Folia Zool. – 57(3): 324–336 (2008)

The use of pelagic habitat by cyprinids in a deep riverine impoundment: Římov Reservoir, Czech Republic

Mojmír VAŠEK[1], Oldřich JAROLÍM[2], Martin ČECH[1], Jan KUBEČKA[1,2], Jiří PETERKA[1] and Marie PRCHALOVÁ[1]

[1] *Institute of Hydrobiology, Biology Centre of the Academy of Sciences of the Czech Republic, v.v.i., Na Sádkách 7, 370 05 České Budějovice, Czech Republic; e-mail: mojmir.vasek@seznam.cz*

[2] *Faculty of Science, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic*

Received 13 June 2007; Accepted 10 June 2008

A b s t r a c t . In the deep and slightly eutrophic dam part of the Římov Reservoir (Czech Republic), the fish use of open water habitat was studied by means of gillnetting, hydroacoustics and diet analyses during the period from April to October 2005. The day and night acoustic surveys revealed majority of pelagic fish present in the upper 5 m of the water column. The highest gillnet catches of planktivorous fish in epipelagic waters were obtained in May and August. The lowest fish catches were recorded in April and October which resulted in significant positive correlation between the gillnet catch per unit effort and water temperature. The majority of captured fish were adults of three cyprinid species: roach *Rutilus rutilus*, bleak *Alburnus alburnus* and bream *Abramis brama*. In the early spring the food of the three species was diversified: bream consumed primarily cyclopoid copepods, bleak fed on terrestrial insects, and gut content of pelagic roach consisted mainly of littoral food components, algae and detritus. In the late spring and summer however, the diets of all three cyprinids were predominated by large cladocerans, thus proving the use of open water habitat abundant in this prey.

Key words: planktivorous fish, epilimnion, seasonal patterns, roach, bleak, bream

Introduction

The region of the Czech Republic entirely lacks large natural lakes. By virtue of increasing demands on freshwater supplies, many dam reservoirs were built in the Czech Republic during the past century, and up to date they are in use as water sources for human consumption, industrial production and cooling, hydropower generation, irrigation and recreation, as well as they provide a flood control. First extensive ecological studies on fish populations in Czech dam reservoirs come from the sixties of the past century (O l i v a & H o l č í k 1965, H o l č í k 1967) and many papers have been published since the time, some of them providing even long-term description of the fish stock development in particular reservoirs (H o l č í k 1977, P i v n i č k a 1992, S e ď a & K u b e č k a 1997, Ř í h a 2007). Nevertheless, an overwhelming majority of these studies have been based on fish collection in littoral areas, with little attempt to include sampling in pelagic zones – mainly due to methodological and financial constraints. Nowadays, advanced hydroacoustic techniques (S i m m o n d s & M a c L e n n a n 2005) together with implementation of multi-mesh gillnetting (A p p e l b e r g 2000) make the scientific sampling of fish in the pelagic zones of lakes and reservoirs much easier. Consequently, there are many recent reports providing information on the use of pelagic habitat by fish in large and deep European lakes (G e o r g e & W i n f i e l d 2000, B e i e r 2001, M e h n e r & S c h u l z 2002, K a h i l a i n e n et al.

2004, D i e k m a n n et al. 2005). However, relatively little is still known about how various fish species utilise the pelagic habitat in large and deep European reservoirs (K a h l & R a d k e 2006). To expand this knowledge, the present study examined the use of the pelagic space and prey in a guild of common cyprinid fish occupying the Římov Reservoir, a deep eutrophic impoundment located in South Bohemia, Czech Republic. Gillnet catches were combined with hydroacoustic observations and diet analyses in order to describe seasonal patterns in the cyprinid exploitation of the open water habitat.

Study Area

Římov Reservoir (48°50' N, 14°30' E; South Bohemia, Czech Republic) is a deep, canyon-shaped impoundment of the Malše River. Main purpose of the reservoir is the supply of drinking water. The reservoir is ~10 km long, with a maximum surface elevation of 471 m a.s.l., an area of 210 ha and a volume of 33 x 10^6 m^3. The mean depth is 16 m, the maximum depth is 45 m and the mean theoretical retention time is approximately 100 days. The reservoir is dimictic and summer stratification develops from April to October. A pronounced longitudinal trophic gradient exists in the Římov Reservoir, with nutrient concentrations decreasing downstream within the impoundment. According to seasonal average of total phosphorus concentration the dam part of the reservoir has slightly eutrophic status, while the upstream reservoir region close to the inflowing river is highly eutrophic (e.g., S e ď a & D e v e t t e r 2000). There is no commercial fishery at the reservoir, and sport fishing is entirely prohibited. To some extent however, poaching done by local inhabitants persists on the reservoir, focusing mostly on attractive species like pike-perch (*Sander lucioperca*) and pike (*Esox lucius*). In an attempt to enhance populations of piscivores, reservoir managers from the Vltava River Authority stock predatory fish species (mainly asp *Aspius aspius*, pike-perch, and pike) every year to the Římov Reservoir, usually in a quantity up to 2 kg ha^{-1} (Ř í h a 2007). Czech Fishing Union regularly stocks salmonids (mainly brown trout *Salmo trutta* and rainbow trout *Oncorhynchus mykiss*) in the Malše River above the reservoir, and consequently the fish migrating downstream after stocking may enter the impoundment (H l a d í k 2005).

