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The effect of depth, distance from dam and habitat on spatial distribution of fish in an artificial reservoir

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Abstract – Spatial distribution of the fish community in the deep canyon-shaped Římov Reservoir, Czech Republic, was studied using overnight gillnetting fishing in 1999–2007. Effects of depth, distance from the dam to the tributary and habitat type (benthic and pelagic) on fish community structure, catch per unit of effort (CPUE), biomass per unit of effort (BPUE) and average weight were tested. Fish were recorded in all sampled depths and parts of the reservoir. Redundancy analysis revealed that effects of three environmental variables were significant and most variability was explained by depth, then by distance from the dam and habitat type. CPUE and BPUE of all species decreased with depth and responses of individual species to depth were similar for juvenile and adult fish. Number of species, CPUE and BPUE of all species except perch increased heading towards the tributary and peaked close to or at the tributary part of the reservoir. Responses of juvenile fish to distance from the dam differed from that of adult fish. Structure of fish community differed in benthic and pelagic habitats with species preferably occupying epipelagic (bleak, asp, rudd and juvenile bleak, roach and bream) or littoral waters (perch, pikeperch, ruffe, roach, bream and juvenile percids). This study showed that fish distribution in the reservoir followed distinct patterns, which were probably shaped by a combination of physiological constraints plus trade-off between food resources and competition.

M. Prchalová[1,2], J. Kubečka[1,2], M. Čech[1,2], J. Frouzová[1,2], V. Draštík[1,2], E. Hohausová[1,2], T. Jůza[1,2], M. Kratochvíl[1,2], J. Matěna[1], J. Peterka[1,2], M. Říha[1,2], M. Tušer[1,2], M. Vašek[1,2]

[1]Biology Centre of the Academy of Sciences of the Czech Republic, v.v.i., Institute of Hydrobiology, České Budějovice, Czech Republic, [2]Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic

Key words: horizontal distribution; vertical distribution; gillnet; reservoir; Cyprinidae; Percidae; redundancy analysis

M. Prchalová, Biology Centre of the Academy of Sciences of the Czech Republic, v.v.i., Institute of Hydrobiology, Na Sádkách 7, 370 05 České Budějovice, Czech Republic; e-mail: marie.prchalova@prf.jcu.cz

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Introduction

The spatial distribution of fish within a water body is not random. At the first level, abiotic conditions determining the environment are heterogeneous. Fish utilise habitats within a water body that are physiologically convenient mainly in terms of oxygen concentration and water temperature (the ‘to be or not to be’ rule) (Straškraba 1974; Brandt 1980; Kubečka & Wittingerová 1998; Brosse & Lek 1999; Gido & Matthews 2000; Matthews et al. 2004). Biotic factors also play role – food availability, predation risk and competition (the ‘to eat and not be eaten’ rule) (Bohl 1980; Eckmann & Imbrock 1996; Mous et al. 2004; Gliwicz et al. 2006). It means that for each ontogenetic stage of fish (ecospecies; Brosse et al. 2007), biotic and abiotic conditions cross at an equilibrium which represents an optimum for spatial occurrence within a specific water body.

During nine summers, we sampled fish community of the Římov Reservoir, Czech Republic. The reservoir has one tributary and is located in a narrow valley. The water column has well-developed thermal stratification during summer. According to this, the

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reservoir has distinct longitudinal and vertical gradients of abiotic factors as water temperature, oxygen and phosphorus concentrations (Straškrabová et al. 1994; Hejzlar & Vyhnálek 1998; Sed'a & Devetter 2000; Mašín et al. 2003; Šimek et al. 2003). Also biotic features such as phytoplankton biomass, primary production, chlorophyll *a* concentration, rotifers and cladoceran densities follow the gradient of abiotic factors (Seďa & Devetter 2000; Jezbera et al. 2003; Vašek et al. 2003). Other studies on juvenile fish in pelagic and in inshore habitats (Čech & Kubečka 2006; Vašek et al. 2006; T. Jůza, unpublished data) and adult fish in pelagic habitats (Vašek et al. 2003, 2004; Draštík et al. 2008) show that majority of fish species prefer the most productive areas and the warmest depth layers within the reservoir.

The aims of this study are to model the distribution of the fish community along the vertical and longitudinal gradients, and in pelagic and benthic habitats. The vertical gradient is represented by depth and the longitudinal gradient is referred as a distance from the dam of the reservoir. We expect fish to inhabit the upper part of the stratified water column in both types of habitats. We assume that the density of fish is highest at the tributary part of the reservoir in both types of habitats.

Many authors lament the lack of knowledge regarding habitat use and the preferences of individual fish ecospecies (e.g. Brosse & Lek 2002; Brosse et al. 2007) as there could be serious intra- and inter-species (Vondracek et al. 1989; Čech et al. 2005; Prchalová et al. 2006) and inter-water body differences (Rowe 1994; Jeppesen et al. 2006). Therefore, we analyse juvenile (0+ year old) and adult fish (1+ year and older) individuals of each species separately as well as the community as a whole expecting that different ecospecies have different preferences in spatial distribution.

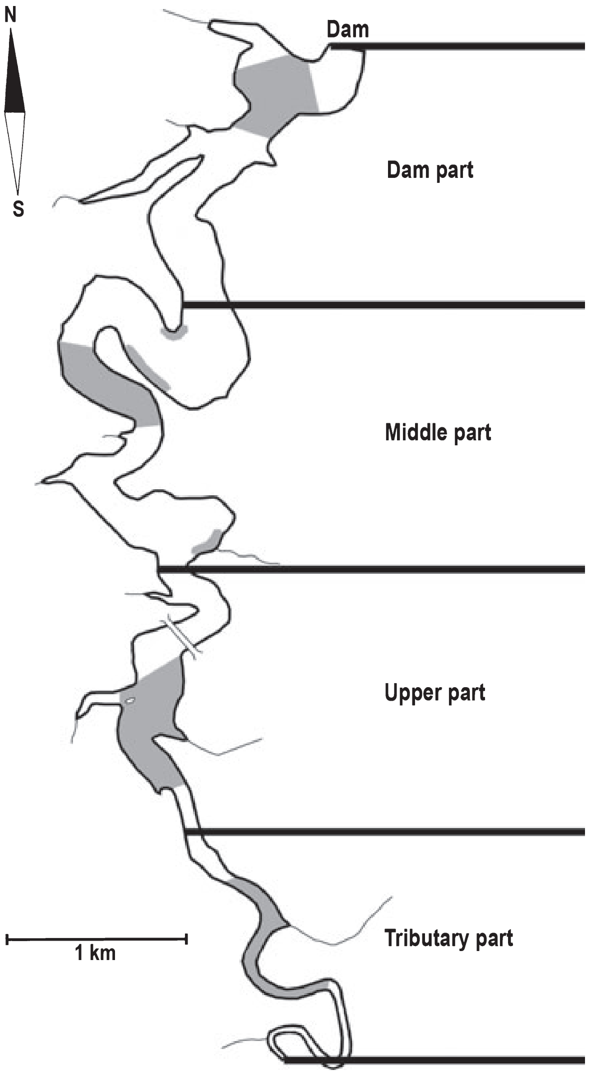

Fig. 1. Map of the Římov Reservoir, Czech Republic. The shaded areas show locations for fish community samplings during the 9 years of the study.

