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Distribution and Diet of 0+ Fish within a Canyon-Shaped European Reservoir in Late Summer

key words: juvenile fish; spatial heterogeneity; reservoirs; perch; roach

Abstract

The distribution and diet of age 0+ fish were studied in the deep canyon-shaped Římov Reservoir (Czech Republic), which is characterized by a longitudinal trophic gradient. During late summer of two years, 0+ fish were sampled from inshore and offshore habitats along the longitudinal reservoir axis. Offshore catches of 0+ fish from the surface layer were dominated by roach (*Rutilus rutilus*), bream (*Abramis brama*) and perch (*Perca fluviatilis*), whereas in the deeper open water perch predominated. Inshore catches of 0+ fish were constituted mainly by perch and roach. The proportions of roach in the inshore catches were highest at the upper and most eutrophic part of the reservoir, whereas the proportions of perch in the inshore catches were higher at the downstream areas. Total catches of both inshore and offshore 0+ fish increased upstream in the reservoir. Offshore 0+ perch were of consistently smaller size than inshore 0+ perch. Inshore 0+ perch had significantly smaller size at the upstream reservoir part than at the downstream, more lacustrine regions. The diet of both inshore and offshore 0+ fish consisted predominantly of crustacean zooplankton. Perch diet was generally dominated both by cladocerans and copepods, whereas roach diet consisted chiefly of cladocerans.

1. Introduction

Recent studies from large lakes and reservoirs recognized the within-system spatial heterogeneity in the distribution patterns and feeding habits of fish as an important ecological issue (e.g., HORPPILA *et al.*, 2000; WINFIELD *et al.*, 2002; VAŠEK *et al.*, 2003). Both from scientific and management point of view, there is no doubt that exploring this issue is needed for more realistic predictions about the structure and functioning of lake or reservoir ecosystems (MEHNER *et al.*, 2002). In Europe, the study of juvenile fish populations in artificial water bodies like reservoirs has received little attention in comparison to natural lakes. However, because reservoirs have some special characteristics compared to natural lakes (e.g., strong water level fluctuations, length/width ratio, small and unstructured littoral area) they can provide new and interesting insights into the fish distribution patterns and population dynamics. A special type of man-made lakes is the canyon-shaped dam reservoir (or the deep valley reservoir, in other words) characterized by elongate morphometry and pronounced longitudinal environmental gradients (LIND *et al.*, 1993; STRAŠKRABA, 1998). Canyon-shaped reservoirs thus offer an excellent possibility to study both the large-scale (along the longitudinal reservoir axis) and the relatively small-scale (littoral to pelagial, vertical) within-system spatial variation in fish parameters.

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In this study we aimed to explore the spatial variation in distribution and diet of 0+ fish within the deep and elongated Římov Reservoir, South Bohemia (Czech Republic). Previous research conducted recently on the Římov Reservoir by means of an extensive gill-netting has indicated pronounced spatial gradients in the distribution of fish (VAŠEK *et al.*, 2004). It was found that during summer majority of fish in the Římov Reservoir occupied epilimnetic layers and the total relative abundance of fish in the offshore habitat increased considerably upstream in the reservoir – toward the most eutrophic tributary region. The present study is entirely focused on the 0+ fish spatial characteristics within the Římov Reservoir and supplements our previous research of similar scope, which was concentrated mostly on adult fish stages (VAŠEK *et al.*, 2003, 2004). We sampled 0+ fish along the longitudinal axis of the Římov Reservoir by using active sampling gears in both inshore and offshore habitats. Sampling was performed in late summer because at this time 0+ fish community composition manifests recruitment success of different fish species throughout whole growing season, i.e. reflects in summary both the spawning success of adult fish and the survival success of 0+ juveniles before passing the first winter. Our aims were to evaluate: (i) whether 0+ fish density and community composition show any strong spatial patterns along the longitudinal reservoir axis, (ii) whether differences in size of 0+ fish of dominant species exist between inshore and offshore habitats and upstream and downstream reservoir regions, and (iii) whether diet composition of 0+ fish exhibits spatial variation within the reservoir. We hypothesized that total density of 0+ fish would be higher upstream than downstream in the reservoir, because of riverine origin of the reservoir fish fauna and also due to more productive character of the reservoir tributary part. We expected that community composition, growth (reflected in fish sizes) and diet of 0+ fish might change along the longitudinal reservoir axis because of pronounced longitudinal gradients of limnological parameters (e.g., water transparency, total phosphorus and chlorophyll-*a* concentrations) that exist in the reservoir.

2. Material and Methods

2.1. Study Site

The research was conducted in the canyon-shaped Římov Reservoir, a narrow and deep man-made lake situated in South Bohemia (48°50' N, 14°29' E), Czech Republic. Římov Reservoir was built for drinking-water storage in 1978 on the Malše River, which is a single major reservoir tributary. The reservoir has a surface area of 210 ha, volume of 33.6×10^6 m³, length of 12 km and maximum surface elevation of 471 m a.s.l. The mean depth of the reservoir is 16 m, the maximum depth is 45 m and the mean theoretical retention time is about 95 days. Římov Reservoir is dimictic and the thermocline depth in the lacustrine part of the reservoir is about 4 m in late summer (August). The littoral region is deprived of aquatic macrophytes due to steep banks and water level fluctuations. The trophic status of the reservoir can be characterized as mesotrophic to highly eutrophic, with phosphorus and chlorophyll-*a* concentrations decreasing downstream in the reservoir (e.g., SEĎA and DEVETTER, 2000). In August 1999, epilimnetic total phosphorus and chlorophyll-*a* concentrations (samples taken from 0.5 m depth) at the dam area of the reservoir were 21 and 9 µg l⁻¹, respectively, and Secchi depth in that area reached 3.3 m. At the uppermost end of the reservoir, in contrast, total phosphorus and chlorophyll-*a* concentrations were 125 and 94 µg l⁻¹ at the same time, respectively, and Secchi depth attained only 0.9 m (databank of the Hydrobiological Institute, České Budějovice).

2.2. Sampling 0+ Fish and Zooplankton

0+ fish were sampled in mid-August 1999 and 2001 in inshore and offshore habitats at three different areas of the Římov Reservoir (Fig. 1). Hereafter, these areas are referred as the dam, middle and tributary areas, respectively, each roughly representing one third of the reservoir length. The inshore

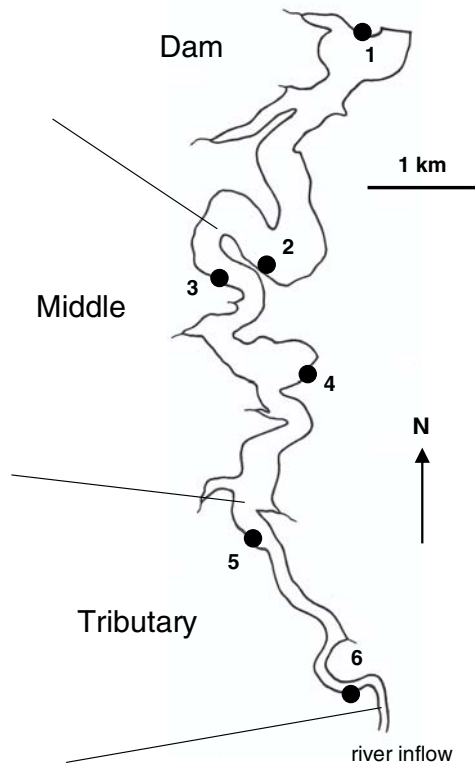


Figure 1. Map of the Římov Reservoir with three different areas (dam, middle, tributary) defined. Sites (1–6) where inshore 0+ fish were collected are shown by dots.