Material and Methods

Fish, zooplankton and water temperature were sampled in the open water habitat (c. 20–40 m deep, 200–400 m wide) near the reservoir dam (Fig. 1) from April to October 2005 on eleven occasions. On each occasion, temperature was measured 0.5 m under the water surface and zooplankton (sampled on 8 occasions only) was collected by duplicate vertical net hauls (net diameter 20 cm, mesh size 200 μm) through 0–5 m depth stratum, which approximately corresponded to the extent of epilimnion during the studied period. Zooplankton samples were always taken in late afternoon and immediately preserved in 4% formaldehyde solution. Densities of the main zooplankton taxa were estimated in the laboratory by the usual method of microscopic counting in a Sedgewick-Rafter chamber. Fish were sampled with Nordic multi-mesh survey gillnets consisting of twelve 4.5 x 2.5 m (height x width) panels with mesh sizes from knot to knot of 5.5, 6, 8, 10, 12.5, 16, 19.5, 24, 29, 35, 43, 55 mm extended by four larger mesh sizes of 70, 90, 110 and 135 mm with the same panel dimensions. The gillnets were set as epipelagic nets, that is with their headlines at the water surface. Four to 13 gillnets

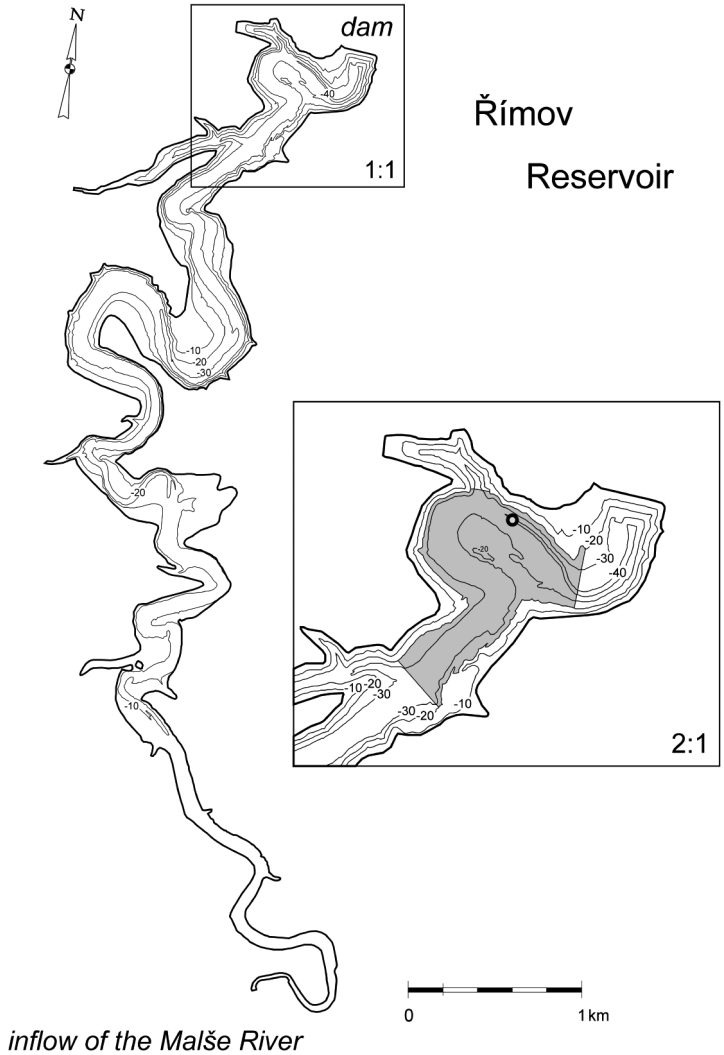

Fig. 1. Bathymetric map of the Římov Reservoir with the dam part magnified. Shading indicates the area where pelagic gillnets were exposed and black circle shows the location of upward beaming transducer.

were installed two hours before the sunset and lifted two or tree hours after the sunset on each sampling occasion. The exposition time throughout sunset was chosen on the basis of our previous studies that found increased gillnet catchability at twilight periods (V a š e k et al., accepted) and gut fullness of planktivorous fish markedly higher during the day and evening than in the morning and at night (V a š e k & K u b e č k a 2004).

On the first sampling date (11 April, shortly after the spring overturn) and on the last sampling date (11 October, at the beginning of fall mixing), mesopelagic and bathypelagic gillnets were used to sample fish in addition to epipelagic (i.e., surface) gillnets. Four mesopelagic gillnets were set with their headlines 5 m below the water surface and four bathypelagic gillnets were installed with their footlines in 5 m distance above the bottom in the deepest zone on both occasions. The nets had the same dimensions and mesh sizes

as the epipelagic gillnets and also their exposition time was the same as for the epipelagic gillnets. We used these nets in April and October as thermal and oxygen stratifications were developed relatively weakly at this time and we expected fish dispersed across the whole water column. For sampling throughout the rest of the season we used only epipelagic gillnets because our previous studies (Vašek et al. 2004, Prchalová 2008) clearly showed that majority of pelagic fish in the Římov Reservoir occupied the epilimnion in summer.

All captured fish were identified and measured to the nearest 0.5 cm standard length (SL). The total catches per unit effort (CPUE; individuals per 100 m^2 net per hour) were calculated for the non-piscivorous fish guild (i.e., the guild of potential zooplanktivores – hereafter referred as planktivorous fish). Pikeperch, pike and large (>20 cm standard length) perch (*Perca fluviatilis*), asp, chub (*Leuciscus cephalus*), brown trout and rainbow trout were assumed piscivorous and excluded from the calculation.

Beside gillnetting, vertical fish distribution in the open water habitat was studied also acoustically with SIMRAD EY 500 split-beam echosounder, working with a frequency of 120 kHz. The data were collected during day and night periods on 14–16 April, 30 May – 3 June and 10–13 August 2005. Similarly to the study of Čech & Kubečka (2002) from the same reservoir, a circular transducer ES 120-7G (7° nominal angle) was fixed on the bottom at the depth of 38.8 ± 0.2 m (i.e., near the deepest point in the dam area) beaming up towards the water surface. The threshold was set to the minimal volume backscattering strength (S_v) of -65 dB (pulse length 0.1 ms, pinging rate 5 pings s^{-1}, power performance 63 W). For data analysis, the water column was divided into 0.7 m thick layers (excluding the uppermost 0.2 m thick stratum under the water surface to avoid surface-bound disturbances) down to a depth of 22 m below the water surface. For each water layer, acoustic fish biomass was calculated as the volume backscattering coefficient s_v (m^2 m^{-3}). The post-processing software Sonar 5 (Balk & Lindem 2005) was used for calculations and the results are presented separately for day and night periods as a mean s_v derived from 8 to 12 records – each c. 80 min long (only records taken through weather with no rain were used). Concurrently with sampling acoustic data, vertical patterns in the temperature and dissolved oxygen were measured with a calibrated WTW OXI 196 probe.