Study area

The Římov Reservoir was built in 1978 on the Malše River (South Bohemia, Czech Republic) as a water supply reservoir with an additional function of preventing floods. Reservoir canyon-shaped morphometry corresponds to the original deep valley (Fig. 1). Typical retention time is approximately 100 days. The maximum depth of the reservoir is 45 m at the dam. The average depth is 16 m. The maximum volume is 33.6 millions m^3 and the surface area is 210 ha at elevation of 417 m a.s.l. It is a dimictic reservoir with thermal stratification developing from April through October (Fig. 2) and water transparency (Secchi depth) in the dam part reaches approximately 1.5 m during late summer. Structural heterogeneity of the littoral zone as well as water macrophyte growth are limited because of water level fluctuations and steep banks. The last 15 years of the development of the fish community of the reservoir were characterised by very stable cyprinid dominated fish assemblage (M. Říha, unpublished data) and by stable annual concentrations of total phosphorus (TP) at the dam (average 30.39, SD 3.29 μg·l^{-1}; Annual Reports of the Institute of Hydrobiology).

As a water supply reservoir, the proximate surrounding of the reservoir is protected area with prohibited access. The only activities on the reservoir are limited to shore maintenance by the Vltava River Authority and research by the Institute of Hydrobiology. During 9 years of this study, no permanent or even temporal flocks of piscivorous birds were recorded on the reservoir. Thus, the distribution of fish in the Římov Reservoir was unlikely to be affected

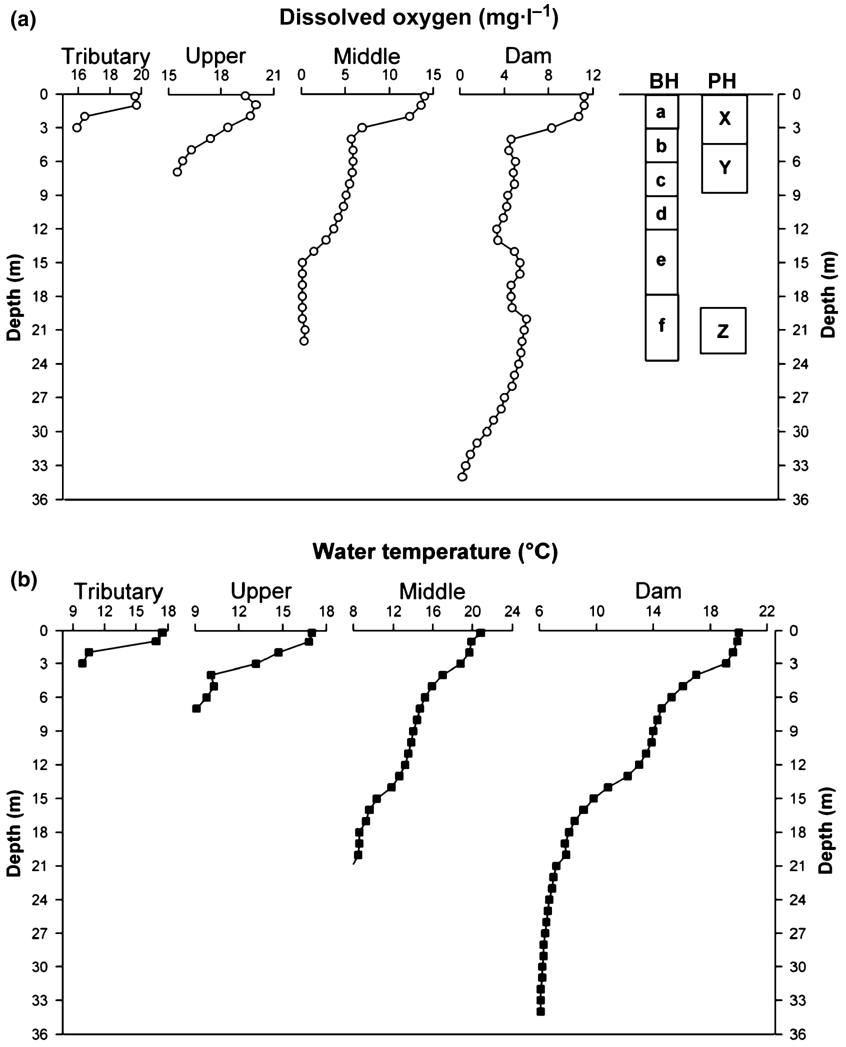

Fig. 2. Example of the vertical distribution of dissolved oxygen (a) and water temperature (b) in four parts of the Římov Reservoir (see Fig. 1), August 2005. Columns below BH and PH abbreviations show sampled depth layers of benthic (BH a–f) and pelagic habitats (PH X–Z): a ~ 0–3 m, b ~ 3.1–6 m, c ~ 6.1–9 m, d ~ 9.1–12 m, e ~ 12.1–18 m, f ~ >20 m, X ~ 0–4.5 m, Y ~ 5–9.5 m and Z ~ 9.5–5 m from the bottom.

by human activities (Scheuerell & Schindler 2004), piscivory by avian predators (Eckmann & Imbrock 1996) as well as by the water transparency and presence of water marcophytes (Bohl 1980; Jacobsen et al. 2004; Mous et al. 2004; Jeppesen et al. 2006).

Methods

Gillnet sampling

Benthic and pelagic gillnets (Pokorný-sítě, Brloh, Czech Republic) were used to sample benthic and pelagic habitats. Benthic habitat was defined as a water layer 1.5 m above the bottom and was sampled by benthic gillnets with a height of 1.5 m. Benthic gillnets were set to the depth layers 0–3, 3.1–6, 6.1–9, 9.1–12, 12.1–18 and >20 m (Fig. 2a), parallel to the shore. Pelagic habitats were defined as volumes of the stratified open water, having no contact with the bottom or shore – with a minimum distance of 1.5 m from the closest bottom. Pelagic gillnets were of three types (Fig. 2a): Surface gillnets were set from the surface down to 4.5 m, supported by big floats on the upper line. Gillnets set to the depth layer 5–9.5 m were equipped with floats on 5 m long strings. Gillnets with weights on 5 m strings attached to the lead line were set to the depth layer 9.5–5 m above the bottom. In the tributary part, a surface pelagic gillnet 3 m high was used.

Benthic and pelagic gillnets were of the same structure. Multimesh gillnets were used in 2004–2007. These gillnets consisted of 2.5 m long blocks of mesh sizes that were sewn together along the full height (Nordic type; Appelberg et al. 1995). During 1999–2003, a series of single gillnet blocks were used – 25 m long blocks of different mesh sizes were tied together. In both periods, 16 mesh sizes were used. Twelve mesh sizes (5, 6.25, 8, 10, 12.5, 15.5, 19.5, 24, 29, 35, 43 and 55 mm, knot-to-knot) were made as given by European Standard Document EN 14757 (2005). Four larger mesh sizes were added to enable the catching of larger fish: 70 and 90 mm (thread diameter 0.25 mm) and multifilament 110 and 135 mm (4 and 6 × 0.15 mm respectively).

