Effects of the construction of a reservoir on the fish assemblage in an inflow river

M. Hladík^{1,2}, J. Kubečka^{1,2}, T. Mrkvička², M. Čech¹, V. Draštík^{1,2}, J. Frouzová¹, E. Hohausová¹, J. Matěna^{1,2}, V. Matěnová², M. Kratochvíl^{1,2}, J. Peterka¹, M. Prchalová¹, M. Vašek¹

ABSTRACT: The construction of the Římov Reservoir on the Malše River in 1978 significantly influenced the fish assemblage within the river, above the reservoir. Fish species that had successfully colonised the reservoir after impoundment expanded to the inflowing river. The changes in the riverine fish assemblage up to the first impassable weir (4 km upstream) reflected the development of the reservoir assemblage after an impoundment boom of pike (*Esox lucius*), then the perch (*Perca fluviatilis*) dominated phase and later the final cyprinid-dominated phase. The changes in the fish fauna over the period 1978–2002 were significant (χ^2 , P < 0.001). During the cyprinid-dominated phase, roach (*Rutilus rutilus*) became the most abundant species both in the reservoir and in the river, outnumbering the pristine river species. We conclude that the cyprinid-dominated assemblage in the reservoir can be more aggressive in interfering with the river assemblage than the percid-dominated one.

Keywords: riverine fish; assemblage development; Czech Republic; reservoir tributary; electrofishing

The construction of artificial reservoirs has been one of the most important modifications of natural river environments. Petts (1984) summarised the effect of damming on riverine ecosystems, including many examples of changes in pristine lotic fish assemblages; even the extinction of some fish species from entire river basins. The species that are most affected are usually anadromous and catadromous migrants (Jungwirth et al., 1998), however some potamodromous freshwater fish can also disappear from entire catchments after impoundment due to changes in natural conditions as well as to the interruption of migratory routes.

Extensive studies carried out in North America have shown that after the construction of artificial

reservoirs large changes occur in fish assemblages in rivers (Martinez et al., 1994; Lienesch et al., 2000; Phillips and Johnston, 2004). The portions of rivers downstream from the reservoirs were usually influenced by changes in physical conditions in the stream and by the input of juvenile fish hatched in the reservoir. Fewer studies have focused on the effects on the upstream fish fauna (Penczak, 1992; Lienesch et al., 2000). The riverine fish assemblage, upstream of the reservoirs, was mainly influenced by fish migrating out from the reservoir (Martinez et al., 1994); and also by their isolation from feeding grounds and refuges located downstream (Kelsh, 1994). The construction of reservoirs in Europe and their influence on inflowing rivers have received

Supported by Czech Science Foundation (Projects Nos. 206/02/0520, S6017004, Programs Nos. 1QS600170504 and AVOZ60170517).

¹Biological Centre of Academy of Sciences of the Czech Republic, Institute of Hydrobiology, České Budějovice, Czech Republic

²University of South Bohemia, České Budějovice, Czech Republic

only limited attention (Degerman and Sers, 1994; Penczak et al., 1998; Kruk and Penczak, 2003; Kukula, 2003). In the Czech Republic, only the complex studies of Peňáz et al. (1968) and Lusk (1995) dealt with the impacts of reservoir construction on the hydrobiological and ichthyological conditions of rivers. However, none of these studies dealt with long-term development of the fish assemblage within the reservoir and the features of its influence over time on the inflow river assemblage.

After impoundment, the development of fish assemblages in most Central-European reservoirs typically passes through several phases (Holčík, 1989; Kubečka, 1993), characterised by different dominant fish species and leads towards cyprinid dominance. In the natural environment, such as lakes, fish are known to make spawning and feeding migrations into inflowing streams (L'Abée-Lund and Vřllestad, 1985; Lilja et al., 2003). Similar behaviour has also been found for reservoir fish (Koščo and Košuth, 1995; Hladík and Kubečka, 2003, 2004).