For diet analyses, subsamples of adult roach, bleak and bream were taken from surface gillnet catches on each occasion when their sample sizes were large enough. Additional samples of adult bream for diet analysis were obtained by purse-seining in the open water habitat on 8–9 August 2005 during the late afternoon (purse seine 120 m long and 12 m deep, mesh sizes (front/mid/rear): 6/8/10 mm). Shortly after the capture, digestive tracts of cyprinids were dissected out and preserved in 5–10% formaldehyde solution. In the laboratory, gut fullness code between 0 (empty) to 5 (fully distended) was assigned separately to the three loops of each intestine and the total for the three gut sections combined is presented, giving a score between 0 and 15. Percent composition of the diet by volume was estimated visually for the whole digestive tract. Three categories of food were distinguished: zooplankton, insects and plant material/detritus. When mucus or inorganic material (sand grains) was a component of the gut content, its share was assessed and subtracted from the gut fullness estimates. The composition of ingested zooplankton prey was evaluated with the numerical method, heads or other well recognizable prey remains (e.g. postabdomens and furcas when organisms were seriously disintegrated by mastication) were counted using a binocular microscope. In total, the number of examined guts was 128 for bleak, 96 for roach and 50 for bream.

Table 1. Numbers and standard lengths (range and median) of all fish captured into epipelagic gillnets during the season 2005.

Species	N	SL (cm)	
		Range	Median
Rutilus rutilus	366	5.0–29.0	25.0
Alburnus alburnus	339	9.5–20.0	16.0
Abramis brama	52	5.5–39.0	31.5
Perca fluviatilis	26	13.0–26.0	16.5
Aspius aspius	19	19.0–36.5	26.0
Salmo trutta	17	13.0–26.0	17.5
Rutilus rutilus x Abramis brama	14	10.5–30.0	28.0
Cyprinus carpio	7	41.5–56.0	44.0
Scardinius erythrophthalmus	3	15.0–24.0	15.5
Leuciscus cephalus	2	32.0–39.0	35.5
Sander lucioperca	2	34.0–35.0	34.5
Esox lucius	1		36.0
Oncorhynchus mykiss	1		25.0
Coregonus sp.	1		41.0

Results

The epipelagic gillnet catches were dominated by three cyprinid species – roach, bleak and bream (Table 1). Their percentages in the total number of fish captured over all gillnet samplings were 43%, 40% and 6%, respectively. The majority of these cyprinids were large adult individuals (Table 1). The epipelagic CPUE of fish planktivores was low during early spring and in autumn, attaining only 0.07–0.66 individuals per 100 m^2 net per hour (Fig. 2). The highest values of planktivorous fish CPUE in the epipelagic habitat were obtained in May and August (up to 3.13 individuals per 100 m^2 net per hour) while in July a decline

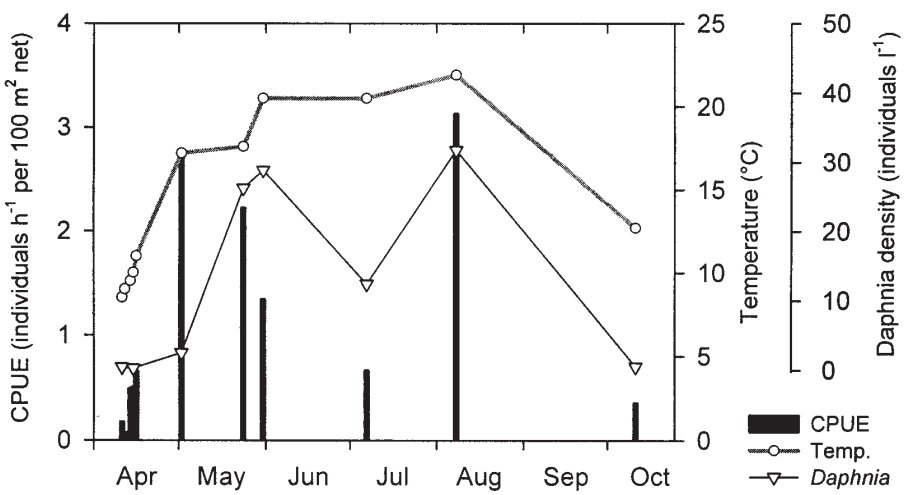

Fig. 2. Seasonal catch per unit effort of planktivorous fish in the epipelagic stratum (0–4.5 m) of the Římov Reservoir, displayed together with *Daphnia* density and water temperature.

in the CPUE was observed (Fig. 2). A significant positive correlation between the epipelagic planktivorous fish CPUE and the water temperature was found (r= 0.74, $F_{1,9}$=10.82, P=0.009). The correlation between the epipelagic planktivorous fish CPUE and the density of *Daphnia* showed a positive trend, however, it was statistically insignificant (r=0.60, $F_{1,6}$=3.44, P=0.113).

On 11 April, shortly after the spring overturn, both mesopelagic and bathypelagic gillnets caught no fish. On 11 October, at the beginning of autumn mixing, the planktivorous fish CPUE in mesopelagic gillnets represented 0.08 individuals per 100 m^2 net per hour, but the catches in the bathypelagic gillnets were null again.

Vertical acoustic surveys of the open water habitat on 14–16 April, 30 May–3 June and 10–13 August revealed majority of fish present in the upper 5 m of the water column, whereas in the deeper strata fish occurrence was negligible or none during both day and night (Fig. 3).