Gillnets were set overnight (installed at 18:00–20:00 hours and lifted the next day at 6:00–8:00 hours) at predefined depth layers at four parts along the longitudinal axis of the reservoir (Fig. 1). The placement depth was measured by an acoustic depth gauge. At each depth layer at each location, a minimum effort of two gillnets and a typical effort of four gillnets was applied each year. Each gillnet then represented a sample in the data analyses.

All fish caught were measured to the nearest 0.5 cm and fish in representative subsamples were weighed to the nearest gram. Weights of the rest of the fish were calculated using species-specific length–weight relationships based on representative subsample. Altogether, 23,794 fish individuals with a total weight of 2733 kg were caught during the study. The results were expressed separately as the catch per unit of effort (CPUE) (fish·1000 m^{-2}·$night^{-1}$; 'abundance' in the further text) for adult fish (1+ year and older) and for juvenile fish (0+ year old), as the biomass per unit of effort (BPUE) of adult fish (kg·1000 m^{-2}·$night^{-1}$; 'biomass' in the further text) and as the average weight of adult fish (g; ratio of absolute BPUE and absolute CPUE). The threshold size separating juvenile and adult fish was set according to the length–frequency distribution supported by the scale reading for each species.

The samplings were carried out every August during the period 1999–2007. The exception was 2002, when the sampling was done in July. When possible, August was chosen as the best time for extensive sampling of the reservoir fish community as juveniles of a majority of fish species are large enough to be sampled using gillnets and identified. Also no spawning or wintering migrations take place during this part of the year (Hladík & Kubečka 2003).

Catchability of gillnets could vary among habitats. Certain studies provided evidence that catchability of fish decreased with decreasing water temperature (e.g. Borgström 1989; Linløkken & Haugen 2006) and with increasing density of fish (e.g. Borgström 1992; Olin & Malinen 2003; Linløkken & Haugen 2006). According to this, it could be misleading to compare habitats with very different water temperature or fish density. However, no guideline for handling this CPUE variance exists and we neglect it in this study.

Data analysis

Direct gradient redundancy analysis (RDA) was used to test effects of depth, distance from the dam and habitat type (benthic and pelagic) on fish community using multivariate statistics (Canoco software, Biometris – Plant Research International, Wageningen, The Netherlands). The unimodal method of the canonical correspondence analysis usually gives a better fit of natural communities' responses, as organisms usually have optima instead of a linear response along a resource gradient (ter Braak & Verdonschot 1995; Gido & Matthews 2000; Irz et al. 2002; Jezbera et al. 2003). However, many of our samples were empty and cannot, therefore, be compared with the others using the chi-square distance, which is implied by unimodal methods. Consequently, we used a linear method, which employed linear Euclidean distances for comparing samples (Lepš & Šmilauer 2003). Besides, the length of the gradient in the detrended correspondence analysis indicated that we could use the linear method.

The environmental (explanatory) variables were: the quantitative variables of depth and distance from the dam and the qualitative dummy (i.e. zero or one) variables for the habitat type (benthic or pelagic) and for each sampled year (1999–2007). The distance from the dam was measured along the middle of the reservoir basin. The variable year was used as a covariate as we did not intent to interpret its effect; however, we wanted to take this effect into account during interpreting effects of the other variables.

Two basic types of data sets were tested: the first type included data sets with only one dependent variable – the total abundance and number of species of juvenile fish, the total abundance, total biomass and number of species of adult fish and the total average weight of adult fish. RDA allowed testing regression in data sets even with one dependent variable, because such analysis fully corresponded with ANOVA (ter Braak & Šmilauer 2002). Excluding number of species, data were log-transformed [$y' = \log_{10}(y + 1)$] and centred by species (no centring for samples were performed). Scaling was focused on inter-sample distances and no post-transformation of species scores were carried out.

The second type of data sets had many dependent variables (equal to number of species) in abundance of juvenile fish community and in abundance, biomass and average weight of the adult fish community. Excluding the number of species, the data were log-transformed [$y' = \log_{10}(y + 1)$] and centred by species (no centring for samples were performed). Scaling was focused on inter-species correlations, species scores were divided by the standard deviation and samples were standardised by norm.

Statistical significances were analysed by Monte Carlo permutation tests. The unrestricted type of permutation tests was performed with blocks defined by covariates to quantify the effect of a given environmental variable (the samples were permuted only within blocks and never across blocks; Lepš & Šmilauer 2003). Species in the adult fish community with more than 20 occurrences and all species in the juvenile fish community were included in the analyses (Table 1).

Both types of effects – marginal and conditional – of environmental variables were observed. The marginal effect was an effect of only one explanatory variable when the effects of other explanatory variables (except covariates) were ignored. In case of the conditional effect, an explanatory variable explained variability in addition to the variability explained by variables already included.

The responses of dependent variables to individual environmental variables were fitted using general linear models (GLMs; CanoDraw software, Petr Šmilauer, Faculty of Science, University of South Bohemia, České Budějovice, Czech Republic). GLMs with the linear and quadratic degree were compared and the degree with significant fit and/or with the better fit (i.e. lower Akaike information criterion, AIC, a measure of the goodness of fit of the model) was selected.

Results

Depth

The depth had the strongest significant effect on every sampled characteristic of the fish community (Tables 2 and 3). Abundance, biomass and the number of species of adult as well as of juvenile fish communities

Table 1. Average species composition in benthic (BH) and pelagic habitats (PH) of the Římov Reservoir derived from the gillnet sampling during summer 1999–2007.

		Benthic habitats			Pelagic habitats		
Common names	Scientific names	A	B	0+	A	B	0+
Cyprinidae							
Roach	*Rutilus rutilus* (L.)	**36.95**	**38.54**	**16.88**	**24.72**	**31.78**	**49.67**
Bream	*Abramis brama* (L.)	**15.11**	**23.07**	**5.68**	**14.35**	**28.15**	**23.76**
Bleak	*Alburnus alburnus* (L.)	**8.70**	**2.30**	**2.04**	**45.83**	**10.36**	**16.38**
Hybrid	*A. brama x R. rutilus*	**2.94**	**5.10**	**0.04**	**1.99**	**3.13**	**0.40**
Asp	*Aspius aspius* (L.)	**1.26**	**1.59**	**0.06**	**3.74**	**4.76**	**0.11**
White bream	*Abramis bjoerkna* (L.)	**0.68**	**0.63**		**0.28**	**0.31**	
Carp	*Cyprinus carpio carpio* L.	**0.61**	**12.14**		**0·48**	**7.23**	
Chub	*Leuciscus cephalus* (L.)	0.09	0.41		**0.11**	**0.26**	
Rudd	*Scardinius erythrophthalmus* (L.)	**0.08**	**0.13**		**0.58**	**0.64**	
Dace	*Leuciscus leuciscus* (L.)	0.07	0.02		0.01		
Gudgeon	*Gobio gobio gobio* (L.)	0.06	0.01	**0.01**			
Prussian carp*	*Carassius gibelio* (Bloch)	0.03	0.06		0.04	0.11	
Barbel	*Barbus barbus* (L.)	0.02	0.01				
Tench	*Tinca tinca* (L.)	0.02	0.09				
Percidae							
Perch	*Perca fluviatilis* L.	**11.89**	**8.46**	**38.22**	**3.90**	**3.27**	**5.24**
Ruffe	*Gymnocephalus cernuus* (L.)	**17.06**	**1.37**	**33.54**	**2.84**	**0.17**	**3.39**
Pikeperch	*Sander lucioperca* (L.)	**4.15**	**4.71**	**3.55**	**0.92**	**1.63**	**1.05**
Esocidae							
Pike	*Esox lucius* L.	**0.21**	**1.13**		**0.09**	**7.93**	
Coregonidae							
Whitefish*	*Coregonus* sp.	0.01	0.02		0.03	0.19	
Salmonidae							
Rainbow trout*	*Oncorhynchus mykkis* (Walbaum)	0.01	0.01		0.01	0.01	
Brown trout	*Salmo trutta fario* L.				0.03	0.08	
Siluridae							
Wells	*Silurus glanis* L.	0.08	0.22		0.06	0.03	
Depth layers	Number of nets	Average values (fish.1000 m^{-2}·$night^{-1}$, kg.1000 m^{-2}.$night^{-2}$)					
0–3 m BH/0–4.5 m PH	135 BH/89 PH	480.39	61.29	190.23	271.58	44.53	34.16
3.1–6 m BH	53 BH	227.05	40.98	47.38			
6.1–9 m BH/5–9.5 m PH	53 BH/51 PH	72.56	10.30	9.49	21.40	4.68	0.34
9.1–12 m BH	37 BH	18.82	2.74	2.25			
12.1–18 m BH	26 BH	9.80	1.88	0.15			
>20 m BH/9.5–5 m bot PH	18 BH/32 PH	0.76	0.48	0	2.25	1.75	0
Reservoir parts (depth layers 0–3 m BH and 0–4.5 m PH only)							
Dam	24 BH/30 PH	257.82	40.43	116.19	95.41	18.94	4.45
Middle	55 BH/19 PH	488.89	60.71	195.95	257.77	33.27	17.61
Upper	28 BH/22 PH	652.60	81.85	250.49	493.57	97.06	46.92
Tributary	28 BH/18 PH	482.28	59.72	182.21	423.87	46.50	146.72