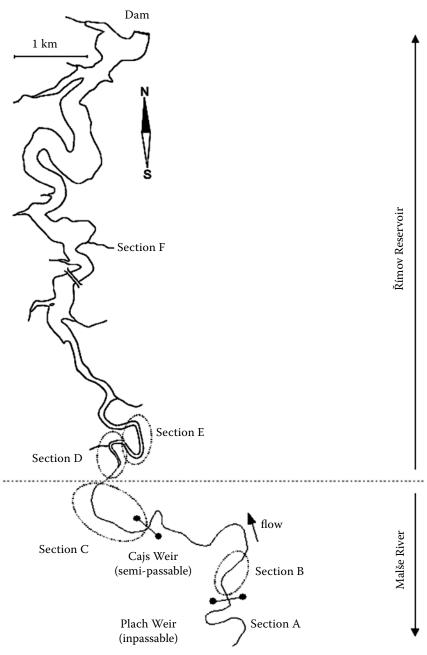


Figure 1. Map of the sampling area

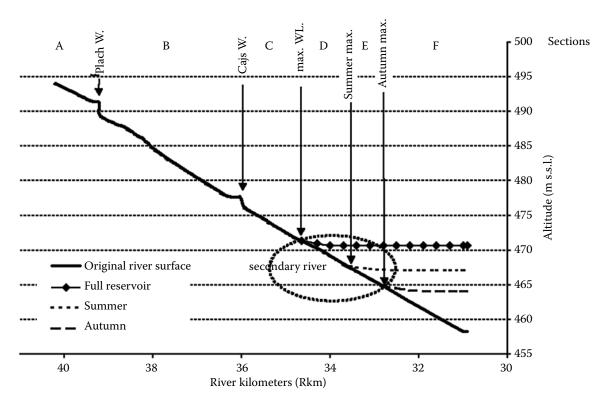


Figure 2. Scheme of the sampling area, location of weirs and usual water levels in the reservoir during the particular periods of each year

Consequently, the composition of fish migrating from the reservoir into the inflowing river can be reflected in the changes of fish assemblage in the inflowing river. In other words, it could be expected that river fish fauna can be reflective of the development phase of the reservoir fish assemblage.

The aim of the present paper is to evaluate longterm effects of the construction of a reservoir upon the fish assemblage in the inflowing river. We hypothesize that the fish community in the reservoir and its development, over twenty years from the impoundment, influences the original riverine fish assemblage in the inflow river. And that the main effect is caused by the migration into the river of those species successful in inhabiting the reservoir.

Description of study sites

The Římov Reservoir (Figure 1) was built in 1978 on the Malše River, south of České Budějovice, Czech Republic (dam coordinates: 48°51'00'N, 14°29'29"E; river kilometre (Rkm) 21.85). The Malše River is a small, sub-mountain river and is the only signifi-

cant inflow into the reservoir. The average width of the river just above the reservoir is 12-15 m, and the average discharge into the reservoir is $4.1 \text{ m}^3/\text{s}$. With regard to physical conditions, the river corresponds to the transition between the trout and grayling zones, according to Huet (1959).

The following sections of the study area were defined (Figures 1 and 2):

Section A – The unaffected part of the Malše River above the Plach weir (Rkm 39.2, the weir was rebuilt after the dam construction to prevent any upstream fish migration from the reservoir and to protect the valuable salmonid fishery in this part of the river). The weir is 2 m high with steep sides. This section was not sampled during the present study.

Section B – The part of the river between the Plach and Cajs weirs (overall section length 3.3 km). The Cajs weir (Rkm 35.9) can be partly overcome by the fish, and few individuals of reservoir-marked roach and bleak were able to penetrate to this area (Hladík, unpublished data).

Section C – Downstream of the Cajs weir to the river's mouth into the reservoir, at the point of the maximum reservoir water level (section length

Table 1. The fish species composition (% of total catch) at sampling sections along the Malše River and in the Římov Reservoir: in 1984–86 and after 20-years of development of the fish assemblage in the reservoir (2000–2002)