sampling sites (sites 1 to 6; Fig. 1) were chosen to represent shallow, gently sloping habitats within the reservoir. They had a slope of approximately 10%, whereas most of the reservoir shoreline is much steeper. The bottom consisted of gravel (site 1), sand (sites 2, 3 and 4) and silt material (sites 5 and 6). No macrophytes as well as no potential obstacles (tree stumps and branches, large stones) were present at any inshore site. Inshore 0+ fish were collected by a 30 × 3 m beach seine with 6 mm mesh size in 1999 and by a 10 × 2 m beach seine of 1.7 mm mesh size in 2001. The seine net was set parallel (by its entire length) to the shoreline at a distance of 15 m from the bank and was drawn to the shore by means of ropes fixed on the net ends.

In 1999, inshore fish were sampled at sites 1, 3 and 6 on three consecutive dates with calm weather conditions. Sampling was carried out in 3-h intervals during one 24-h period at each site. Usually one haul only was conducted at each 3-h interval, since it yielded a sufficient number (at least several tens) of 0+ fish. The exception was the seining at site 3, where we observed 0+ fish moving in large shoals along the shoreline. We performed three replicate hauls regularly spaced along the shore of this site when we started the diel sampling, it means at the first two 3-h intervals of the 24-h period (13:00 and 16:00 hours). In both time intervals, one of the replicate hauls yielded huge amounts of 0+ fish (more than thousand of individuals), whereas the other two replicates represented none or negligible catches (<10 individuals). In further day-time intervals of the diel trial, we performed non-replicated hauls just in those parts of shoreline where shoals of 0+ juveniles were present (the position of shoals were visually checked before each seining). It means always one “aimed” haul successful in capturing large number of 0+ fish was carried out in each daytime interval. During night period, no shoals of juveniles were observed in the littoral and therefore the night hauls were not “aimed” and only

a single haul was performed at each night-time interval. The night hauls yielded large catches of 0+ fish. To allow a rough comparison of the relative abundances of 0+ fish among the inshore sites along the longitudinal reservoir axis, the catches of non-replicated hauls taken in daytime at site 3 were divided by a factor of 3. We assume the results of replicated seining at this site justified this measure.

When the total 0+ fish catch per haul represented a volume ≤ 2 litres (2 l ~ 400–600 individuals of 0+ fish), all juveniles were killed with an overdose of MS-222 (tricaine methane sulphonate) and preserved in 10% formaldehyde. When the amount of fish per haul was larger, a 2 l subsample was fixed and the rest of 0+ fish was released. A specific problem represented the catch in the tributary area (site 6) where about 50 l of fine mud mixed with hundreds of 0+ fish was obtained by each haul. Due to the time and manpower restrictions, 0+ fish were picked from only one third of the mud volume in each haul (their number was tripled for relative abundance comparison among sites) and preserved for later analyses. In 2001, 0+ fish were sampled at all six inshore sites. Three replicate hauls regularly spaced along a shore were taken at each site during the day (11:30–16:00) and night (22:00–0:30) periods.

Offshore 0+ fish were sampled with a fixed-frame pelagic trawl (mouth opening 3×3 m, length 5.4 m, mesh size 6.5 mm, cod end of mesh size 3 mm with a funnel preventing fry escape) pulled 100 m behind a vessel at a speed of 0.9 m s^{-1} . The trajectory of pulling was not straight so the sampling was outside the area disturbed by the boat. Tows were made for the duration of approximately 10 minutes (8–16 min) and were performed at depths of the upper trawl rim of 0 m and 3 or 4 m (i.e. the trawl sampled 0–3, 3–6 or 4–7 m depth stratum). At one occasion, the tow was conducted at the depth of the upper trawl rim of 6 m (sampling in 6–9 m stratum). Trawling was carried out in mid-August (always at calm weather) both during day and night in 1999, or only during the night in 2001. Trawling in the surface open water (0–3 m) was performed in all three reservoir areas (Fig. 1), whereas trawling in the deeper open water (below 3 m) was conducted only in the dam and middle areas. The whole 0+ fish catch from each trawl tow was immediately preserved in 10% formaldehyde. In the laboratory, 0+ fish from each seine or trawl haul were identified and counted. Whole catch or a random subsample of 100–300 individuals of the dominant 0+ fish species from each habitat and part of the reservoir was usually measured to determine the standard length (SL) of 0+ juveniles.

Concurrently with fish sampling in 1999, inshore and offshore zooplankton was collected at the three reservoir areas. Inshore zooplankton was taken at sites 1, 3 and 6 with a 30.7 l Schindler sampler fitted with a 200 μm mesh net. At each site, three Schindler samples were taken close to the shore at the depth of 0.7–1 m in 12-h intervals during a diel cycle. The sampling times were 14:00, 2:00 and 14:00 hours in the middle and tributary sites and 12:00, 24:00 and 12:00 hours in the dam site. Offshore zooplankton was collected in the open water areas (above the maximum depth) adjacent to the inshore sites 1, 3 and 6. Samples were taken as vertical hauls through the epilimnetic layer with an Apstain plankton net (mouth diameter 28.5 cm, mesh size 200 μm). The depth of the epilimnion was 4.5, 4.0 and 1.3 m at the dam, middle and tributary areas, respectively. At each area, one non-replicate haul was taken in 4-h intervals during a diel cycle. At the middle and tributary sites, sampling started at 14:00 hours and finished at 10:00 hours of the consecutive day. At the dam site, sampling started at 12:00 hours and finished at 8:00 hours of the consecutive day. For the day-night comparison of zooplankton density, samples taken during 8:00–18:00 h period are treated as the day samples and samples taken during 20:00–6:00 h period are treated as the night samples.

2.3. Diet Analyses

In 1999, 15–20 individuals of the dominant 0+ fish species were randomly taken from each sample, whenever possible, and subjected to digestive tract content analysis. These fish were measured for standard length, blotted with tissue paper and weighed to the nearest 0.01 g wet weight (excluding digestive tract contents) with an electronic balance. In perch (*Perca fluviatilis* L.), the content of every stomach was scrutinized in a grid-etched Sedgewick-Rafter chamber under a binocular microscope at either 40 \times or 100 \times magnification. Prey items were identified to the relevant taxonomic categories and counted (prey items in perch stomachs were usually intact and occasional prey fragments were easily identifiable). Since cyprinids lack a morphologically separated stomach, the content of the first third of every gut was analyzed in case of roach *Rutilus rutilus* (L.) and bream *Abramis brama* (L.). Firstly, the whole digestive tract was removed under a dissecting microscope and divided into three sections, corresponding to the three loops of the gut. Then the anterior loop was opened and the content placed into polyvinyl alcohol medium on a microscope slide. This permanent mount was examined under a binocular micro-

scope at a 100× magnification. As the food organisms in cyprinid guts were considerably disintegrated, well recognizable remains of prey were identified and enumerated as individuals. For instance, cladoceran postabdomens or (pairs of) mandibles, copepod furcas and head capsules of insects were counted. Whenever possible, the body lengths of undamaged individuals (in cyprinids guts, this was usually possible for small-bodied cladocerans with thick exoskeleton like bosminids and chydorids) or the lengths of recognizable remains were measured in 5–10 cases for each prey category in every gut (stomach) using an eye-piece micrometer. When the latter approach was applied, body lengths of individuals were estimated from relationships between measurements of prey fragments and corresponding prey body lengths found in the literature (MEHNER *et al.*, 1995) or derived from our zooplankton samples. Median body lengths of prey found in perch stomachs and cyprinid guts were converted to wet weights using formerly published taxon-specific length–weight regressions (BOTTRELL *et al.*, 1976; MEHNER *et al.*, 1995; HOEHN *et al.*, 1998).