Proportion of species (%) in abundance (A) and biomass (B) of adult fish and in abundance of juvenile fish (0+).

*Marks nonindigenous species in the reservoir catchment. Species in bold were selected for RDA analysis. Lower rows give average values of catch per 1000 m^2 of gillnets in various depth layers and parts of the reservoir in benthic and pelagic habitats.

Table 2. Effects of individual and all (row Sum) environmental variables, expressed as a proportion of the explained variability (%) of the adult fish community in terms of its total abundance, total biomass, total average weight, number of species and in terms of its community structure in abundance, biomass and average weight.

Environmental variables	Total abundance	Total biomass	Total average weight	No. of species	Abundance	Biomass	Average weight
Depth	62.5*	53.1*	30.3*	45.5*	23.5*	20.9*	4.0*
Distance	23.5*/4.8*	24.1*/6.2*	5*/0.1^{NS}	27.2*/9.1*	15.6*/6.7*	14.1*/6.5*	3.1*/1.5*
Habitat	5.8*/1.6*	2.9*/0.4**	0^{NS}/0.3^{NS}	0.2^{NS}/0.6**	10.2*/9.2*	3.4*/3*	0.8**/1.4*
Sum	68.9*	59.6*	30.7*	55.2*	39.4*	30.5*	7.2*

Numbers before the slash are marginal effects of variables; numbers behind the slash denote conditional effect of the variable.
*P = 0.001; **P < 0.05; NS, not significant.

Table 3. Effects of individual and all (row Sum) environmental variables, expressed as a share of the explained variability (%) of juvenile fish community in terms of its total abundance, community structure in abundance and number of species.

Environmental variables	Total abundance	Abundance	No. of species
Depth	31.6*	9.6*	25*
Distance	15.8*/4.5*	5.4*/2.1*	19.3*/7.9*
Habitat	3.8*/3.7*	6.3*/5.6*	4.7*/1.6**
Sum	42.1*	17.3*	34.4*

Numbers before the slash are marginal effects of variables; numbers behind the slash denote conditional effect of the variable.
*P = 0.001; **P < 0.05.

decreased steeply with the depth (Figs. 3–6). The total average weight of adult fish slightly increased with depth, which was caused by several catches of very large individual fish in depth layers below 18 m (Fig. 3c).

Abundance and biomass of all species decreased with the depth (Figs. 3d–f, 4, 5c and d, 6). However, the response of each species differed from each other (Table 4, Figs. 3d–f and 5c, d). Adult bleak, asp, white bream and rudd showed the steepest decrease in abundance with depth (regression coefficient B in range −0.7 to −0.9, Table 4). A slower decrease was found in adult roach, bream, perch, pikeperch, pike and roach × bream hybrid (B ~ -0.3 to -0.4). Abundance of adult ruffe and carp demonstrated the lowest decrease with depth (B ~ -0.2). Juveniles of roach and perch showed the steepest decrease with depth (B ~ -0.7). Juvenile bleak and pikeperch decreased moderately (B ~ -0.5) and juvenile bream and ruffe demonstrated the lowest decrease with depth (B ~ -0.3). GLM depth model was significant for all tested ecospecies and their responses successfully fit the model with a linear degree (Table 4).

Responses of average weight of adult fish to depth differed among species more than responses of their abundance (Fig. 3). The most common response was a more or less steep decrease of average weight with the increasing depth as in the case of roach, bream, bleak, asp, pike, white bream and rudd (B in range −0.1 to −0.9; Fig. 3g–i). Models of response of average weight to depth were significant for all tested species.

Distance

The distance from the dam had the second strongest effect on fish community characteristics (Tables 2 and 3). Both marginal and conditional effects of the distance were significant with the exception of the conditional effect on total average weight.

The total abundance and biomass of adult fish (Fig. 7a) and the total abundance and the number of species of juvenile fish (Fig. 8a and b) continuously increased heading away from the dam and reached the optimum close to the tributary approximately 6 km from the dam. The number of species of adult fish reached maximum at the tributary part (Fig. 7b). The average weight of adult fish was highest at the dam and in the middle part of the reservoir (Fig. 7c).

Responses of individual species of adult fish community to distance from the dam differed from each other. In general, the community in the dam part was similar to the community in the middle part and these two differed from the community in the upper and tributary parts of the reservoir (Figs. 4 and 6). The most common response was modelled significantly with the quadratic degree with values increasing continuously from the dam and peaking close to the tributary (Table 4, Fig. 7). All tested species were found in all parts of the reservoir. Only white bream were strictly bounded to the tributary and the upper parts of the reservoir (Fig. 7e).

Responses of most species of the juvenile community differed from those of the adult fish (Fig. 8). All species fit better with the quadratic degree of the significant model (Table 4).

Modelling of responses of average weight of adult fish to the distance from the dam showed that fish of different sizes inhabited different parts of the reservoir. Roach, pikeperch and ruffe had significant fit with the linear degree of the model: The largest individuals of roach were caught at the dam (Fig. 7g) and average weight of pikeperch and ruffe increased from the dam to the tributary (Fig. 7h and i). Asp and white bream had significant fit with the quadratic degree of the model: The largest asp were recorded around 5.5 km from the dam and the largest white bream were caught at the tributary part (Fig. 7g).