	:	Pristine					Sections of Malse Kiver	Malse Kiv	/er				VIIIIO	MILLION NESELVOIL
	Sampling site	fish stock	В			C				D		Е		F
	Year	1976–78*	2001	1984	1984-86**	2000	2000-02	19	1986**	200	2000-02	2001	1984–86	2000-03
	Sampling period	VI.	VI.	VII.	XXII.	VIVII.	VIIIX.	VII.	XXI.	VIVII.	VIIIX.	×	VIIIX.	VIIIX.
Brook lamprey	Brook lamprey Lampetra planeri (Bloch. 1784)	0.1												
Brown trout	Salmo trutta m. fario (L.)	18.3	18.8	5.1	7.0	0.5	0.5			9.0	0.1	0.3		
Grayling	Thymallus thymallus (L.)	1.3	0.2	2.2	4.2		0.1							
Minnow	Phoximus phoximus (L.)	4.8	1.1											
Rainbow trout	Oncorh. mykiss (Walbaum. 1792)									0.1	0.1			
Burbot	Lota lota (L.)		6.0	8.0	1.0					0.1	0.1			
ट्ट g Stoneloach	Barbatula barbatula (L.)	8.0	1.3				0.3			0.2	8.0			
Nase	Chondrostoma nasus (L.)						0.1							
Barbel	Barbus barbus (L.)	11.3			0.1			0.3						
Gudgeon	Gobio gobio (L.)	5.9	0.2	1.5	1.2	6.0	2.2	0.4		5.4	6.4	9.0		9.0
Riffle minnow	Alburnoides bipunctatus (Bloch. 1782)	0.2												
EelA	Anguilla anguilla (L.)	0.1		8.0	0.1	0.4	0.1	6.0		0.3	0.3			0.1
Bullhead	Cottus gobio (L.)	2.6	11.1	8.0	2.9	4.0	8.6			4.0	3.4			
Dace	Leuciscus leuciscus (L.)	26.1	12.7	13.3	8.2	6.1	18.5	6.0		2.1	3.9	3.1	0.0	4.4
Chub	Leuciscus cephalus (L.)	27.9	10.2	30.3	44.5	6.7	6.7	17.7	52.6	7.8	7.2	5.3	1.2	0.0
Perch	Perca fluviatilis (L.)	0.2	9.0	37.8	25.8	16.4	5.6	56.8	26.3	10.2	7.3	14.4	69.2	4.9
Roach	Rutilus rutilus (L.)		40.6	8.0	4.9	9.69	51.5	7.6	5.3	55.0	67.0	74.9	23.7	41.9
Pike	Esox lucius (L.)	0.1		8.0	0.2	0.1	1.3	9.9	1.8	0.1	0.3		0.1	0.2
Bream	Abramis brama (L.)				0.3	2.1		7.2	10.5	10.7	2.3		4.1	32.3
Bleak	Alburnus alburnus (L.)		2.5			3.0				2.5			0.1	5.0
Hybrid	Abramis \times Rutilus (L.)									0.1		0.3	0.1	0.5
Ruffe	Gymnocephalus cernuus (L.)					0.1	0.2			0.1	0.4	0.3	6.0	6.4
Asp	Aspius aspius (L.)									0.2		0.3	0.1	2.7
Catfish	Silurus glanis (L.)									0.2	0.1			
White hream	Rlicea bioontraa (I)										,			

data from *Vostradovská and Vostradovský (1983); **Kubečka and Křivanec (1990)

Table 1. to be continued

		Pristine				S 3	Sections of Malše River	Malše Riv	er				Římov I	Římov Reservoir
	Sampling site	fish stock	В			C				D		Е		F
	Year	1976-78*	2001	1984	1984-86**	2000	2000-02	19	1986**	200	2000-02	2001	1984–86	1984-86 2000-03
	Sampling period	VI.	VI.	VII.	XXII.	XXII. VIVII. VIIIX.	VIIIX.	VII.	XXI.	XXI. VIVII. VIIIX.	VIIIX.	×	VIIIX.	VIIIX. VIIIX.
ië Tench	Tinca tinca (L.)	0.1						1.3	1.8					
Carp Spec	Cyprinus carpio (L.)												0.1	0.1
Rudd	Scardinius erythrop. (L.)								1.8				0.2	0.1
Grass carp	Ctenoph. idella (Valenciennes 1844)													
ਦ L Pikeperch	Stizostedion lucioperca (L.)												0.1	8.0
		100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0	100.0
	Number of species	15	12	11	13	12	13	10	7	19	16	6	13	15
	H (Shannon diversity, In)	1.8	1.7	1.7	1.6	1.4	1.5	1.4	1.3	1.6	1.3	6.0	6.0	1.6
	Km sampled	6.0	0.3	4.2	13.5	1.5	6.0	1.8	2.0	1.5	0.2	0.2		
	Abundance (inds.)	1 683	640	1 333	986	3 118	851	226	57	2 153	367	319		
	Density (infds./km)	1 781	2 133	317	73	2 079	946	126	29	1 435	1 835	2 127		

1.2 km to Rkm 34.7). In this section, there is no obvious barrier for fish migration between the river mouth and reservoir.

The sections further downstream are located in the area of the reservoir impoundment, and their character changed according to the seasonal changes in water levels in the reservoir. The maximum water level was usually reached after snowmelt in early spring; then it gradually decreased towards winter by several meters, except during periods of higher rainfall.

Section D – The upper part of the reservoir (1.2 km), characterised by slowing water current and increasing depth during the early spring maximum water level. This section becomes a "secondary river" with typical riverine features since late spring, due to the declining water level in the reservoir.

