton populations.

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