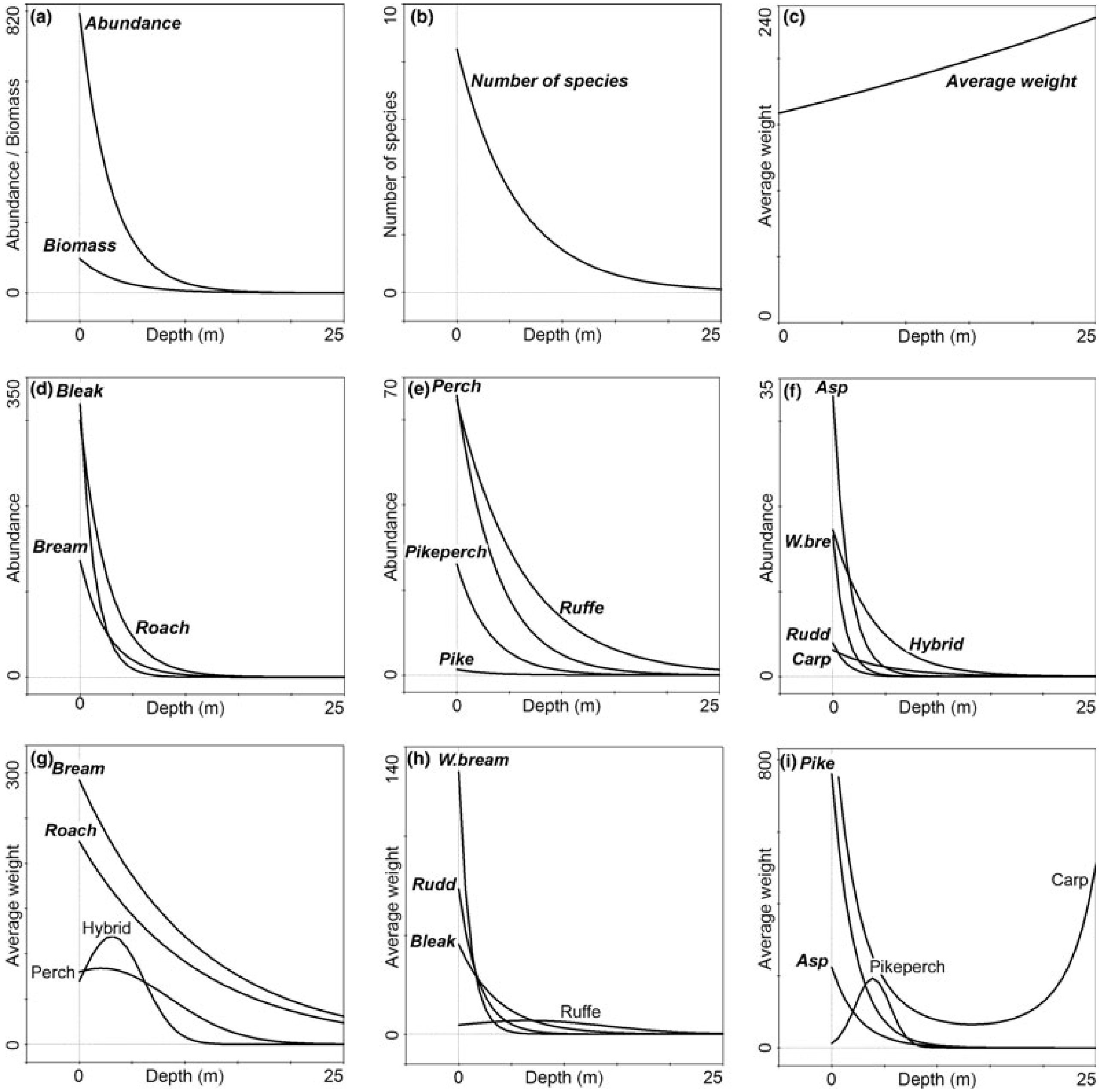

Fig. 3. Responses of the adult fish community as a whole (a–c), individual species (d–f) and average species weight (g–i) to depth. Responses of biomass of individual species are similar to responses of their abundance (d–f) and are not portrayed here. Characteristics and species with bold italic labels have responses modelled with a linear degree of GLM. Characteristics and species with the regular (nonbold, nonitalic) labels have responses modelled with a quadratic degree of GLM. Units of abundance – fish·1000 m^{-2}·$night^{-1}$, units of biomass – kg·1000 m^{-2}·$night^{-1}$, units of average weight – g.

Habitat type

Habitat-type variable explained the smallest part of the variability of sampled characteristics (Table 2). Both the marginal and conditional effects were significant with the exceptions of the effect on total average weight and number of species of adult fish.

The structure of the adult as well as the juvenile fish communities clearly differed between benthic and pelagic habitats (Table 1). However, all dominant species occupied both habitat types. The fish community was dominated by adult roach and juvenile perch and ruffe in benthic habitats. The pelagic habitats were dominated by adult bleak, roach and also bream and juvenile roach, bream and bleak.

According to ordination analyses, the adult fish community could be interpreted as three groups of species (Fig. 4): The first group consisted of pelagic

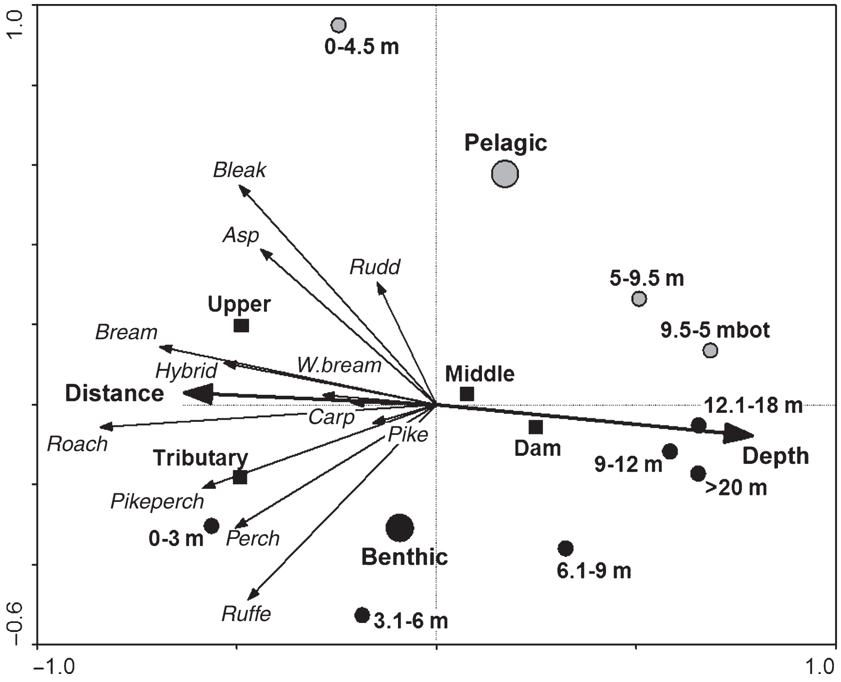

Fig. 4. Ordination biplot of the adult fish abundance with environmental variables depth, distance from the dam, affiliation to benthic (black circles) and pelagic habitat (grey circles) together with plotting of individual depth layers and parts of the reservoir (black squares). Numbers beside circles indicate depth layers, 9.5–5 mbot is the layer 9.5–5 m above the bottom. Values of variables increase in direction of the arrow. Correlations are displayed by angles between arrows (acute angle ~ positive correlation, obtuse angle ~ negative correlation and right angle ~ no correlation). Order of habitats with the highest abundances can be read from order of their right angle projections to a species arrow. Projections to elongation of an arrow to the negative space behind the point [0;0] indicate values below average. Similarity of samples are higher with higher proximity of their projections. Note that the ordination biplot represents 2D projection of multidimensional feature.

cyprinids, bleak, asp and rudd, with maximal abundance in epilimnetic waters. The second group was created by littoral percids, perch, pikeperch, ruffe and by pike with abundances higher in the benthic depth layers 0–3 and 3.1–6 m (and 6.1–9 m for ruffe also). The last group was represented by roach, bream, white bream, carp and roach × bream hybrid with the highest abundances in both littoral and epipelagic waters.