Early in the season, gut fullness of cyprinids caught in the open water habitat was relatively low or varied considerably, but from the end of May throughout the summer it was generally high in all three species (Fig. 4). Gut contents of roach in April consisted mainly of filamentous algae and detritus, while from May throughout the summer zooplankton was

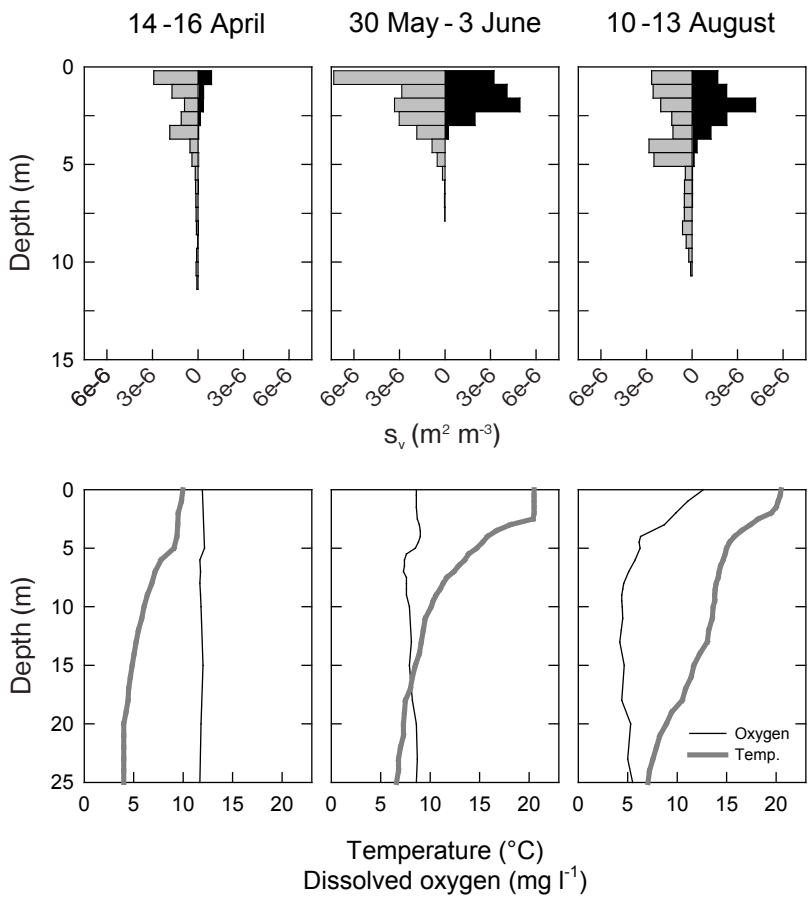

Fig. 3. Vertical distribution of acoustic fish biomass (s_v) during the day (▒) and night (■), and temperature and oxygen profiles in the pelagic zone of the Římov Reservoir on three sampling occasions in 2005. No fish echoes were recorded below the depth of 15 m.

the dominant food component of pelagic roach (Fig. 4b). The diet of bleak in the early spring was comprised mostly of terrestrial insects collected from water surface. Cereal grains and groats, probably remains of the fishing bait, constituted a part of bleak gut contents in mid-April. From late May to October, bleak consumed predominantly zooplankton, but terrestrial insects were also an important prey (Fig. 4d). Zooplankton dominated the diet of bream almost exclusively in both spring and summer periods (Fig. 4f).

Total abundance of limnetic zooplankton was highest at the end of May and in August (Table 2). On the same dates, maximum population densities of daphnids (almost exclusively *Daphnia galeata*) were recorded. Cyclopoid copepods dominated zooplankton during the spring. *Leptodora kindtii*, the largest zooplankton species, attained maximum density of