Diet composition of fish was described by prey frequency of occurrence, percentage of prey numbers and percentage of prey wet weight. A total of 676 perch stomachs and 145 roach and 50 bream intestines were analyzed. The graphical method of COSTELLO (1990), modified by AMUNDSEN *et al.* (1996), was used to examine feeding strategy of 0+ fish. Ratios of reconstructed stomach content wet weight to body wet weight were used to measure perch stomach fullness and to determine perch diel feeding patterns. Principal component analysis (PCA), a linear multivariate technique for indirect gradient analysis (LEPŠ and ŠMILAUER, 2003), was used to describe the main sources of variation in diet composition of the dominant offshore-sampled 0+ fish in 1999. Mean percentage diet composition (by numbers and wet weight, respectively) of individual fish species (i.e. the weighted means from 15–20 dissected specimens of each species) from particular trawl tows represented the sampling units (i.e. statistical individuals) in the PCA performed. The transformation $\log(x + 1)$ was applied to the data matrix.

3. Results

3.1. Distribution and Size of 0+ Fish

Mean total catch per unit effort of inshore 0+ fish (pooled day and night samples) was lowest at the dam area and increased upstream within the reservoir in both years (Fig. 2). Inshore 0+ fish catches were dominated by perch and roach, bream occurred much less frequently in both years (Fig. 2). Ruffe (*Gymnocephalus cernuus* (L.)) was the third most frequent species collected in the inshore habitat in 2001. Comparing the composition of inshore 0+ fish assemblages along the longitudinal reservoir axis, lowest proportions of perch and highest proportions of cyprinids, mainly roach, were found at the tributary area in both years. A total of 13 trawl tows were carried out at offshore locations in 1999: all 6 tows performed during night successfully captured 0+ fish, while out of the 7 daytime tows only two were successful in capturing 0+ fish. Therefore, in 2001 only night trawling was conducted. Densities of offshore 0+ fish in different depths and parts of the reservoir are presented in Table 1. According to trawl catches from the surface stratum (depth 0–3 m), total offshore 0+ fish density increased upstream within the reservoir in both years. 0+ fish catches from the surface layer were dominated by roach (1999) or bream and roach (2001). Perch, in contrast, strongly dominated offshore catches obtained from the deeper layers during both years (Table 1).

Mean standard length (SL) of offshore perch at different reservoir areas attained 42.7–49.8 mm in 1999 and 44.3–48.5 mm in 2001. In both years, mean SL of offshore perch was consistently smaller than mean SL of inshore perch that reached 52.2–59.6 mm (1999) and 51.5–60.6 mm (2001) at different reservoir areas and day periods (Fig. 3 and Fig. 4). SL of inshore perch differed significantly along the longitudinal reservoir axis, mean perch SL was found smaller at the tributary area compared to the dam or middle area in both years (ANOVA, post hoc Tukey HSD tests, $p < 0.05$ for both day and night samples). Mean SL (± 1 SD) of offshore roach in the surface layer (0–3 m) at different reservoir areas reached 44.5 (± 2.9) – 45.6 (± 2.7) mm in 1999 and 43.5 (± 2.4) – 43.7 (± 4.2) mm in 2001. Roach col-

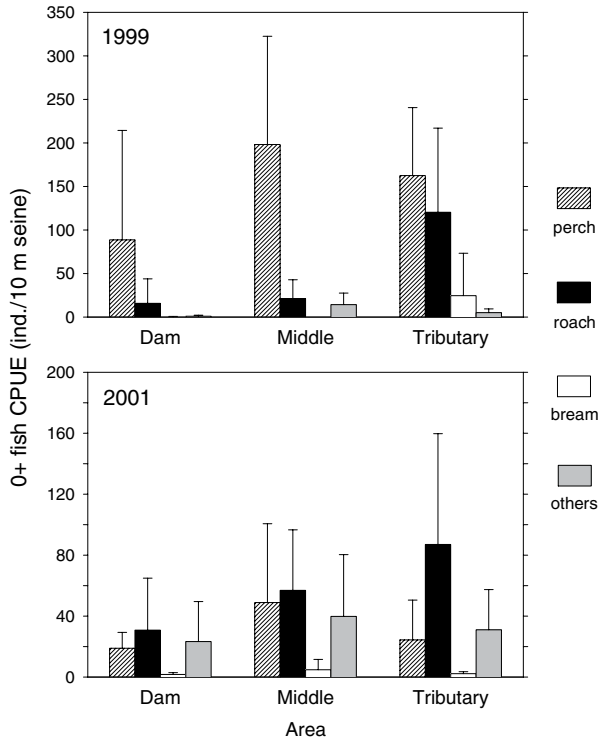


Figure 2. Mean catches per unit effort (+1 SD) of inshore 0+ fish at the three reservoir areas in August 1999 and 2001. Day and night samples were pooled.

Table 1. Densities of offshore 0+ fish at the three reservoir areas and different depth strata in August 1999 and 2001 (*N* number of trawl tows performed). Numerical proportions of three dominant species (perch, roach, and bream) on total 0+ fish catches are presented.

Area	Year	Period of day	Depth (m)	N	Density (ind./100 m ³)	Catch composition by species		
						perch	roach	bream
Dam	1999	day	0–3	1	0	–	–	–
Middle	1999	day	0–3	2	0	–	–	–
Tributary	1999	day	0–3	1	0	–	–	–
Dam	1999	day	4–7	2	1.78	0.54	0.42	0.02
Middle	1999	day	4–7	1	0	–	–	–
Dam	1999	night	0–3	1	6.26	0.01	0.99	–
Middle	1999	night	0–3	2	16.10	0.04	0.92	0.03
Tributary	1999	night	0–3	1	25.63	0.03	0.91	0.04
Dam	1999	night	4–7	1	1.10	0.78	0.22	–
Middle	1999	night	4–7	1	18.79	0.89	0.10	0.01
Dam	2001	night	0–3	2	0.84	0.43	0.14	0.31
Middle	2001	night	0–3	2	2.45	0.42	0.20	0.37
Tributary	2001	night	0–3	1	11.38	0.05	0.02	0.92
Dam	2001	night	3–6	2	0.79	1.00	–	–
Middle	2001	night	3–6	1	1.91	0.89	0.03	0.05
Dam	2001	night	6–9	1	0.04	1.00	–	–