Similarly, the community of juvenile fish consisted of two clearly separate groups of species – the pelagic group of cyprinid species roach, bream and bleak and the littoral group of percid species perch, pikeperch and ruffe (Fig. 6). For roach and bream, higher than average abundances were also found in the benthic depth layer 0–3 m.

Patterns of vertical and longitudinal distribution of fish community were similar between benthic and pelagic habitats; with the exception of juveniles in pelagic habitats, where numbers were highest in the tributary part of the reservoir (Table 1).

Discussion

This study of the spatial distribution of the fish community in the Římov Reservoir found distinct spatial patterns. Generally, most fish were located in the upper depth layers in both benthic and pelagic habitats and their abundances increased heading away from the dam towards the tributary.

The vertical distribution of fish was apparently driven by the physical constraint of thermal and oxygen stratifications – most fish avoided depth layers below the thermocline i.e. with a water temperature below 16 °C and oxygen concentration below ca 5 $\text{mg} \cdot \text{l}^{-1}$ (Fig. 2). Fish recorded in depth layers below the thermocline (below 6 m in benthic habitats and below 5 m in pelagic habitats) represented approximately 13% and 8% of the total catch of adult fish in benthic and pelagic habitats, respectively (Table 1). Catches in these deeper layers included species with moderate (roach, perch, bream, roach × bream hybrid) and the lowest decreasing responses (ruffe) to depth (Fig. 3). For these species, which were able to tolerate temporarily lower water temperature and oxygen concentration, competition was probably the driving force for their vertical distribution. This type of situation was described for perch from the Římov Reservoir (Vašek et al. 2008), in the Saidenbach Reservoir (Kahl & Radke 2006) and in the Lake Vesijärvi (Horppila et al. 2000). Zooplankton, as the preferred food item of the most abundant fish species

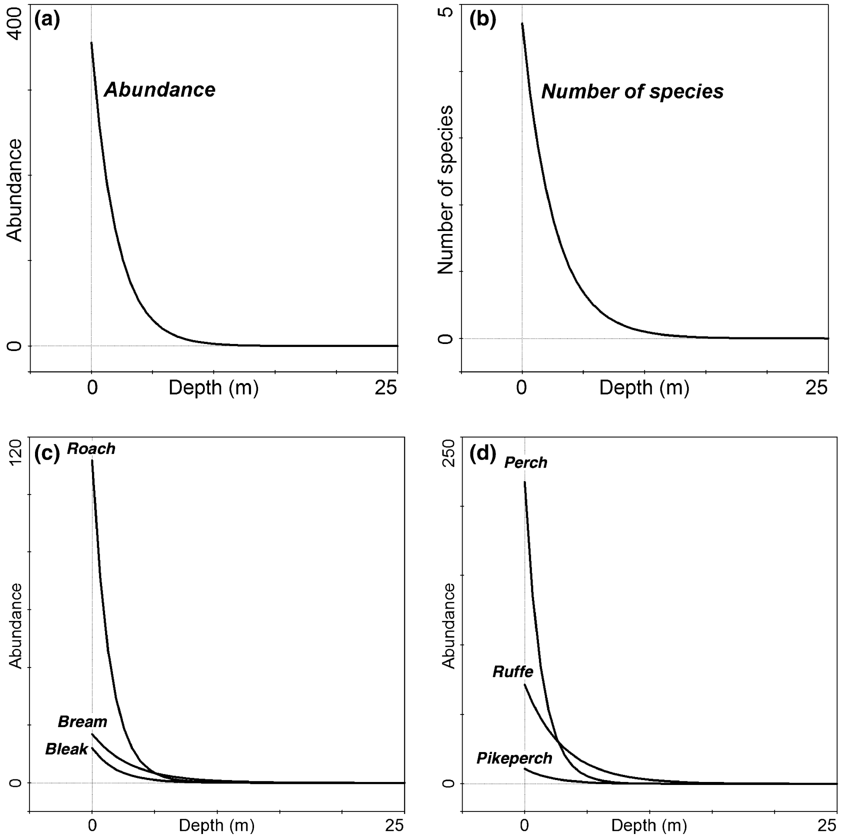

Fig. 5. Responses of the juvenile fish community as a whole (a and b) and individual species (c and d) to depth. All characteristics and species have response modelled with a linear degree of GLM. Units of abundance – fish·1000 m^{-2}·$night^{-1}$, units of biomass – kg·1000 m^{-2}·$night^{-1}$, units of average weight – g.

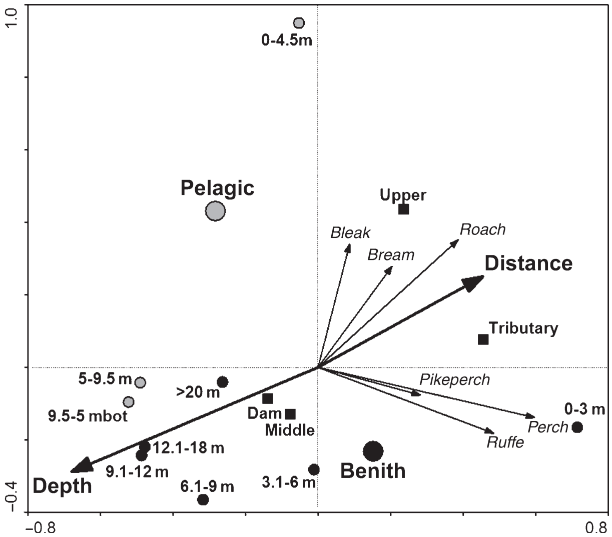

Fig. 6. Ordination biplot of the juvenile fish abundance with environmental variables of depth, distance from the dam, affiliation to benthic (black circles) and pelagic habitat (grey circles) together with plotting of individual depth layers and parts of the reservoir (black squares). Numbers beside circles indicate depth layers, 9.5–5 mbot is the layer 9.5–5 m above the bottom. For interpretation of the ordination biplot see Fig. 4.

in the Římov Reservoir (Vašek et al. 2003; Vašek & Kubečka 2004), was distributed to some extent throughout the entire water column with maxima in epilimnetic waters (Sed'a et al. 2007a,b). Larger cladocerans were found at the thermocline or closely under it and the uppermost depth layers were dominated mainly by rotifers and small bodied cladocerans during daytime in the thermally stratified reservoir Dubník II with relatively high predation pressure caused by both fish and invertebrate (chaoborus larvae) predators (Hudcovicová & Vranovský 2006). Accordingly, we can assume that fish occurring below the thermocline can profit from their tolerance of lower temperature and oxygen concentration because of the availability of prey.