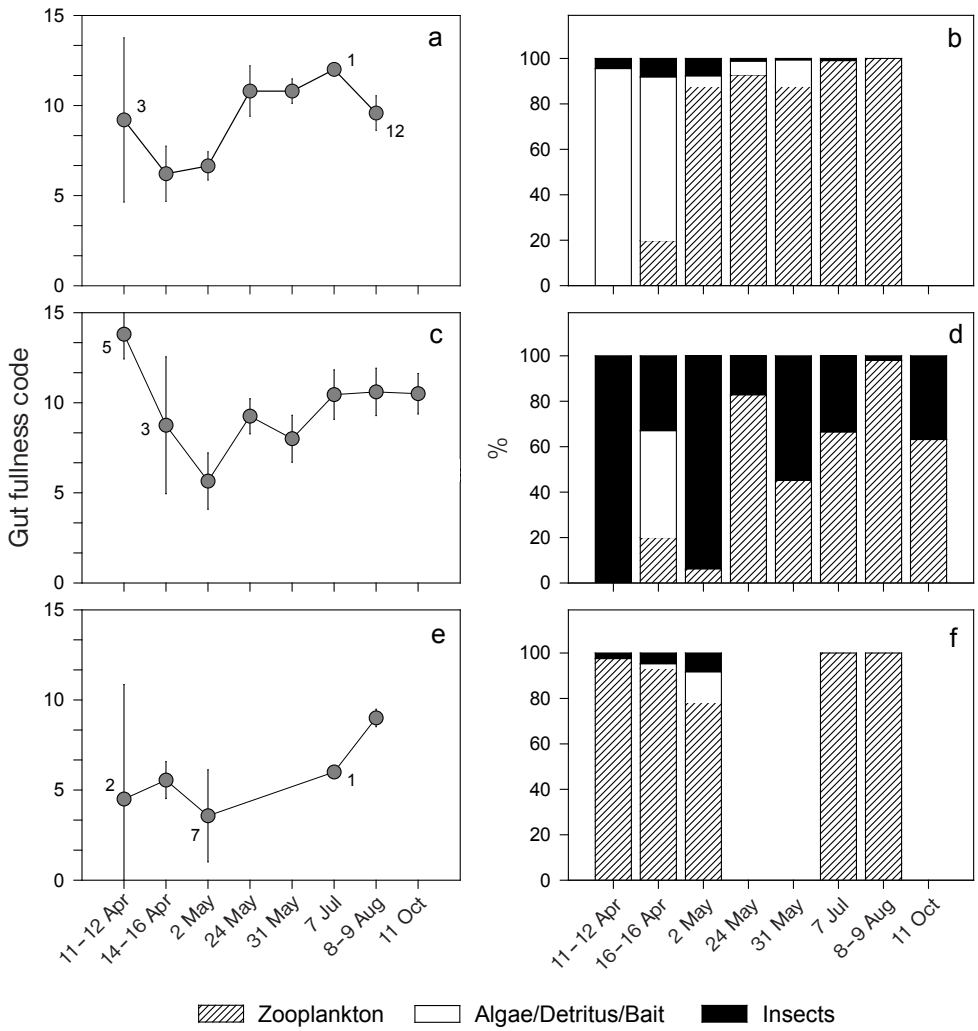

Fig. 4. Mean gut fullness code (± 95% confidence limits) and volume percentage composition of the diet of roach (a, b), bleak (c, d) and bream (e, f) in the Římov Reservoir in 2005. Whenever possible, gut contents of 20 large individuals of each species were examined on each sampling occasion (the numbers near dots indicate smaller sample sizes only). Mean standard lengths (and range) of examined fish were as follow: roach 25.4 (19.5–29.0) cm; bleak 16.1 (13.0–19.5) cm; bream 31.3 (25.5–35.5) cm.

Table 2. Seasonal changes in the density (ind. l^{-1}) of major planktonic crustaceans in the epipelagic stratum (0–5 m) of the Římov Reservoir in 2005.

Crustacean taxa	Date							
	11 Apr	15 Apr	02 May	24 May	31 May	07 Jul	08 Aug	11 Oct
Cladocera:								
Daphnia spp.	0.44	0.27	2.47	26.21	28.81	12.33	31.72	0.51
Diaphanosoma brachyurum	-	-	-	-	0.32	7.32	35.44	-
Leptodora kindtii	-	-	0.08	-	0.16	0.08	0.64	-
Ceriodaphnia quadrangula	-	0.05	0.08	0.53	-	0.95	1.32	32.53
Bosminidae	0.52	0.16	1.19	8.49	6.68	0.48	3.21	0.32
Copepoda:								
Eudiaptomus gracilis	0.48	0.45	1.43	1.17	3.18	9.39	2.11	0.19
Cyclopidae	14.56	6.87	42.73	47.96	36.45	5.49	12.84	1.97
Total crustacean density	16.00	7.80	47.99	84.46	75.92	36.05	87.29	35.52

0.64 ind. l^{-1} in August. On the same date, *Diaphanosoma brachyurum* was the most abundant cladoceran, while *Ceriodaphnia quadrangula* predominated in zooplankton in autumn (Table 2). Daphnids were the major zooplankton prey consumed by pelagic roach, bleak and bream from May throughout the summer (Table 3). Early in the spring, when densities of daphnids in the reservoir were extremely low, cyclopoid copepods constituted significant proportions of zooplankton prey taken by the three cyprinids, but the quantity of total zooplanktonic food in guts of cyprinids was very low at that time (Fig. 4). Although numerically the proportions of *Leptodora kindtii* in cyprinid diets were not large (Table 3), this largest cladoceran species contributed significantly to total volume of gut contents of sampled cyprinids, particularly in August. Bosminids were important prey for bleak in late May (Table 3). *Polyphemus pediculus*, a typically littoral cladoceran, numerically formed 11.7% of total zooplankton prey taken by bleak in early July and was present in 35% of inspected bleak guts at this time. In October, zooplankton consumed by bleak was dominated by daphnids. No roach and bream were caught into epipelagic gillnets at this time.

Discussion

Water temperature is undoubtedly one of the most important abiotic factors influencing the living processes in ectothermic aquatic vertebrates. Cyprinid species abundant in eutrophic ecosystems of temperate Europe generally prefer warmer water temperatures since their foraging and growth rates are maximised under these conditions. In roach, for example, growth and feeding rates are maximal between 20 and 27°C, and at temperatures below 12°C growth ceases (H a r d e w i g & v a n D i j k 2003). In open waters of the Římov Reservoir, we obtained low catches of cyprinids during early spring and autumn, when the water temperature was below 13°C. On the other hand, cyprinid catches were relatively high in late spring and summer, indicating increased fish abundance and activity in the open water habitat throughout the period of increased water temperatures (17–22°C). The intensity of pelagic habitat use by cyprinids thus coincided with the period when growth and feeding rates are expected at seasonal maximum.

In our previous studies based on extensive summer-time gillnetting (V a š e k et al. 2004, P r c h a l o v á 2008), we found that cyprinids inhabiting open waters of the Římov

Table 3. Proportions of different microcrustacean taxa (% by number) in cyprinid guts during the season 2005. Number of analysed guts (N) containing planktonic crustaceans is given for each species and sampling date, for the standard lengths of examined fish see caption of Fig. 4. Cycl: Cyclopidae; Daph: *Daphnia*; Bosm: Bosminidae; Diap: *Diaphanosoma*; Lept: *Leptodora*; Others: other microcrustaceans including also littoral/benthic species.