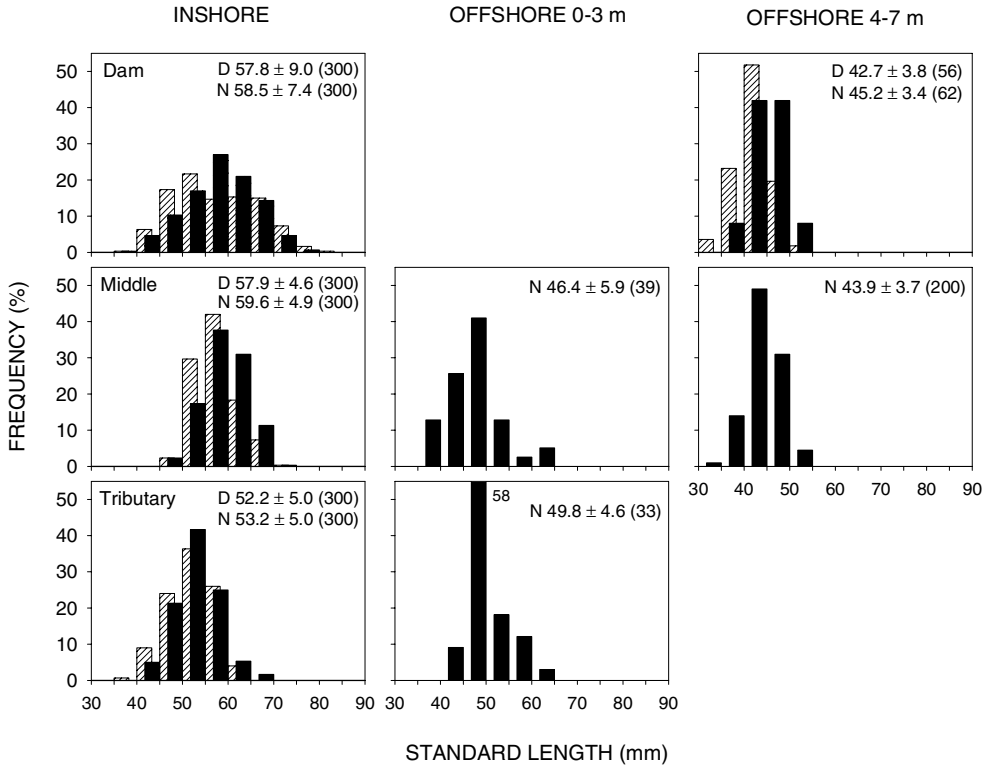


Figure 3. Length-frequency distribution of inshore and offshore 0+ perch at the three reservoir areas in mid-August 1999. Mean standard lengths ± 1 SD (mm) of perch sampled during day (*D*; hatched bars) or night (*N*; black bars) period are given above each histogram, the numbers of fish measured are given in parentheses.

lected inshore at different reservoir areas averaged 41.7 (± 3.2) – 45.2 (± 4.3) mm in 1999 and 44.7 (± 3.9) – 45.5 (± 3.3) mm in 2001. No consistent pattern in size differences of roach between inshore and offshore habitats or along the longitudinal reservoir axis was found. Mean SL (± 1 SD) of inshore and offshore bream at the tributary area in 1999 was 44.7 (± 3.5) and 42.8 (± 4.7) mm, respectively. Mean SL of bream collected offshore in 2001 ranged from 42.6 (± 4.6) to 43.0 (± 5.0) mm at different reservoir areas.

3.2. Diets of 0+ Perch, Roach and Bream

0+ fish foraged predominantly on crustacean zooplankton in both inshore and offshore habitats in August 1999. Zooplankton densities at different areas of the Římov Reservoir during this time are illustrated in Figure 5. Total densities of planktonic crustaceans were highest at the tributary area where they reached similar values in both offshore and inshore habitats. At this area, cyclopoid copepods were by far the most abundant component in zooplankton. By contrast, cladocerans prevailed over copepods in the zooplankton at the dam and middle areas and total zooplankton densities at these areas were markedly higher offshore compared to the inshore habitat. Generally, no pronounced differences between day and night densities of individual crustacean taxa were observed at the particular areas.

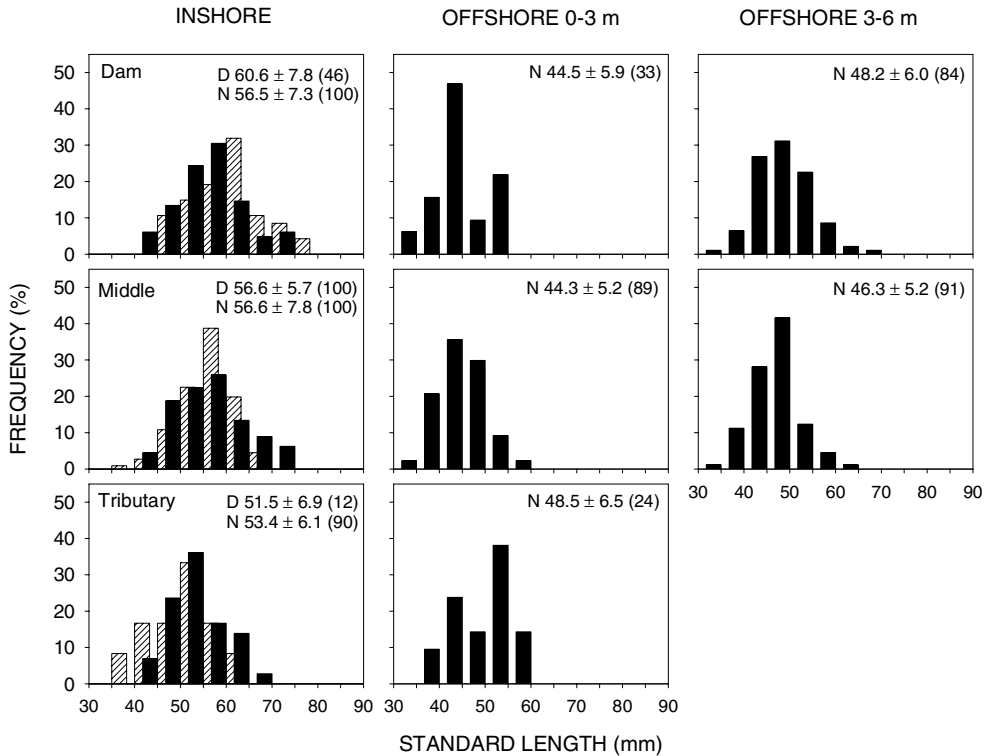


Figure 4. Length-frequency distribution of inshore and offshore 0+ perch at the three reservoir areas in mid-August 2001. Mean standard lengths ± 1 SD (mm) of perch sampled during day (D; hatched bars) or night (N; black bars) period are given above each histogram, the numbers of fish measured are given in parentheses.

