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Distribution of the bathypelagic perch fry layer along the longitudinal profile of two large canyon-shaped reservoirs

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The distribution of the bathypelagic perch *Perca fluviatilis* fry (BPF) layer and its qualitative and quantitative changes were studied along the longitudinal profiles of the large canyon-shaped Slapy and Orlík Reservoirs (Czech Republic), using acoustic methods (SIMRAD EY500 echosounder, split-beam transducer, Sonar5 post-processing software). In Slapy Reservoir (sampled in late May), the BPF layer created by the mass of non-shoaling perch larvae and juveniles (average total length, L_T, 10·4 mm) was recorded from the dam for 29 km upstream. The BPF layer only vanished in the upper third of the reservoir due to the extremely cold hypolimnetic water discharged from Orlík Reservoir, which is situated upstream in the cascade. Both abundance and size of BPF increased significantly upstream following, in Slapy Reservoir, the trophic gradient. In Orlík Reservoir (sampled in late June), the BPF layer was created predominantly by shoaling perch fry individuals (average L_T 31·8 mm), recorded along the whole longitudinal profile of the reservoir (>50 km, filled with relatively warm water). Both the sizes of BPF and their shoaling activity again increased significantly from the dam towards the inflow following, in Orlík Reservoir, the trophic gradient. Pooling the data from both reservoirs, it was evident that the tendency to flock in a dense layer and, much later, to create distinct shoals, increased continuously with the size of BPF. A number of variables describing the BPF layer in Slapy and Orlík Reservoir are given.

Key words: echosounder; Orlík Reservoir; *Perca fluviatilis*; shoal; Slapy Reservoir; Sonar5.

INTRODUCTION

The marine origin of percids (Bănărescu, 1990) probably predetermined the early pelagic phase in their life cycles. Similarly, in the early life history of perch *Perca fluviatilis* L. there is an obligate pelagic phase (Guma'a, 1978; Coles, 1981; Treasurer, 1988; Urho, 1996). Recently, Čech *et al.* (2005) gave

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evidence of sympatric surface-confined, or epipelagic, perch fry (EPF) and deep water, or bathypelagic, perch fry (BPF) communities occurring simultaneously in Slapy Reservoir during spring. While EPF are well documented in the work of many authors [Guma'a, 1978; Coles, 1981; Viljanen & Holopainen, 1982; Craig, 1987; Treasurer, 1988; Wang & Eckmann, 1994; Matěna, 1995; Urho, 1996; Wanzenböck *et al.*, 1997 for perch and Whiteside *et al.*, 1985; Post & McQueen, 1988 for the closely related yellow perch *Perca flavescens* (Mitchill)] the community of BPF, which is present as a several metre thick scattering layer, that could be followed by the echosounder, has been overlooked for decades. Except for a few observations (V. Hruška, unpubl. data; J. Kubečka, unpubl. data) the phenomenon of the BPF layer was restricted to the role of an interfering noise on the screen of commercial fishermen's echosounders. The BPF community, however, may represent significant (Čech *et al.*, 2005; Čech & Kubečka, 2006), and in special cases, the only portion of the whole pelagic perch fry community (Čech *et al.*, 2007).

In their recent work, Čech & Kubečka (2006) have shown that, in the small, canyon-shaped Římov Reservoir, the BPF layer was evenly distributed along most of the longitudinal profile of this reservoir from late May to early September. The only exception was the uppermost, very shallow, riverine part of the reservoir where the BPF layer was either absent due to inflowing water pushing the fry community further downstream into the reservoir, or changed to bottom-dwelling fish staying well hidden from any sampling techniques. A spring flood in May and migration for overwintering in September were also suggested to be factors that should be considered in explaining the absence of the BPF layer in the riverine part of this reservoir.

The present study investigated the distribution of the BPF layer along the longitudinal profiles of two large canyon-shaped reservoirs (four and five times longer then Římov Reservoir). The main questions were (1) whether the BPF layer is really evenly distributed along the whole longitudinal profile of these large reservoirs and (2) whether there could be any qualitative or quantitative changes (*e.g.* abundance, size of fish and shoaling activity) recorded along the longitudinal profile of such a BPF layer.

MATERIALS AND METHODS

STUDY AREA

The study was carried out in two large, canyon-shaped Czech reservoirs, Slapy and Orlík Reservoirs (Fig. 1). The meso- to eutrophic Slapy Reservoir (49°49′28″ N; 14°25′58″ E, 40 km south of Prague) has an area of 1392 ha (length 42 km, mean width 313 m), a volume of 269×10^6 m^3, and maximum depth of 58 m. The reservoir was built in 1954 by damming the River Vltava as the third of nine Vltava River cascade reservoirs. Because of a relatively high mean annual inflow of 85 m^3 s^{-1}, the average theoretical retention time (reservoir volume divided by the inflow discharge) is only 38·5 days (Hrbáček & Straškraba, 1966). During acoustic and complementary net sampling in late May 2002 the bathypelagic fry community of Slapy Reservoir was composed of 95·5% perch, 3·2% zander *Sander lucioperca* (L.) and 1·3% ruffe *Gymnocephalus cernuus* (L.) (Čech *et al.*, 2005).