Date	N	Prey taxa					
		Cycl	Daph	Bosm	Diap	Lept	Others
Rutilus rutilus							
16 Apr	14	40.34	59.12	0.21	-	-	0.33
02 May	20	3.41	90.14	2.03	-	4.38	0.04
24 May	19	0.52	98.54	0.65	-	0.06	0.23
31 May	20	0.61	98.74	0.12	-	0.53	-
07 Jul	1	-	100.00	-	-	-	-
08 Aug	12	0.08	90.98	0.30	1.67	6.82	0.15
Alburnus alburnus							
16 Apr	1	4.80	95.20	-	-	-	-
02 May	10	89.47	5.26	3.52	-	1.75	-
24 May	20	4.36	75.98	16.99	0.12	-	2.55
31 May	19	8.28	53.63	34.16	-	0.15	3.78
07 Jul	19	0.95	84.49	0.07	1.69	1.08	11.72
08 Aug	20	1.62	66.59	0.90	3.86	27.03	-
11 Oct	20	2.35	88.66	7.25	0.12	-	1.62
Abramis brama							
11-12 Apr	2	66.85	33.15	-	-	-	-
14-15 Apr	20	98.34	1.31	0.25	-	-	0.10
02 May	6	25.65	60.53	7.37	-	5.99	0.46
07 Jul	1	1.87	93.46	0.93	0.93	1.88	0.93
08-09 Aug	20	4.36	76.12	1.28	9.85	8.22	0.17

Reservoir remarkably favoured the epilimnetic stratum. Cyprinid catches were by an order of magnitude higher in the surface layer than in the layer just below the thermocline, and catches in the deep hypolimnion were negligible or none. The confinement of pelagic fish to epilimnetic stratum during the summer has been previously documented in the same reservoir also by the acoustic observations of Čech & Kubečka (2002). Similarly, the acoustic observations in the present study clearly showed that through the major part of growing season pelagic fish occupied almost exclusively the upper 5 m of the water column during both day and night. Beside this, the gillnet surveys in April and October also revealed substantially higher fish catches in the surface waters than in the deep waters, even though the water column was thermally stratified only weakly.

There are several factors apparently contributing to cyprinid attraction to surface (epilimnetic) waters. Firstly, cyprinids prefer warm epilimnetic waters because, as mentioned above, they have relatively high optimal temperature requirements. Secondly, cyprinids in the open water habitat of the Římov Reservoir feed predominantly on planktonic crustaceans (Vašek et al. 2003, this study) and zooplankton density is generally highest in the epilimnetic stratum of this reservoir. Moreover, beside that the majority of *Daphnia* population inhabits epilimnetic waters, the diel depth distribution of daphnids in the Římov

Reservoir is static (Seďa et al. 2007), and thus there is no need of planktivorous fish to follow vertical migrations of their preferred prey. Thirdly, planktivorous cyprinids in open waters of the Římov Reservoir feed most intensively during day and dusk periods (Vašek & Kubečka 2004) which adverts to an important role of light intensity in the foraging process. Finally, in addition to temperature, light and prey density, vertical gradient in dissolved oxygen may affect the depth distribution of cyprinids in the Římov Reservoir especially in late summer. At this time fish can be restricted to epilimnetic waters due to hypoxic conditions in hypolimnion, where oxygen concentrations sometimes drop well below 5 mg l^{-1} (databank of the Institute of Hydrobiology, BC AS CR, České Budějovice).

In summary, cyprinids in pelagic waters of the Římov Reservoir meet the most favourable living conditions within well-illuminated and warm surface stratum with abundant prey and sufficient amounts of dissolved oxygen. In accordance with our results, acoustic observations performed in other cyprinid dominated and deep European reservoirs also reported fish density higher in surface waters than in deep waters throughout the period of summer stratification (Kubečka & Wittingerová 1998, Brosse et al. 1999, Swierzowski et al. 2000).

In deep canyon-shaped Římov Reservoir most of the shoreline is comprised by steep rocky banks and thus, as a consequence of the basin morphology, shallow littoral constitutes only small proportion of the total surface area or volume of the reservoir. Moreover, due to water level fluctuation and wind-induced wave action, even the shallow littoral areas are deprived of any aquatic macrophytes. Under these circumstances of relatively small and impoverished littoral zone, pelagic habitat seems to be of particular importance concerning the availability of food resources for fish. Gut content analyses provided in this study clearly indicated that especially limnetic zooplankton is an important food resource for cyprinids in the Římov Reservoir. From the end of May through summer cyprinid gut fullness was generally high and large cladocerans, *Daphnia* and *Leptodora*, were the major prey consumed. The intensive feeding upon cladocerans coincided with the seasonal occurrence of high cladoceran densities in the reservoir. When the availability of cladocerans was largely reduced during the early spring, zooplanktonic food of cyprinids encompassed also cyclopoid copepods. Similar pattern in the seasonal use of copepod and cladoceran prey has been mentioned for cyprinids in few other, deep and mesotrophic/eutrophic, middle European reservoirs (Pociecha & Amirowicz 2003, Kahl & Radke 2006).

In the early spring, only the diet of pelagic bream was comprised almost entirely of zooplankton prey, mainly cyclopoid copepods, while the gut contents of bleak consisted primarily of terrestrial insects and the guts of roach captured in the pelagic zone contained mainly filamentous epiphytic algae and detritus. Bream has a highly protrusible mouth in contrast of the two species, which likely gives him an advantage in capture of evasive prey like copepods (Winfield et al. 1983). The presence of epiphytic algae in roach diet clearly indicated that the roach moved between the littoral and pelagic habitats. Diel shift between habitats and prey types in roach have been documented in many studies (e.g., Horppila 1994, Haertel & Eckmann 2002). According to Lyagina (1972) and Øllestad (1985), a high proportion of algae and detritus in roach diet indicates low availability of animal prey. This seems to comport with the situation in the Římov Reservoir, where the roach consumed algae and detritus during the time before the increase of cladoceran abundance. The diet of bleak, though over the whole season generally consisting of prey taken in the open water habitat (i.e., surface insects, pelagic cladocerans), also provided evidence of diel horizontal migrations since ingested food in May and July included

small amounts of *P. pediculus*, a cladoceran species not present in the limnetic zooplankton but commonly occurring in the shallow littoral of the Římov Reservoir (B r a n d l 1994).