All species in the juvenile fish community preferably occupied the upper depth layers; a strong dependence of their vertical distribution on water temperature could be expected (Brandt 1980). Abundance of no ecospecies increased with the depth was in accordance with findings of Prchalová et al. (2008) from the large canyon-shaped water supply Želivka Reservoir with a similar species assemblage.

The vertical distribution of the fish community in the Římov Reservoir would be different if the proportions of brown trout and whitefish were higher. These species prefer cold water and may inhabit depth layers below the thermocline (Linløkken 1988; Helland et al. 2007). Thus, it is probable that their vertical preferences would be different from the species that were dominant in the fish community in

Table 4. Responses of the fish community as a whole and abundance of individual species to depth and the distance from the dam.

	Depth				Distance				
Dependent variable	*F*	R^2	GLM	*B*	*F*	R^2	GLM	*B*	Optima
Adult fish									
Total abundance	607.9***	0.4	L	−0.3	43.7***	0.7	Q		6.1
Total biomass	317.4***	0.5	L	−0.3	22.9***	0.8	Q		6.0
Number of species	712.9***	0.4	L	−0.2	42.3***	0.7	Q		7.7
Average weight	NS				7.1**	0.9	Q		NA
Asp	171.1***	0.6	L	−0.7	17.6***	0.9	Q		5.5
Bleak	247.2***	0.6	L	−0.7	22.1***	0.8	Q		6.1
Bream	161.8***	0.7	L	−0.4	46.9***	0.7	Q		6.6
Carp	19.1***	0.9	L	−0.2	NS				
Hybrid	51.1***	0.8	L	−0.3	21.6***	0.7	Q		5.7
Perch	104.3***	0.7	L	−0.3	3.9*	0.9	L	−0.1	
Pike	13.8***	0.9	L	−0.3	NS				
Pikeperch	89.7***	0.8	L	−0.3	11.8***	0.9	Q		5.3
Roach	417.7***	0.5	L	−0.4	17.5***	0.8	Q		5.2
Rudd	39.8***	0.8	L	−0.7	NS				
Ruffe	67.6***	0.9	L	−0.2	20.3***	0.9	L	0.2	
White bream	28.5***	0.8	L	−0.9	25.2***	0.7	Q		11.1
Juvenile fish									
Total abundance	232.1***	0.6	L	−0.5	11.9***	0.9	Q		6.6
Number of species	361.6***	0.5	L	−0.4	24.5***	0.9	Q		5.8
Bleak	19.0***	0.8	L	−0.5	11.9***	0.8	Q		12.4
Bream	28.4***	0.9	L	−0.3	20.0***	0.8	Q		7.5
Perch	123.8***	0.7	L	−0.7	5.2**	0.9	Q		3.4
Roach	134.8***	0.7	L	−0.7	21.6***	0.8	Q		7.9
Ruffe	56.8***	0.8	L	−0.3	18.5***	0.8	Q		8.3
Pikeperch	49.9***	0.8	L	−0.5	6.2**	0.9	Q		4.7

Column GLM means linear (L) or quadratic (Q) degree of the model. Column B contains values of the regression coefficient *B*. Optima in km are in the optima column.

***$P < 0.001$, **$P < 0.01$; *$P < 0.05$; NS, not significant, NA, not available.

GLM, general linear model.

the Římov Reservoir and were included in the analyses.

We could interpret changes in fish numbers and community structure on the longitudinal axis of the reservoir as a gradient of fish communities along the general trophic gradient. Fish abundance and biomass increased with trophy and were high in eutrophic waterbodies (e.g. Jeppesen et al. 2002, 2005; Rask et al. 2003; Garcia et al. 2006) as well as in the upstream parts of the Římov Reservoir. Cyprinids prevailed in these parts of the reservoir and waterbodies with high trophy (e.g. Olin et al. 2002, 2006). Contrary, mesotrophic downstream parts of the Římov Reservoir and waterbodies with lower trophy had higher proportion of perch in the community (Persson et al. 1988).

Moreover, high abundances of juvenile fish at the tributary could be positively influenced by tributary spawning of many fish species of the Římov Reservoir (Hladík & Kubečka 2003) followed by a downstream drift of eggs, larvae and juveniles (Peterka et al. 2004). Further, a high number of species could be related to the proximity of the river as a species source (Fernando & Holčík 1991).

However, the tributary part of the Římov Reservoir could be too trophic for many abundant ecospecies. Abundances of these ecospecies had optima not at the tributary but approximately 1–2 km downstream from it. Griffiths (2006) compared many reservoirs and lakes and showed that the lacustrine fish biomass increased up to the concentration of TP of 140 $\mu g \cdot l^{-1}$, in waters with a higher concentration of TP biomass levelled off or decreased. The concentration of TP at the tributary of the Římov Reservoir reached a value of 155 $\mu g \cdot l^{-1}$ (August 1999, depth 0.5 m; Jezbera et al. 2003; Mašín et al. 2003), which could be the value higher than optimum for the above-mentioned ecospecies. Further, the tributary part of the Římov Reservoir was quite shallow and narrow and as such there could be serious lack of space to obtain the highest fish density (Vašek et al. 2003).

The longitudinal distribution of planktonic crustacean had two peaks, the first one in the upper part of the reservoir and the second one in the dam part and partially in the downstream area of the middle part of the Římov Reservoir (Sed'a & Devetter 2000; Sed'a et al. 2007a,b). Experiments with perch and roach showed that perch were better in evaluating predation risk and in taking advantage of different prey availability in refuge habitats (Persson & Eklöv 1995; Eklöv & Persson 1996). So, it seemed that perch could