Section E – The "secondary river" also developed in this section, in summer and autumn, during the continued drawdown of the water level in the reservoir (1.2 km). Riparian vegetation did not develop on the gravel shores during this period of a secondary river.

Section F – The main body of the reservoir, 13.5 km of the former river, area 210 ha, volume 33.8 mil.m³.

Sections A and B have recently been managed by the Czech Anglers Association as a salmonid fishery, while sections C–F are under the control of a special fishing management plan for the water supply reservoir (a ban on fishing, regular stocking of predatory species (Seďa and Kubečka, 1997)).

MATERIAL AND METHODS

The fish assemblage in the Malše River was sampled in three periods: before the construction of the reservoir in 1976–1978 (Vostradovská and Vostradovský, 1983), during the early developmental stages of the fish assemblage in the reservoir from 1984 to 1986 (perch-dominated phase, Kubečka and Křivanec, 1990), and again in 2000–2002 after more than twenty years of fish assemblage development (cyprinid-dominated phase, this study, Table 1). All samplings were made by electrofishing (for detailed description of earlier samplings see Vostradovská and Vostradovský, 1983; Kubečka and Křivanec, 1990). Sampling in 2000–2002 was performed by BMA-Honda electroshocker (230 V, 50 Hz, Bednář Factory, Czech

Table 2. The pristine fish species composition in the Malše River before the Římov Reservoir construction, compared to the fish species composition in river sections B, C and D after the filling of the reservoir in 1984–1986, and in 2000–2002 by both Jaccard index (Ja) and percentage similarity (Ps)

Malše River	Section/ween -	Jaccai	d index	Percentag	ge similarity
waise River	Section/year —	1986	2001-02	1986	2001-02
1976-78	В	_	0.53	_	0.23
	C	0.50	0.37	0.26	0.09
	D	0.11	0.33	0.05	0.09

Republic), with a single pass applied through the river section surveyed. All samplings were performed outside of 'spawning migration peaks', i.e. outside upstream and following downstream migration of fish from the reservoir (Hladík and Kubečka, 2003), to sample resident fish only. Only fish 1+ and older were considered. Since the sampled stretches of the river differed in lengths, the number of fish captured was also expressed as fish density of individuals per km (Table 1).

The estimations of the fish assemblage compositions in the reservoir in the 1980s and in the 2000s were based on night-time shore seining (Seďa and Kubečka, 1997; Říha et al., 2008).

The fish species recorded during the study were split into two groups:

(1) lotic species – species typical for running waters;

(2) lentic species – riverine fish species capable of inhabiting the reservoir standing water (Table 1).

The composition of fish species found in each sampling in the river and the reservoir was compared both between periods and between river sections using: relative abundance (%), total number of species, and Shannon index of diversity (H, ln) (Table 1). Changes in the fish assemblage within the river sections (sections B, C and D), after the reservoir construction and during reservoir aging, were expressed by comparisons with the pristine river fish assemblage using the Jaccard index (Ja) and percentage similarity (Ps) (Ludwig and Reynolds, 1988) (Table 2).

In order to compare the composition of the fish catches in the 1970s, 1980s and 2000s, we used con-

Table 3. The percentage contributions of individual species to the significance of changes in the fish communities (proportional change of individual species), obtained from contingency tables in three sections of the Malše River and in the Římov Reservoir during 1975–2003

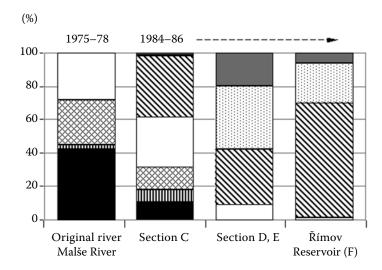
Species/section	Section C	Section D	Section F
Brown trout	11.01	18.67	7.72
Grayling	1.92	1.35	0.52
Minnow	5.11	5.16	1.99
Barbel	12.11	12.22	4.75
Gudgeon	2.24	2.09	1.68
Bullhead	0.39	1.03	1.10
Dace	4.89	23.23	5.85
Chub	11.41	11.78	9.77
'Other lotic species"	0.32	0.40	0.40
Perch	11.01	6.59	48.86
Roach	36.84	14.00	5.83
Bream	0.98	1.75	7.59
Bleak	1.64	0.94	1.58
'Other lentic species"	0.11	0.79	2.36

tingency tables (Everitt, 1992). The changes were analysed for sections C, D, and F, for which data from all three periods were available. Rare species (with abundances of less than five individuals) were pooled together, based on species, into "other lotic" and "other lentic" species groups in order to meet the requirement of the minimum number for the χ^2 test of contingency tables. The null hypothesis of the test was that: no change in the proportion of species in the whole fish assemblage of the studied river sections occurred over the described period. The P-level was set to 0.01. Another outcome of the analysis was the percentage contribution of each species to the total significance of the χ^2 test of the contingency tables, which corresponded to the pro-

portional change in each species in the assemblage during the study period (Table 3).