The daytime underwater video-camera monitoring of the open water in the dam area of the Římov Reservoir in June 2005 (J. P e t e r k a , unpubl. data) found adult bream and roach as the most abundant epilimnetic inhabitants while no records were obtained for bleak. Nevertheless, in this study bleak were frequently captured in the pelagic gillnets set through evening, and thus we assume that bleak in the dam area likely stayed close to shores during the day and migrated to open water at sunset. As bleak due to its small size and slender body may be substantially more vulnerable to gape-limited piscivorous fish (L a m m e n s et al. 1992, S c h u l z e et al. 2006), it is appropriate to expect that the pelagic habitat use in bleak was more strongly influenced by the presence of predatory fish than in large roach and bream. The most abundant pelagic piscivores in the Římov Reservoir are day active asp and large perch, suggesting that the risk of predation in open water habitat should be reduced at night.

In our study we did not sample fish in the inshore area. However, P r c h a l o v á (2008) provided an analysis of fish spatial distribution within the reservoir that is based on nine year (1999–2007) summer-time gillnetting in both inshore and offshore habitats. Her data showed that in the dam part of the reservoir the total adult fish CPUE in the upper open water was on average less than half of the total adult fish CPUE in the littoral zone, both in terms of fish abundance and biomass. In age 0+ juveniles, the total gillnet CPUE in terms of abundance was on average even 25 times lower in the upper open water compared to that in the littoral zone. Such results indicate that in the downstream part of the Římov Reservoir fish use more intensively the littoral habitat than the open water habitat and confinement to the inshore area is pronounced especially in juveniles, which is likely connected with higher risks to predation in open waters (G l i w i c z & J a c h n e r 1992, B r a b r a n d & F a a f e n g 1993).

During spawning, the spatial distribution of cyprinids is certainly confined to areas suitable for deposition of the adhesive eggs. Roach, bream and bleak are phyto-lithophils (B a l o n 1975), i.e., they scatter eggs on macrophytes or gravel substratum usually at shallow depths. In this study, we found that majority of roach females captured on 2 May were egg-laden. The next sampling date, on 24 May, all roach females caught into gillnets were already spent and a vigorous spawning activity of bream was visually observed at shallow littoral areas within the reservoir. In the case of bleak, many captured females were still egg-laden on 24 and 31 May, indicating that this species spawned even later. Consequently, the spawning activity could have been a factor seriously affecting the use of the open water habitat by fish during late spring/early summer. However, we found relatively high CPUE of cyprinids in the pelagic habitat in May while the lowest pelagic CPUE during late spring and summer period was recorded on 7 July, which is rather behind the time of cyprinid spawning, at least that of roach and bream. This indicates that not only spawning activity but also other factors could have contributed to cyprinid willingness to use the open water habitat. The decline in CPUE in July could not be explained by a variation in water temperature since this physical parameter remained constantly high through the period of summer samplings (Fig. 2). Moreover, the weather on the dates of gillnet sampling was relatively similar across the season – sometimes windy during day but always calm at night, and with no rain – thus it did not seem to have apparent impact on the reduced CPUE in July. The decline in *Daphnia* density in July could however contribute to lower fish catches in the pelagic at this time.

In conclusion, cyprinids in the Římov Reservoir utilised the open water habitat most intensively throughout the late spring and summer, when especially large individuals of

roach, bleak and bream occupied epilimnetic waters over the areas of highest reservoir depth and preyed upon large cladocerans. Since the structurally simple open water environment provides little protection against predation risk, a benefit from feeding on limnetic prey can be regarded as the main determinant of pelagic habitat use in reservoir fish.

A c k n o w l e d g m e n t s

We acknowledge FISHECU members (www.hbu.cas.cz/fishecu) for assistance in field sampling and J. Ž a l o u d í k for providing the bathymetric map of the Římov Reservoir. Financial support was provided by the Grant Agency of the Academy of Sciences of the Czech Republic (project no. IAA600170502) and by the Czech Science Foundation (project no. 206/06/P418).

L I T E R A T U R E

Appelberg M. 2000: Swedish standard methods for sampling freshwater fish with multi-mesh gillnets. *Fiskeriverket Informerar 1: 3–32*.

Balk H. & Lindem T. 2005: Sonar4 and Sonar5 post processing systems (operation manual). *University of Oslo, Norway.*

Balon E.K. 1975: Reproductive guilds of fishes: a proposal and definition. *J. Fish. Res. Bd. Can. 32: 821–864*.

Beier U. 2001: Habitat distribution and size structure in freshwater fish communities: effects of vendace on interactions between perch and roach. *J. Fish Biol. 59: 1437–1454*.

Brabrand Å. & Faafeng B. 1993: Habitat shift in roach (*Rutilus rutilus*) induced by pikeperch (*Stizostedion lucioperca*) introduction: predation risk versus pelagic behaviour. *Oecologia 95: 38–46*.

Brandl Z. 1994: The seasonal dynamics of zooplankton biomass in two Czech reservoirs: a long-term study. *Arch. Hydrobiol. Beih. Ergebn. Limnol. 40: 127–135*.

Brosse S., Dauba F., Oberdorff T. & Lek S. 1999: Influence of some topographical variables on the spatial distribution of lake fish during summer stratification. *Arch. Hydrobiol. 145: 359–371*.

Čech M. & Kubečka J. 2002: Sinusoidal cycling swimming pattern of reservoir fishes. *J. Fish Biol. 61: 456–471*.

Diekmann M., Brämick U., Lemcke R. & Mehner T. 2005: Habitat-specific fishing revealed distinct indicator species in German lowland lake fish communities. *J. Appl. Ecol. 42: 901–909*.

George D.G. & Winfield I.J. 2000: Factors influencing the spatial distribution of zooplankton and fish in Loch Ness, UK. *Freshw. Biol. 43: 557–570*.

Gliwicz Z.M. & Jachner A. 1992: Diel migrations of juvenile fish: a ghost of predation past or present? *Arch. Hydrobiol. 124: 385-410*.