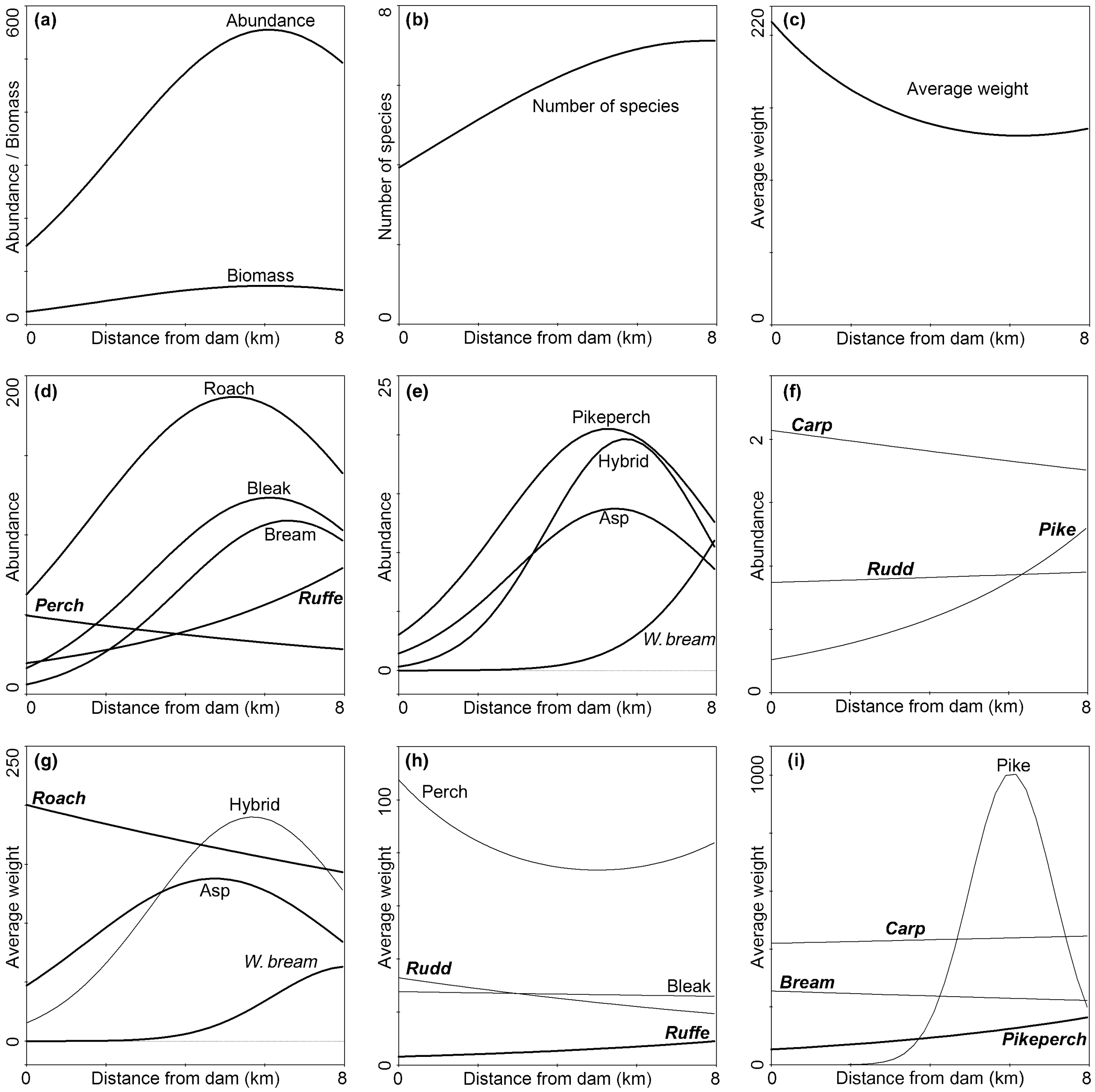

Fig. 7. Responses of the adult fish community as a whole (a–c) and individual species (d–f) and average species weight (g–i) to the distance from the dam. Responses of biomass of individual species are similar to responses of their abundance (d–f) and are not portrayed here. Characteristics and species with the bold italic labels have response modelled with a linear degree of GLM. Characteristics and species with the regular (nonbold, nonitalic) labels have response modelled with quadratic degree of GLM. Thinner lines mean nonsignificant fit. Units of abundance – fish·1000 m^{-2}·$night^{-1}$, units of biomass – kg·1000 m^{-2}·$night^{-1}$, units of average weight – g.

utilise the second density peak of cladoceran zooplankton as the abundance of both adult and juvenile perch were the highest in the downstream part of the Římov Reservoir.

The total CPUE in pelagic habitat represented approximately one-third and one-tenth of the total CPUE in the benthic habitat in terms of adult and juvenile fish, respectively. We assumed that in the reservoir with a very limited littoral zone, pelagic habitats were important for fish community in term of niche utilisation (Kahl & Radke 2006). Therefore, these habitats should be included in routine monitoring of the fish communities (Lauridsen et al. 2008).

In the Římov Reservoir, rudd preferred pelagic habitats which contrasted with the findings of Holčík (1977), Brosse et al. (1999, 2007) and Järvalt et al. (2005) who found rudd preferred near shore habitats with macrophytes in reservoirs and lakes. Jeppesen

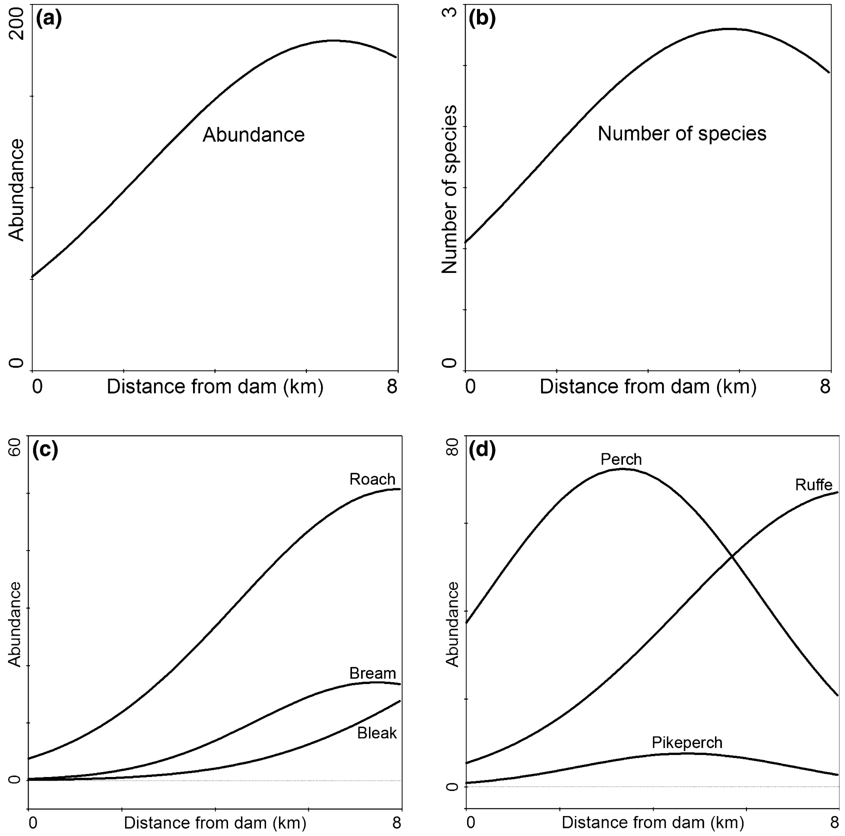

Fig. 8. Responses of the juvenile fish community as a whole (a and b) and individual species (c and d) to the distance from the dam. Characteristics and species with the bold italic labels have response modelled with linear degree of GLM. Characteristics and species with the regular (nonbold, nonitalic) labels have response modelled with quadratic degree of GLM. Units of abundance – fish·1000 m^{-2}·night^{-1}, units of biomass – kg·1000 m^{-2}·night^{-1}, units of average weight – g.

et al. (2006) described a habitat shift of larger rudd (>10 cm) from littoral to pelagic habitats in lakes with lower trophy. Winfield (1986) and Eklöv & Hamrin (1989) found rudd in pelagic habitats in systems with low predation pressure. Therefore, rudd in the Římov Reservoir, facing unfavourable littoral areas with missing macrophytes and a low overall abundance of piscivorous fish (Table 1), could rely on searching for food in pelagic habitats.

To summarise: in the artificial environment of the canyon-shaped Římov Reservoir, the originally riverine fish community colonised all inhabitable reservoir niches with distinct patterns. Habitat preferences, especially for horizontal distribution, changed from species to species and also with ontogeny. As the abundance of fish predators (both fish and birds) was relatively low, the spatial distribution was likely only slightly affected by predation.

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