RESULTS

The results from 1976–1978 showed that the fish assemblage within the river contained a high proportion of lotic species (Figure 3), with prevalence of chub (*Leuciscus cephalus*), dace (*Leuciscus leuciscus*), brown trout (*Salmo trutta* m. *fario*) and barbel (*Barbus barbus*) (Table 1). This composition was considered as the basic fish assemblage for all sections of the river, sampled in later years. The composition of fish species in the inflow river



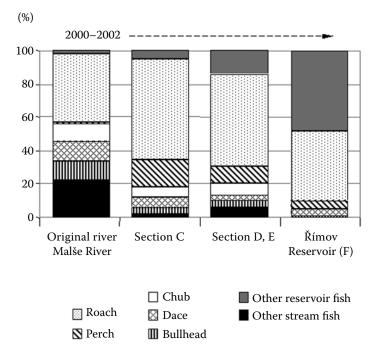


Figure 3. The fish species composition (% of total catch) in the Malše River: before the filling of the Římov Reservoir (1975–78), after the filling of the reservoir (Sections A and B in 1984–1986), and after 20 years of development of the fish assemblage in the reservoir (Sections A, B and C in 2000–2002). The fish species compositions in the Římov Reservoir in 1984–1986 and in 2000–2002 are given in the righthand columns

changed very soon after the reservoir was filled; and the proportions of fish species were changing during the aging of the reservoir, reflecting the fish assemblage development therein.

In 1984–1986, the fish assemblage in the reservoir was in a perch-dominated phase. It was dominated by perch (*Perca fluviatilis*), with roach (*Rutilus rutilus*) being the second most abundant species; and the same species dominated the lower part of the river (section D). Chub remained the only important stream fish in this section (Figure 3). In section C, perch was also very abundant, but approximately 60% of the fish assemblage in this section was still composed of the original stream fish species. The catch per 1 km of stream in the 1980s (30 to 300 individuals/km) was much lower than before the reservoir was constructed, as well as compared to the 2 000s samplings (Table 1). Sections A and B were not sampled during the 1980s.

In the 2000s, the development of the fish assemblage in the reservoir reached a stable cyprinid phase, dominated by cyprinid species (mainly roach, bream Abramis brama, and bleak Alburnus alburnus). The abundance of perch was found to be low in both the reservoir and the river (Table 1). In contrast, cyprinids became dominant in sections D, and also C, and the proportion of lotic fish dropped there to around 20% of the fish assemblage only. The original assemblage of roach in the river, supported by roach migrating from the reservoir and its offspring, managed to increase the relative densities of fish in the river (sections C and D) to a level of 1 000 inds/km. Roach even penetrated through the semi-permeable Cajs weir and gained dominance in section B.

To summarize, the true river (never flooded by the reservoir water) adjacent to the reservoir did not change morphologically, but its fish stock went through substantial succession (Figure 4). Dominant lotic species (chub, dace and brown trout) reduced their abundance several times, some species (barbel, minnow) disappeared completely (Table 1), while roach emerged in 2000–2002 as a new dominant species outnumbering all remaining fishes (Figure 4). The abundance of bleak and bream rose in 2000–2002 as well, but to much lower levels (20–40 inds/km) than roach.

A special temporary transition zone between the river and the reservoir - a secondary river, developed in sections D and E during the regular summer and autumn drawdowns of the reservoir water level (Figure 2). At the time of drawdown, the reservoir fish followed the decreasing water level and left the secondary river zone while riverine fish from upstream sections only entered this temporary habitat in low numbers. Due to this, the temporarily developed secondary river was nearly fishless (Table 1). This phenomenon was especially apparent during the perch phase in the 1980s, when the relative fish catch was below 200 inds/km. During the cyprinid phase in the reservoir, the fish fauna of the secondary river was represented mainly by age 1+ and 2+ roach, 1+ perch, and a few other fish (Figure 3). The relative abundance per km of stream was around 2 000 inds/km, similar to the original level in the 1970s.