Haertel S.S. & Eckmann R. 2002: Diel diet shift of roach and its implications for the estimation of daily rations. *J. Fish Biol. 60: 876–892*.

Hardewig I. & van Dijk P.L.M. 2003: Is digestive capacity limiting growth at low temperatures in roach? *J. Fish Biol. 62: 358–374*.

Hladík M. 2005: Importance of the tributary zone for development of fish population in a reservoir. *PhD Thesis, University of South Bohemia, Faculty of Biological Sciences, České Budějovice, 74 pp*.

Holčík J. 1967: Life history of the roach – *Rutilus rutilus* (Linnaeus, 1758) in the Klíčava valley reservoir. *Věst. Čs. Spol. Zool. 31: 213–229*.

Holčík J. 1977: Changes in fish community of Klíčava reservoir with particular reference to Eurasian perch (*Perca fluviatilis*), 1957–72. *J. Fish. Res. Board Can. 34: 1734-1747*.

Horppila J. 1994: The diet and growth of roach (*Rutilus rutilus* (L.)) in Lake Vesijärvi and possible changes in the course of biomanipulation. *Hydrobiologia 294: 35–41*.

Kahilainen K., Malinen T., Tuomaala A. & Lehtonen H. 2004: Diel and seasonal habitat and food segregation of three sympatric *Coregonus lavaretus* forms in a subarctic lake. *J. Fish Biol. 64: 418–434*.

Kahl U. & Radke R.J. 2006: Habitat and food resource use of perch and roach in a deep mesotrophic reservoir: enough space to avoid competition? *Ecol. Freshwat. Fish 15: 48–56*.

Kubečka J. & Wittingerová M. 1998: Horizontal beaming as a crucial component of acoustic fish stock assessment in freshwater reservoirs. *Fish. Res. 35: 99–106*.

Lammens E.H.R.R., Frank-Landman A., McGillavry P.J. & Vlink B. 1992: The role of predation and competition in determining the distribution of common bream, roach and white bream in Dutch eutrophic lakes. *Environ. Biol. Fish. 33: 195–205.*

Lyagina T.N. 1972: The seasonal dynamics of biological characteristics of the roach (*Rutilus rutilus* L.) under conditions of varying food availability. *J. Ichtyol. 12: 210–226.*

Mehner T. & Schulz M. 2002: Monthly variability of hydroacoustic fish stock estimates in a deep lake and its correlation to gillnet catches. *J. Fish Biol. 61: 1109–1121.*

Oliva O. & Holčík J. 1965: The estimation of the fish population in the Klíčava valley water reservoir. *Věst. Čs. Spol. Zool. 29: 249–254.*

Pivnička K. 1992: The Klíčava reservoir, Czechoslovakia: a 30 year study of the fish community. *Fish. Res. 14: 1–20.*

Pociecha A. & Amirowicz A. 2003: An attempt to determine the share of zooplankton in food consumed by fish in the limnetic zone of a eutrophic dam reservoir. *Oceanological and Hydrobiological Studies 32: 15–31.*

Prchalová M. 2008: Gradients of fish distribution in reservoirs. *PhD Thesis, University of South Bohemia, Faculty of Science, České Budějovice, 72 pp.*

Říha M. 2007: Long-term development of fish populations in the Římov Reservoir. *MSc Thesis, University of South Bohemia, Faculty of Biological Sciences, České Budějovice, 30 pp.*

Schulze T., Dörner H., Hölker F. & Mehner T. 2006: Determinants of habitat use in large roach. *J. Fish Biol. 69: 1136–1150.*

Seďa J. & Kubečka J. 1997: Long-term biomanipulation of Římov Reservoir (Czech Republic). *Hydrobiologia 345: 95–108.*

Seďa J. & Devetter M. 2000: Zooplankton community structure along a trophic gradient in a canyon-shaped dam reservoir. *J. Plankton Res. 22: 1829–1840.*

Seďa J., Kolářová K., Petrusek A. & Macháček J. 2007: *Daphnia galeata* in the deep hypolimnion: spatial differentiation of a "typical epilimnetic" species. *Hydrobiologia 594: 47–57.*

Simmonds E.J. & MacLennan D.N. 2005: Fisheries acoustics. *Blackwell, Oxford.*

Świerzovski A., Godlewska M. & Półtorak T. 2000: The relationship between the spatial distribution of fish, zooplankton and other environmental parameters in the Solina reservoir, Poland. *Aquat. Living Resour. 13: 373–377.*

Vašek M., Kubečka J. & Seďa J. 2003: Cyprinid predation on zooplankton along the longitudinal profile of a canyon-shaped reservoir. *Arch. Hydrobiol. 156: 535–550.*

Vašek M. & Kubečka J. 2004: *In situ* diel patterns of zooplankton consumption by subadult/adult roach *Rutilus rutilus*, bream *Abramis brama*, and bleak *Alburnus alburnus*. *Folia Zool. 53: 203–214.*

Vašek M., Kubečka J., Peterka J., Čech M., Draštík V., Hladík M., Prchalová M. & Frouzová J. 2004: Longitudinal and vertical spatial gradients in the distribution of fish within a canyon-shaped reservoir. *Internat. Rev. Hydrobiol. 89: 352–362.*

Vašek M., Kubečka J., Čech M., Draštík V., Matěna J., Mrkvička T., Peterka J. & Prchalová M. (in press): Diel variation in gillnet catches and vertical distribution of pelagic fishes in a stratified European reservoir. *Fisheries Research.*

Vøllestad L.A. 1985: Resource partitioning of roach *Rutilus rutilus* and bleak *Alburnus alburnus* in two eutrophic lakes in SE Norway. *Holartic Ecology 8: 88–92.*

Winfield I.J., Peirson G., Cryer M. & Townsend C.R. 1983: The behavioural basis of prey selection by underyearling bream (*Abramis brama* (L.)) and roach (*Rutilus rutilus* (L.)). *Freshw. Biol. 13: 139–149.*