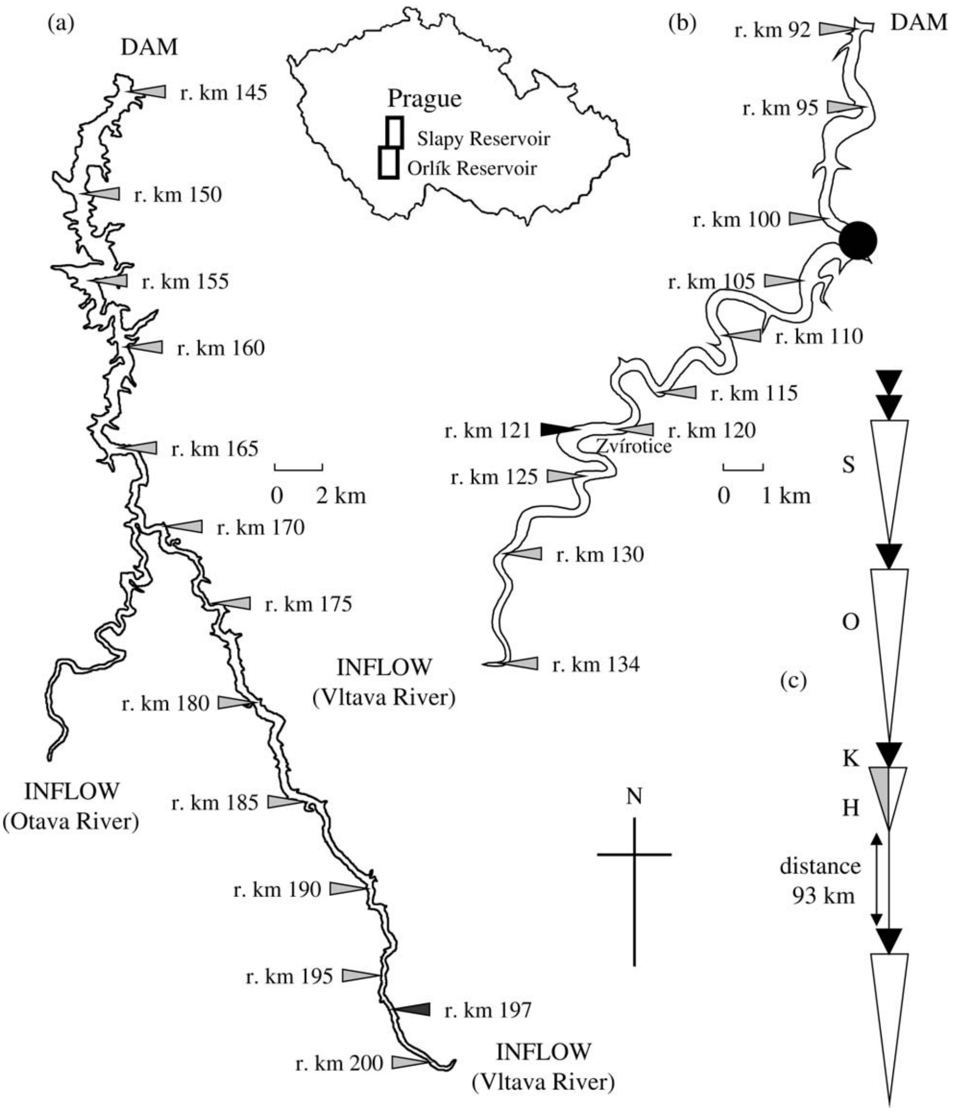

FIG. 1. A map of (a) Orlík and (b) Slapy Reservoir and their locations in the Czech Republic. R. km, river km, *i.e.* distance from the mouth of the Vltava River into the River Elbe. (▶), (r. km 197 in Orlík and r. km 121 in Slapy), the uppermost record of the bathypelagic perch fry (BPF) layer. ●, Slapy Reservoir, shows the area where diel vertical migrations and diet of BPF were intensively studied (Čech *et al.*, 2005; M. Kratochvíl & J. Peterka, unpubl. data). (c) A scheme of the Vltava River cascade reservoirs. 'Black' reservoirs serve to regulate water level fluctuations, 'white' reservoirs accumulate water for hydroelectric power stations, the 'grey-white' reservoir also ensures water for Temelín nuclear power station. H, Hněvkovice Reservoir; K, Kořensko Reservoir; O, Orlík Reservoir; S, Slapy Reservoir.

The eutrophic Orlík Reservoir (49°36′30″ N; 14°11′00″ E, 70 km south of Prague) has an area of 2733 ha (length of the main stream 55 km, mean width 390 m), a volume of 717×10^6 m^3, and maximum depth of 72 m. This reservoir was built in 1960 by damming the River Vltava (upstream of Slapy Reservoir) as the sixth of nine Vltava River cascade reservoirs. A relatively high mean annual inflow of 83 $m^3 s^{-1}$ results in the average theoretical retention time of 100 days (Straškraba *et al.*, 1973). In addition to Slapy (Čech *et al.*, 2005) and Římov (Čech & Kubečka, 2006), Orlík is another reservoir in the Vltava River basin where the BPF layer was observed (Čech *et al.*, in press; J. Kubečka, pers. data). In this reservoir, in mid June 2004, the bathypelagic fry community was composed of 67·5% perch, 31·1% zander and 0·8% ruffe (Čech *et al.*, 2007).