Contingency tables revealed that the changes in species composition in sections C, D, and F were highly significant between the sampling periods (P < 0.001). The percentage contribution to total

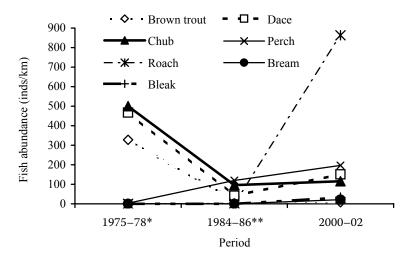


Figure 4. Changes in the abundance of dominant fish species in the section C of the Malše River before and after the construction of the Římov Reservoir

significance of the χ^2 test was highest in roach, brown trout, barbel, chub, and perch (Table 3). The proportion of these species changed considerably in the river (sections C and D, Figure 4). In the reservoir (section F), the changes in the proportion of perch mainly dictated the development of the community structure. We can conclude that the tested hypothesis (of no changes in the species proportions) of the river sections studied over the described period can be rejected.

The highest number of species was found in section D, which was supported by the secondary river, a transition zone between lotic and lentic environments, inhabited by riverine as well as reservoir species (Table 1). The species richness of this zone included 22 species. The Shannon index of diversity (H') was highest for the pristine river assemblage before the reservoir construction (1.8). Then it decreased slightly and fluctuated within the range of 1.3–1.7 in the tributary during all later samplings. Low values of the Jaccard index and percentage similarity, comparing pre- and post-impoundment periods in the river (Table 2), demonstrated the importance of changes in the fish assemblage.

DISCUSSION

Assessment of current and past data allows for an overview of processes of fish assemblage development from the original river system to a system modified by the reservoir construction. Although the set of presented historical and current data lacks a systematic sampling design, we attempted to educe the main signs of fish development in the reservoir and in the river over the targeted period. Background data of Vostradovská and Vostradovský (1983) give the species composition of the Malše River only within the recent section F (before flooding by the reservoir water) and results of five quantitative estimates: below section F (1 estimate), in the section F (1) and in the section A (3 estimates). One site (below the town of Kaplice in section A) had significantly higher abundance and biomass than other sites and was termed as outlier by the authors. Thus we also excluded this site from our comparisons. We considered the species composition available in Vostradovská and Vostradovský (1983) to be usable as background historical data for all sections A-F because (i) their quantitative estimates did not vary much, (ii) the composition was supported by qualitative statements of Vostradovský (1978) and (iii) the catch was relatively abundant (1 683 fishes). Later samplings were not taken systematically either with respect to the sampling period and effort, which added to the variation of the presented data (Table 1). However the shifts of fish communities were highly significant irrespective of the variation.

The fish species from the pristine river assemblage differed in their resistance to the variety of factors probably influencing their community, such as interference of reservoir fish (potential predation, food and/or habitat competition) and stream fragmentation. Some riverine species disappeared from the studied part of the river, e.g. barbel and the rare riffle minnow (Alburnoides bipunctatus); other species substantially decreased in abundance (dace (Leuciscus leuciscus), brown trout, rainbow trout (Oncorhynchus mykiss) and grayling (Thymallus thymallus), while some pristine fish were not affected, such as chub (Leuciscus cephalus). Some species could even profit from changes in the fish community, like bullhead (Cottus gobio).

Species typical of the barbel zone (Huet, 1959), such as barbel, have also been documented to be highly sensitive to river damming elsewhere. Kukula (2003) reported the extinction of two species of barbel from the San River after the construction of a reservoir; Penczak et al. (1998) recorded the extinction of anadromous vimba (*Vimba vimba*) and nase (*Chondrostoma nasus*) from the Warta River catchment after the construction of the Jerzinsko reservoir; additionally, a rapid decrease in the abundance of nase was found in the impounded Svratka River. Lusk (1995) even suggested that the effect of the construction of reservoirs was equal to the destruction of the whole fish assemblage in the upstream river zones.

Dace showed a decrease in relative abundance from 26% in the pristine river to 12% in section B, 6.5–18% in section C and 0.9–3.9% in section D after the reservoir filling. Brown trout, rainbow trout and grayling decreased in section C although these species were regularly stocked upstream by a local fishery, and a considerable number of brown trout and rainbow trout was recorded during downstream migration after stocking (Hladík and Kubečka, 2003). Interference of the salmonids and the reservoir fish and/or their offspring colonising the river from spawning grounds can be assumed, but other possible unidentified factors cannot be omitted completely. Chub was found in similar relative abundance like in the pristine assemblage in

the period 1984–1986, but dropped in 2000–2002 in all sampled places. Despite of this decrease, chub showed the highest relative abundance among original riverine fish in 2000–2002.