The diet spectra of inshore perch collected at the three reservoir areas during the whole diel cycle are described in Figure 6. Perch diets at the dam and middle areas were dominated by the cladocerans *Daphnia galeata* Sars and *Diaphanosoma brachyurum* (LÉVIN) and by calanoid copepod *Eudiaptomus gracilis* (Sars). In terms of wet weight, the large cladoceran *Leptodora kindtii* (Focke) was also an important food component. No obvious diel shifts in diet composition of these perch were observed, except for somewhat increased proportions of *L. kindtii* during the night in perch diet at the dam area. Otherwise, proportions of different prey items in the diet within the 24-h sampling periods were of rather consistent pattern (dam area) or showed some kind of random fluctuations (middle area). Inshore perch at the tributary area consumed *D. galeata*, *D. brachyurum* and cyclopoid copepods. *E. gracilis* was of negligible importance in the diet of perch at this area. Pronounced changes in diet composition of perch throughout the 24-h period were observed at the tributary area. Proportions of *D. galeata* in the diet increased during the night hours. This was especially evident from the diel pattern of diet composition based on prey numbers. Furthermore, examining the diel diet composition by wet weight, a marked contrast in proportions of the two dominant prey items in perch diet was revealed between the start and end of the 24-h sampling cycle. At the beginning of the trial *D. galeata* and cyclopoid copepods constituted 75% and 15% of the diet, respectively, while 24 hours later the reverse was seen and the same prey comprised 16% and 69% of the diet, respectively (Fig. 6).

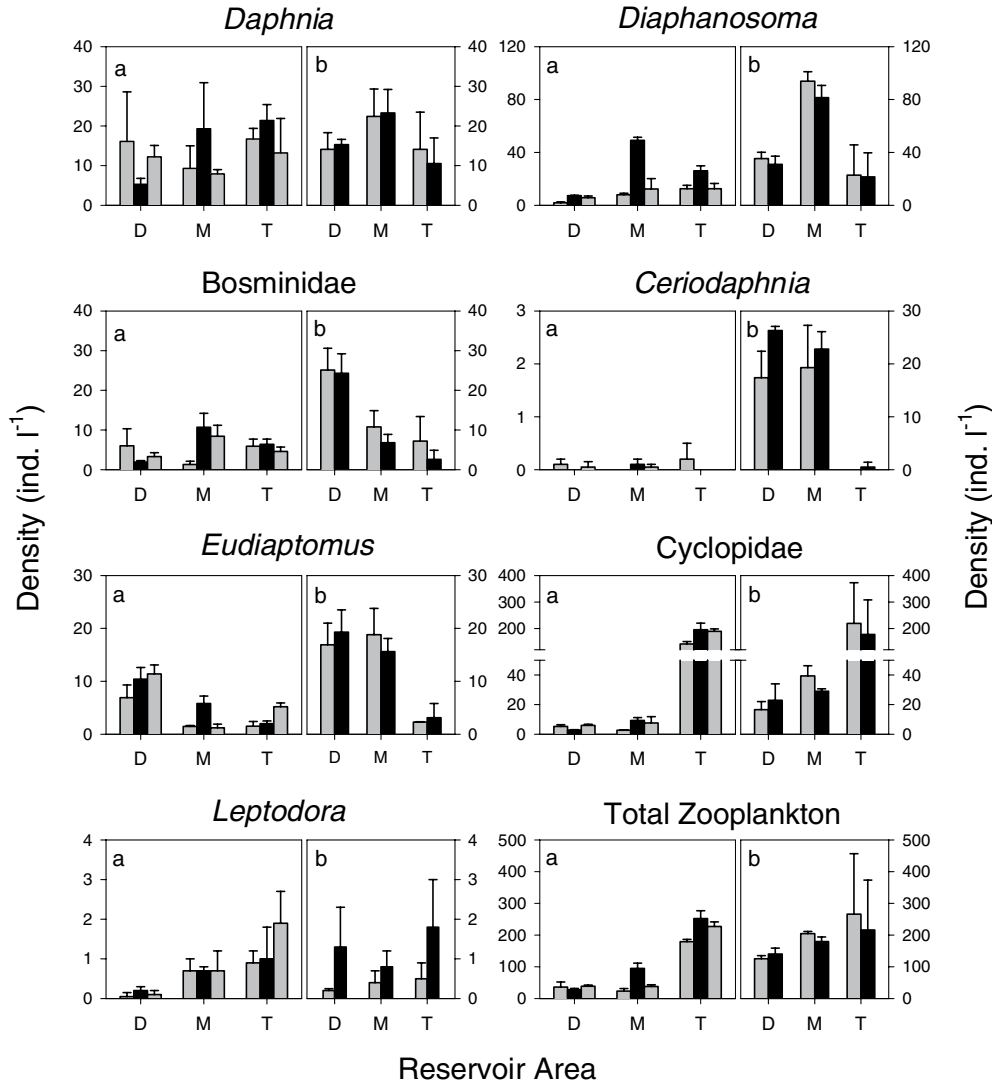


Figure 5. Densities of inshore (a) and offshore (b) crustacean zooplankton at three reservoir areas (*D* dam, *M* middle, *T* tributary) in mid-August 1999. Means (+1 SD) are based on three replicates. Daytime samples are presented by grey bars, night samples by black bars. The daytime densities on two consecutive days are shown for zooplankton in the inshore habitat. Note different scaling of y-axis for different zooplankton taxa. Within a taxon, the scaling of y-axis for inshore and offshore habitats is the same, except for *Ceriodaphnia*.

The diet (on a wet weight basis) of inshore roach caught at the dam area around noon was dominated by *D. galeata* (88%) and *L. kindtii* (8%) and diet of inshore roach caught at the tributary area at the same time was dominated by *D. galeata* (75%), cyclopoid copepods (13%) and *L. kindtii* (8%). The diet of inshore bream at the tributary area consisted of sediment-dwelling chydorids (76% of wet weight), *D. galeata* (10%), chironomid larvae (6%) and cyclopoids (4%). Detritus and periphyton occurred in 20% of both roach and bream guts

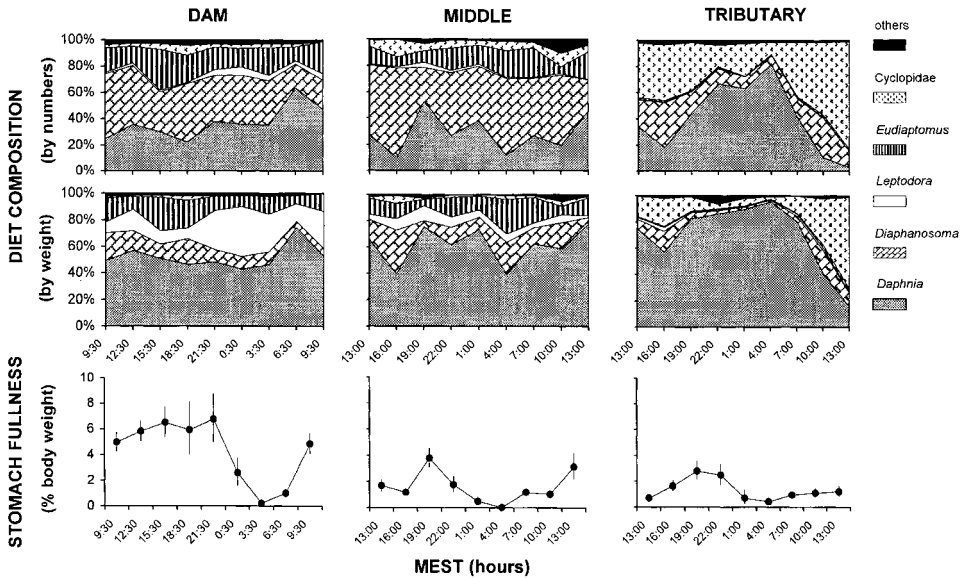


Figure 6. Diel variation in diet composition (% by numbers and wet weight) and stomach fullness (% of body wet weight) of inshore 0+ perch at the three reservoir areas in mid-August 1999. Stomach contents of 20 individuals were examined at each area and time interval, stomach fullness is shown as a mean with 95% confidence limits. Sunset and sunrise were at 20:15 and 5:55 h of the Middle European summer time (MEST).

in the tributary area, but only in negligible amounts. These food components were therefore not considered in computation of the diet compositions and the diet spectra presented here reflect purely an animal food of cyprinids.