Fish typical of the upstream river zones were able to benefit from the reservoir construction only in a few cases. Koščo and Košuth (1995) described an increase in the abundance of Balkan barbel (*Barbus meridionalis*) in inflow streams after the construction of the Starina Reservoir (eastern Slovakia); and Rodriguez-Ruiz and Granado-Lorencio (1992) documented massive migration of barbel (*Barbus sclateri*) and Iberian nase (*Chondrostoma polylepis willkommii*) from a reservoir to spawning grounds in the tributary river.

On the other hand, in some cases, stream cyprinids such as chub and dace in our study were also able to withstand the consequences of the reservoir construction or even benefit from it. A considerable portion of the chub population within the river used the reservoir as a winter refuge (Hladík and Kubečka, 2003). Dace were able to utilize the still-water conditions in the reservoir and accounted for 4.4% (on average) of the reservoir fish assemblage in 2000–2002 (Říha et al., 2008). On the contrary, Koščo and Košuth (1995) documented the expansion of dace from the Starina Reservoir into the inflow streams.

By contrast, bullhead (*Cottus gobio*) was very abundant in all sampled parts of the river in the 1980s and 2000s. Its resistance was probably supported by the decrease in the abundance of brown trout, which is the main predator of the bullhead.

Development of the fish assemblage of Central-European reservoirs typically passes through several phases (Holčík, 1989; Kubečka, 1993), including a pike phase, percid phase, and finally a cypriniddominated phase. The percid phase in the Rímov Reservoir lasted for about six years (ca 1983–1989; Kubečka and Křivanec, 1990; Seďa and Kubečka, 1997), which was the period of possible perch influence on the riverine fish assemblage. The cyprinid phase began to dominate the reservoir in the early 1990s (Seďa and Kubečka, 1997). This phase is usually the final one (Holčík, 1989), and thus the longest lasting phase, of Central-European reservoirs. We conclude that the cyprinid-dominated assemblage can be considered more aggressive in interfering with the river assemblage, due to its long-term and thus stronger overall effect than is the short-term perch-dominated assemblage. In addition, the intensive spawning migration of cyprinids (Hladík and Kubečka, 2003) can intensify the effect. However, other mentioned factors, such as stream fragmentation and/or fish stocking could play a role.

The construction of the Římov Reservoir fundamentally affected the fish assemblage in the Malše River, up to the first impassable weir. The fish assemblage in the river sections adjacent to the reservoir developed from a predominance of river species toward percid-dominated, and then later to cyprinid-dominated assemblages, reflecting the fish assemblage development in the reservoir. Roach were especially successful in replacing riverine fauna, both qualitatively and quantitatively.

The effort to restore and protect natural riverine ecosystems throughout Europe, stimulated by the Water Framework Directive, involves the construction of bypasses in order to facilitate fish migration through weirs and dams. On the other hand, means for the protection of the riverine ecosystems upstream of the reservoir against fish expansion from the artificial water body should be still considered.

Acknowledgement

We greatly appreciate the help of the members and friends of the ichthyology working-group of the Institute of Hydrobiology and Povodí Vltavy, with extensive fieldwork. We thank Magdalena Žofková, David Hardekopf, Peter R. Lemkin and Robin Welcomme for their help with completion of the manuscript.

REFERENCES

Degerman E., Sers B. (1994): The effect of lakes on the stream fish fauna. Ecology of Freshwater Fish, 3, 116–122.

Everitt B.S. (1992): The Analysis of Contingency Tables (Monographs on Statistics and Applied Probability 45) $2^{\rm nd}$ ed., Chapman and Hall, London, UK, 164 pp.

Hladík M., Kubečka J. (2003): Fish migration between a temperate reservoir and its main tributary. Hydrobiologia, 504, 251–266.

Hladík M., Kubečka J. (2004): The effect of water level fluctuation on tributary spawning migration of reservoir fish. International Journal of Ecohydrology and Hydrobiology, 4, 449–457.

Holčík J. (1989): The Freshwater Fishes of Europe. AULA-Verlag Wiesbaden, 1/II, 469 pp.

Huet M. (1959): Profiles and biology of West European streams as related to fish management. Transactions of the American Fisheries Society, 88, 155–163.