In general, feeding strategy analysis revealed a high specialization of inshore 0+ fish toward a single or a few prey items. An example of the feeding strategy plots based on diet composition by wet weight is given in Figure 7. Beside this high level of specialization, several other prey items were included commonly in the diet of most fish individuals but their contribution to the digestive tract contents of fish was low.

Variation in diet composition of offshore 0+ fish in August 1999 is summarized by PCA biplots (Fig. 8) based on percentage numerical and wet weight data, respectively. For the PCA of prey numbers, the first two ordination axes explained 81.6% (52.0 + 29.6) of the total variation in the diet composition data. For the PCA of prey wet weight, the first two axes accounted for 80.9% (59.1 + 21.8) of the total variability. In both analyses, the first axis clearly reflected the difference between roach and perch diets. Roach consumed mainly cladocerans *L. kindtii* and *D. galeata*, whereas perch foraged significantly also on copepods (Cyclopidae, *E. gracilis*) and cladoceran *D. brachyurum*. The second axis separated occasionally taken daytime samples of 0+ fish from the rest of the night samples. The prey item contributing most to this separation was *Ceriodaphnia quadrangula* (O. F. MÜLLER), which was a significant food component for the daytime caught offshore fish while in the diets of fish sampled during night it has a minor importance.

According to the feeding strategy analysis, also offshore 0+ fish showed a specialization toward a single or a few prey items (Fig. 9). However, especially in the case of perch, a relatively high intra-individual (within-phenotype) diet variation was sometimes found, indicating rather a generalized feeding strategy toward the different zooplankton prey (see first

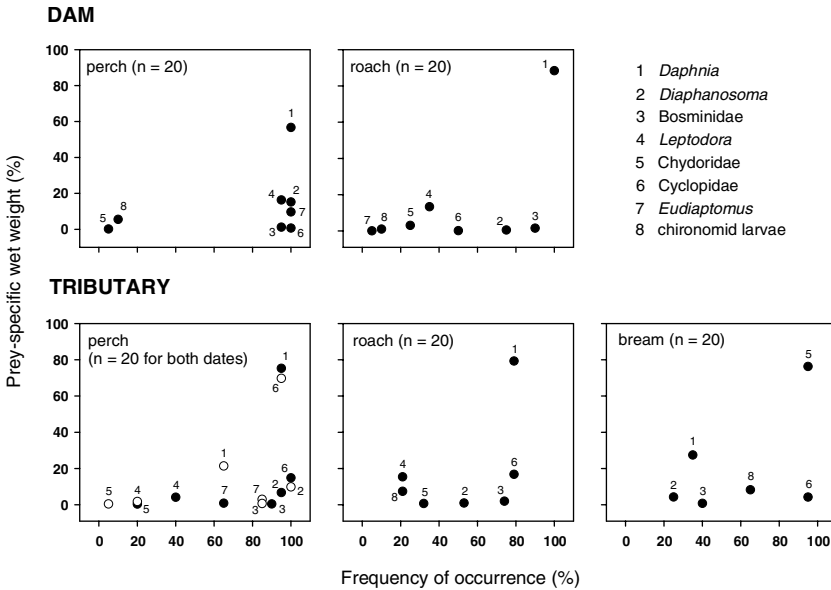


Figure 7. Feeding strategy plots of inshore 0+ perch, roach and bream in August 1999. Fish were sampled at 12:30 h at the dam area and 13:00 h at the tributary area. Diet composition of perch at the tributary area was assessed during two consecutive days (filled dots – 16 August; empty dots – 17 August). Numbers of non-empty digestive tracts analyzed are given in parentheses. Prey-specific wet weight is defined as the percentage a prey category comprised of total wet weight of all prey items in the digestive tracts of only those fish in which the actual prey occurred (AMUNDSEN *et al.*, 1996).

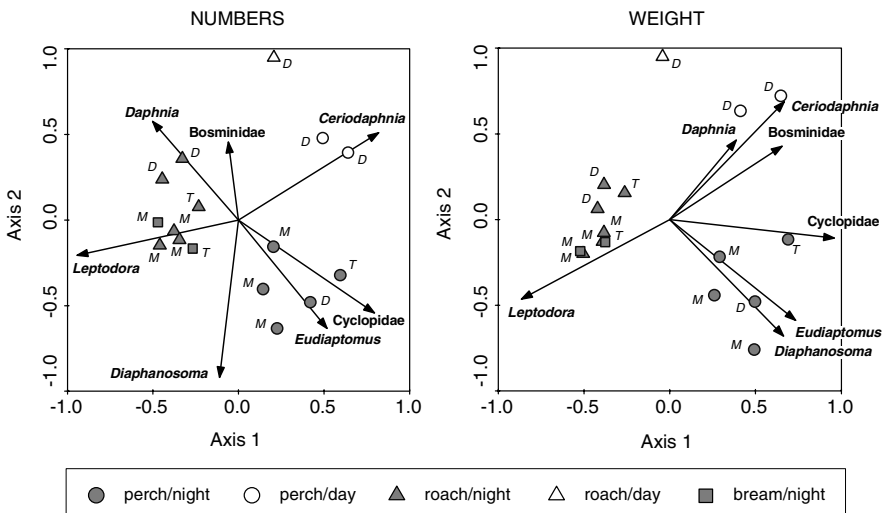


Figure 8. Principal component analysis (PCA) biplots of diet composition of offshore 0+ fish, separated for numerical and wet weight data. Sample points represent the mean percentage diet composition of the individual fish species (i.e. the weighted means from 15–20 dissected individuals of each species) originated from particular trawl tows. The code near each point indicates the reservoir area: *D* dam, *M* middle, *T* tributary. Prey arrows are centered, that is the mean value of each transformed variable coincides with the origin of the biplot. The transformation $\log(x + 1)$ was applied to the data matrix.

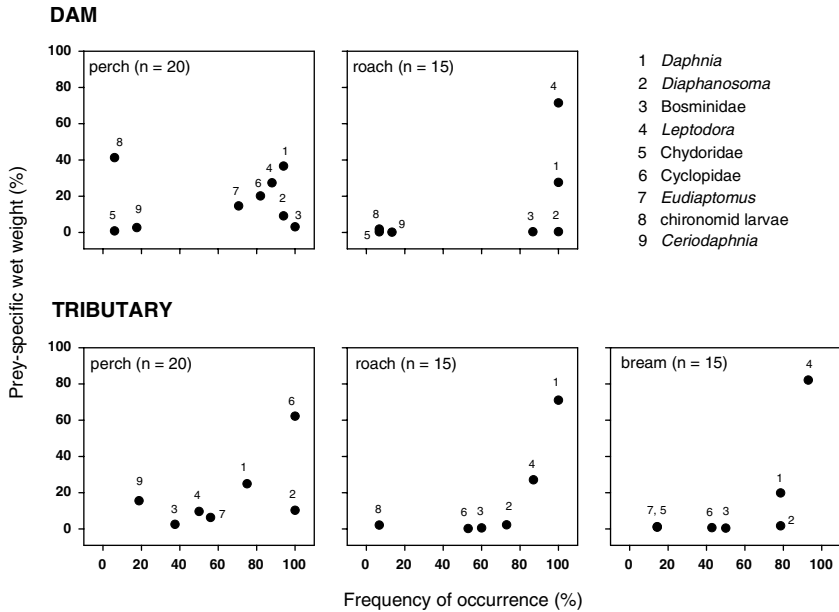


Figure 9. Feeding strategy plots of offshore 0+ perch, roach and bream in August 1999. Fish at the dam area were collected at 22:00 h from the depth of 4–7 m, fish at the tributary area were collected at 21:15 h from the depth of 0–3 m. Numbers of non-empty digestive tracts analyzed are given in parentheses. For the definition of prey-specific wet weight see caption of the Figure 7.

plot in the Fig. 9). In general, considering the diet of fish of the same species taken from the same sample, no large inter-individual (between-phenotype) diet variation was revealed, i.e. the diet was homogeneous amongst the individuals. No evidence of piscivorous feeding was found in both inshore and offshore 0+ perch at any reservoir area.

Stomach fullness (SF) patterns over the 24-h periods indicated that inshore 0+ perch were diurnal feeders at all three reservoir areas (Fig. 6). Maxima in perch SF were observed during late afternoon or dusk and consequently they were followed by a decline until the next morning. Mean SF of perch at the dam area during 9:30–18:30 hours ranged between 4.9 and 6.5% of body wet weight, whereas mean perch SF at the middle and tributary areas attained, respectively, 1.0–3.8 and 0.7–2.8% of body wet weight throughout the time period 10:00–19:00 hours. Offshore perch originating from the only two daytime samples (dam area) had a mean SF of 2.7 and 2.9% of body wet weight. Mean SF of perch sampled offshore during night varied from 0.8 to 1.5% of body wet weight.

4. Discussion

Using trawling, 0+ fish were readily caught in the open water habitat of the Římov Reservoir during night. In contrast, catches of 0+ fish in the same habitat during daytime were rather exceptional. Such very low daytime catches of offshore 0+ fish could be a result of several different causes. Firstly, we cannot exclude the possibility that 0+ fish avoided the trawl in daytime because they can see the net (NOBLE, 1970). Secondly, aggregated distribution of fish during daytime compared to more even distribution at night

(TISCHLER *et al.*, 2000; MASSON *et al.*, 2001) might be another reason for the low daytime catches in offshore areas since fish shoals have a higher avoidance capability, or simply due to the fact that hitting of a fish aggregation by relatively low number of tows is less probable. Finally, 0+ fish could spend daytime in the littoral zone (BOHL, 1980; GLIWICZ and JACHNER, 1992) or deeper open water strata (see further text) leaving the surface open water practically unoccupied. In the Římov Reservoir, most abundant piscivorous fish of the open water habitat are asp (*Aspius aspius*) and large perch (VAŠEK *et al.*, 2004). Due to the presence of these daytime active pelagic piscivores, the surface open water habitat seems to be suitable for 0+ fish foraging rather during nighttime, when the predation risk is presumably reduced. This assumption coincides well with the negligible daytime catches of 0+ fish obtained at offshore areas.

In the present study, we found that 0+ perch were of consistently smaller size in the offshore habitat than those perch in the inshore habitat in late summer. It is well known from previous studies on lakes and reservoirs that perch larvae after hatching in the littoral zone disperse into the open water habitat and stay there for at least several weeks. Then, at the end of the larval period or as late as during the juvenile stage, it is common that young-of-the-year perch populations shift back to the littoral zone (for review see URHO, 1996). The timing of such shoreward movement seems to take place gradually with respect to perch size (larger individuals return to the littoral sooner) and to be flexible both within and between populations (URHO, 1996). In our case, the presence of smaller perch juveniles in the offshore habitat could therefore indicate that these individuals did not complete their shoreward shift from the open water habitat. A year-round acoustic study carried out on the Římov Reservoir in 1996 found 0+ fish present in the pelagic habitat down to 17 m depth through the period from May to September (ČECH and KUBEČKA, 2006). Authors in this study documented that in August the 0+ fish that occupied reservoir hypolimnion (most probably perch) were distributed mainly in depths 5–10 m during daytime. In another deep Czech reservoir, ČECH *et al.* (2005) observed diel vertical migrations of bathypelagic 0+ perch. These bathypelagic perch migrated to epilimnion at dusk and returned to hypolimnion at dawn, and were significantly smaller in comparison with littoral 0+ perch. The presence of smaller perch in the nighttime pelagic samples observed in the present study might therefore be due to vertically migrating bathypelagic perch, which are smaller than inshore perch and reside at considerable depth during the day. This assumption is supported by the fact that, in mid-August, we never caught 0+ perch of SL below 35 mm in the inshore habitat, whereas from the offshore habitat we obtained several such specimens in both years. Thus, a part of 0+ perch cohort in the Římov Reservoir likely did not shift to the littoral habitat until August, which is similar to findings from large and deep Lake Constance (WANG and ECKMANN, 1994). On the other hand, 0+ perch populations in small and shallow lakes seem to complete the migration to the littoral rather early in the season (POST and MCQUEEN, 1988; URHO, 1996).

Apart from the probability of 0+ fish vertical migrations, our diet analyses proved that at least some 0+ fish individuals (not only perch) had to move between inshore and offshore habitats, since we occasionally found small amounts of typically littoral prey (chironomid larvae, Chydoridae) in the digestive tracts of offshore collected fish. The potential reason for such horizontal migrations could be higher zooplankton densities in the pelagic zone than in the littoral zone, observed in the lacustrine part of the reservoir in late summer 1999.

Sampling in the offshore habitat revealed that roach and bream were the major species in the surface stratum (depth 0–3 m), whereas perch prevailed in the deeper layers (depth 3–9 m). This inverse dominance between 0+ cyprinids and perch along the vertical depth gradient was consistent across both studied years. GLIWICZ and JACHNER (1992) found similar distribution pattern of young-of-the-year roach and perch in the open water of a mesotrophic Poland lake. PERSSON (1986) reported the vertical segregation between roach and perch in Swedish lakes and, in laboratory experiments he revealed that the feeding efficiency between roach and perch differs with the temperature. Thus, it can be hypothesized

that the depth segregation between 0+ cyprinids and perch observed in this study might have been the result of a temperature-induced competitive segregation. Considering the distribution of 0+ fish along the longitudinal reservoir axis, we found increasing densities of offshore 0+ fish from the dam toward the tributary area in both studied years. The total catches of inshore 0+ fish per unit effort also tended to increase upstream in the reservoir. Highest overall catches of 0+ roach and bream in both inshore and offshore habitat were found at the reservoir tributary area. Large numbers of adult bream and roach inhabiting the Římov Reservoir use the tributary area and the river section above the reservoir for spawning (HLADÍK and KUBEČKA, 2004) and this might explain the increased abundance of 0+ cyprinids at the uppermost reservoir end. Besides that, however, a more productive character of the tributary area apparently supports its importance as the feeding ground for cyprinid larvae and juveniles.