- Jungwirth M., Schmutz S., Weiss S. (1998): Fish Migration and Fish Bypasses. Fishing New Books. Blackwell Science, 438 pp.
- Kelsh S.W. (1994): Lotic fish-community structure following transition from severe drought to high discharge. Journal of Fish Biology, 9, 331–341.
- Koščo J., Košuth P. (1995): Ichthyofauna of river basin of Starina water reservoir. Roczniki Bieszcadzkie, 4, 143–154.
- Kruk A., Penczak T. (2003): Impoundment impact on assemblages of facultative riverine fish. Annales de Limnologie-International Journal of Limnology, 39, 197–210.
- Kubečka J. (1993): Succession of fish communities of Central and East European reservoirs. In: Straskraba M., Tundisi J.S., Duncan A. (eds.): Comparative Reservoir Limnology and Water Quality Management. Kluwer, Dordrecht, Germany, 153–168.
- Kubečka J., Křivanec K. (1990): Influence of the Římov Reservoir on the fish stock of upper parts of Malše River. Ichthyofauna of the Malše River and the Římov Reservoir, Museum of South Bohemia, České Budějovice, ČR, 134–141.
- Kukula K. (2003): Ichthyofauna of a mountain river upstream from a big dam reservoir (the upper San River, South-eastern Poland). Archiv Für Hydrobiologie, 157, 413–431.
- L'Abée-Lund J.H., Vøllestad L.A. (1985): Homing precision of roach *Rutilus rutilus* in Lake Arungen, Norway. Environmental Biology of Fishes, 13, 235–239.
- Lienesch P.W., Lutterschmidt W.I., Schaefer J.F. (2000): Seasonal and long-term changes in the fish assemblage of a small stream isolated by a reservoir. The Southwestern Naturalist, 45, 274–288.
- Lilja J., Keskinen T., Marjomäki T.J., Valkeajärvi P., Karjalainen J. (2003): Upstream migration activity of cyprinids and percids in a channel, monitored by a horizontal split-beam echosounder. Aquatic Living Resources, 16, 185–190.
- Ludwig J.A., Reynolds J.F. (1988): Statistical Ecology: A Primer on Methods and Computing. Wiley, New York, USA.
- Lusk S. (1995): Influence of valley dams on the changes in fish communities inhabiting streams in the Dyje River drainage area. Folia Zoologica, 44, 45–56.

- Martinez P.J., Chart T.E., Trammel M.A., Wullschleger J.G., Bergersen E.P. (1994): Fish species composition before and after construction of a main stream reservoir on the White River, Colorado. Environmental Biology of Fishes, 40, 227–239.
- Penczak T. (1992): Fish production in the Warta river postimpoundment study. Hydrobiologia, 242, 87–93
- Penczak T., Glowacki L., Galicka W., Koszalinski H. (1998): A long-term study (1985–1995) of fish assemblages in the impounded Warta River, Poland. Hydrobiologia, 368, 157–173.
- Petts G.E. (1984): Impounded Rivers. Chichester: Wiley, USA.
- Peňáz M., Kubíček F., Marvan P., Zelinka M. (1968): Influence of the Vír river valley reservoir on the hydrobiological and ichthyological conditions in the River Svratka. Acta Scientiarum Naturalium Academiae Scientiarum Bohemoslovacea, Brno, 2, 1–60.
- Phillips B.W., Johnston C.E. (2004): Fish assemblage recovery and persistence. Ecology of Freshwater Fish, 13, 145–153.
- Rodriguez-Ruiz A., Granado-Lorencio C. (1992): Spawning period and migration of three species of cyprinids in a stream with Mediterranean regimen (SW Spain). Journal of Fish Biology, 41, 545–556.
- Říha M., Kubečka J., Seďa J., Matěna J., Hladík M., Čech M., Draštík V., Frouzová J., Hohausová E., Jarolím O., Jůza T., Kratochvíl M., Peterka J., Prchalová M., Tušer M., Vašek M. (2008): Long-term development of fish populations in the Římov Reservoir. Fisheries Management and Ecology. (in press)
- Seďa J., Kubečka J. (1997): Long-term biomanipulation of the Římov reservoir, Czech Republic. Hydrobiologia, 345, 95–108.
- Vostradovská M., Vostradovský J. (1983): The Prognosis and actual development of the stocking rate in water reservoirs (Římov and Lučina). Czech Journal of Animal Science, 28, 801–807.
- Vostradovský J. (1978): Forecasted development of fishery relations in the water-supply reservoir Římov. Vertebrathogical News, Brno, CR, 61–65.

Received: 2008–05–13 Accepted after corrections: 2008–08–28

Corresponding Author

Doc. RNDr. Jan Kubečka, CSc., Biological Centre of Academy of Sciences of the Czech Republic, Institute of Hydrobiology, Na Sádkách 7, 37005 České Budějovice, Czech Republic Tel. +420 387 775 848, e-mail: kubecka@hbu.cas.cz