Both inshore and offshore 0+ fish fed predominantly on planktonic crustaceans along the whole longitudinal axis of the Římov Reservoir. Presumably due to low structural complexity of the littoral habitat (no macrophytes) the inshore 0+ fish utilized the same food as the offshore fish, i.e. the limnetic zooplankton. By contrast, in the year of a high water level, when flooded terrestrial vegetation covered some parts of the inshore zone of the Římov Reservoir, typically littoral animals (*Polyphemus pediculus* (L.), Chydoridae, chironomid larvae, *Stylaria* sp.) were observed to be a significant component in diets of 0+ fish (MATĚNA, 1995). According to the feeding strategy analysis, diet of 0+ fish of the same species collected at the same site and time was largely homogeneous which evidently reflected foraging in unstructured environment on relatively homogeneously distributed food. However, beside this within sample species-specific diet homogeneity we observed some interspecific, spatial and diel variations in diets of 0+ fish. Considering the interspecific differences in diet composition, we found that perch diet was generally dominated both by planktonic cladocerans (*Daphnia*, *Leptodora*, *Diaphanosoma*) and copepods (Cyclopidae, *Eudiaptomus*), whereas roach diet consisted chiefly of cladocerans (mainly *Daphnia* and *Leptodora*) with only a minor share of copepods. Previous observations from natural habitats where diets of 0+ perch and roach were studied simultaneously also pointed out this difference (HAMMER, 1985; COOK and BURGIS, 1988; JACHNER, 1991; MATĚNA, 1995) suggesting perch should be more efficient feeder on copepods than roach. This is in contrast, however, with findings of PERSSON (1987) who has observed that roach had higher foraging efficiency than perch when feeding on cyclopoids. Assuming such discrepancy, it seems that further laboratory investigations should provide more evidence to draw any strong conclusions about foraging capacity of juvenile perch and roach on copepod prey. In this study, cyclopoid copepods constituted significant proportions in perch diets especially at the upper end of the reservoir. This appears to reflect their availability, since abundance of cyclopoids was by far the highest just at the upper end of the reservoir. At more downstream locations, where cyclopoid densities were much lower and similar to densities of the calanoid copepod *E. gracilis*, perch preyed considerably also on *E. gracilis*.

Concerning the diet of 0+ bream, planktonic cladocerans (*Daphnia*, *Leptodora*) usually predominated in the guts of offshore sampled individuals whereas benthic cladocerans (Chydoridae) comprised the majority in the guts of inshore sampled individuals at the tributary area. The diet of inshore bream at the tributary area thus differed almost entirely from the diets of roach and perch. Apparently, inshore 0+ bream foraged close to or in the bottom sediment, since their major prey, chydorids, were practically absent (<0.1 ind./l) in littoral zooplankton taken concurrently with fish. This further suggests that for inshore bream the profitability of benthic cladocerans was probably higher than that of planktonic microcrustaceans. The importance of benthic cladocerans in food of juvenile bream has been reported also by other authors (WINFIELD *et al.*, 1983; PERSSON and BRÖNMARK, 2002).

Considering the diel changes in the 0+ fish diet composition, we found increased proportions of daphnids in the diet of inshore perch collected at the tributary area during night.

Due to the fact that daphnid density in both inshore and offshore habitat at the tributary area did not differ significantly between day and night (inshore area: ANOVA, $P = 0.417$; offshore area: t -test, $P = 0.616$) as well as there was no statistically significant difference in the daphnid density between the two areas at night (t -test, $P = 0.082$), we assume the diet shift was not associated with the daphnid distribution nor with the predator migration but rather with changes in prey detection over the period of reduced light intensity (MILLS *et al.*, 1986). Larger daphnids (median size 1.6 mm in perch stomachs during the night) with poor escape abilities were apparently easily detected and captured under the low light conditions compared to smaller and evasive cyclopoids (median size 0.9 mm). Another pronounced difference in diet composition between the day and night was found for offshore collected 0+ fish. These fish ate *Ceriodaphnia* more during the daytime (23–54% of the diet by numbers) than in the night (<7% of the diet by numbers) although density of *Ceriodaphnia* was even somewhat lower in the daytime samples of offshore zooplankton than in the night-time samples. Perhaps foraging on this relatively small-bodied cladoceran under the low light conditions, when the reaction distance of fish is known to be reduced considerably (MILLS *et al.*, 1986; RICHMOND *et al.*, 2004), was less profitable than during the period of an adequate light. No *Ceriodaphnia* was found in the digestive tracts of inshore 0+ fish, both during the day and night, apparently due to the negligible abundance of this cladoceran in the inshore zooplankton.

The diel observation of stomach fullness of inshore 0+ perch revealed that perch foraged intensively at daytime and dusk, and fed very little or not at all during late night and before dawn. Stomach fullness of offshore perch caught during the daytime was also higher than that of offshore perch caught during the night. Such daytime and dusk feeding activity of 0+ perch is in accordance with earlier reports describing diel feeding patterns of juvenile *P. fluviatilis* and its American congener *P. flavescens* (SPANOVSKAYA and GRYGORASH, 1977; ZALEWSKI *et al.*, 1990; POST, 1990; GRANT and KOTT, 1999).

We found that inshore perch in both years were of smaller size at the tributary area than at the more downstream areas. Since catches of 0+ fish (this study) and older planktivorous fish (VAŠEK *et al.*, 2003, 2004) were highest at the tributary area of the Římov Reservoir in late summer, we suggest more intense competition for food within the abundant fish assemblage at the tributary area as a likely explanation for the smaller size of 0+ perch. It can be also hypothesized that high algal turbidity regularly occurring in the tributary area of the Římov Reservoir in summer could decrease foraging efficiency of visually hunting 0+ perch, which consequently resulted in their slower growth (LJUNGGREN and SANDSTRÖM, 2002).

To conclude, 0+ fish in the Římov Reservoir exhibited certain patterns of spatial distribution during the period of late summer. Total 0+ fish densities (or catches per unit of effort) were higher at the upstream, relatively shallow and eutrophic part of the reservoir. At the same area, the highest catches of roach and bream were obtained. Roach, bream and perch were the major species of 0+ fish in the surface layer of the open water, in the deeper open water perch predominated. Perch from pelagic and littoral habitats differed in body size, pelagic perch being consistently smaller. These distribution patterns likely were the result of a different foraging success of individual species under spatially variable environmental conditions in the reservoir. However, our study was focused only on a short time period at the end of a growing season. Future research in the Římov Reservoir should be directed to study food consumption, growth and survival of 0+ fish throughout the whole growing season. We should then understand the spatio-temporal dynamics of 0+ fish characteristics more properly.

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