SAMPLING

Acoustic data were collected during continuous sampling surveys of Slapy Reservoir on 28 May 2002 [period 1100–1800 hours; the day before the study referred to by Čech *et al.* (2005)] and on 29–30 June 1997 (period 1000–1700 hours) in the case of Orlík Reservoir. Both reservoirs were scanned acoustically along the whole longitudinal profile from the dam to the inflow. Surface temperature was measured continuously using a calibrated YSI 556 MPS (Slapy) and WTW OXI 196 (Orlík) probe.

The investigation was carried out using a SIMRAD EY500 split-beam scientific echosounder, working with a frequency of 120 KHz. The pulse repetition rate was 10 pings s^{-1}, the pulse duration was 0·1 ms (frequency bandwidth 12 KHz). The circular transducer (SIMRAD ES120-7G) with a nominal beam angle of 7·1° was used in the case of Slapy Reservoir, the elliptical transducer (SIMRAD ES120-4) with nominal beam angles of 9·1 × 4·3° was used in the case of Orlík Reservoir. The transducer, beaming vertically, was held by a remotely controlled aluminium plate on the frame construction in front of the Ota Oliva (Slapy) and Dory 13 (Orlík) research vessel. Acoustic data were stored on the hard disk of a notebook computer for later analysis. The whole sonar system was calibrated with a standard calibration copper sphere of 23 mm diameter (Foote *et al.*, 1987). To detect all young-of-year (YOY) fishes, including the smallest fish larvae, the threshold for the primary noise filtering of the acoustic record during fieldwork was set to a minimal target strength (TS; Simmonds & MacLennan, 2005) of –80 dB in the case of Slapy Reservoir (Čech *et al.*, 2005) and of −70 dB for Orlík Reservoir (Čech & Kubečka, 2006).

The acoustic data were analysed using the automatic tracking facilities of the post-processing software, Sonar5, developed at the University of Oslo (Balk & Lindem, 2005). The water column was divided into 1 m thick layers down to a depth of 16 m (Slapy) and 28 m (Orlík) below the water surface. Below these depths, no fry were observed. The uppermost 2 m (Slapy) and 4 m (Orlík) of the water column were not accessible to acoustic analysis due to the near field of the transducer (0·97 m for the circular transducer; 3·75 m for the elliptical transducer), possible avoidance of fry in front of the vessel and the low sampling volume at closer ranges. For each of the other 14 (Slapy) and 24 (Orlík) 1 m-thick layers, the abundance of fry was then calculated separately for each 1 km long transect (river km) of the reservoir. This was done in a classical way using echointegration, and by scaling the echointegrated energy with the average backscattering cross-section σ_{bs} (Simmonds & MacLennan, 2005). The backscattering cross-section came from the analysis of a single target population, and its quality was further improved by tracking (almost 16 000 fish fry tracked in the case of Slapy Reservoir and >20 000 in Orlík Reservoir; Table I). The area backscattering coefficient s_a for the layers 2–16 m (Slapy) and 4–28 m (Orlík) was used as a measure of the water column acoustic biomass, while the volume backscattering coefficients s_v were used to characterize acoustic biomass in individual layers (MacLennan *et al.*, 2002). Following Čech & Kubečka (2006), the BPF layer was defined as all the consecutive 1 m thick layers where s_v exceeds 5% of s_a and the depth of the main layer was defined as the 1 m thick layer of the water column with the highest s_v.

For an indication of aggregating behaviour (the aggregation index I_A), the proportion of the acoustic biomass of multiple (overlapping, shoaling) targets in the total s_a was calculated according to Čech & Kubečka (2006) as follows: $I_A = 100(s_a - s_{a\ \mathrm{single}})s_a^{-1}$, where $s_{a\ \mathrm{single}}$ is the area backscattering coefficient of single targets in a particular transect. An I_A of 100% means that no single targets were present. All sizing of acoustically

TABLE I. Tracking variables for Slapy and Orlík Reservoir: minimum track length, minimal number of detections to track a fish (hits in beam); maximum ping gap, maximal number of missing pings per track; gating range, maximal range between detections; minimum and maximum TS threshold, minimal and maximal threshold in between which bathypelagic perch fry (BPF) were assumed according to previous studies (see below). Total length (mm) of BPF in parenthesis calculated using TS to L_T conversion according to Frouzová & Kubečka (2004)

	Slapy Reservoir (28 May 2002)	Orlík Reservoir (29–30 June 1997)
Layer (m)	2–16	4–28
Minimum track length (ping)	2	2
Maximum ping gap (ping)	0	0
Gating range (m)	0·07	0·07
Minimum TS threshold (dB)	−70 (6·2 mm)[†]	−65 (10·7 mm)[‡]
Maximum TS threshold (dB)	−57 (26·0 mm)[†]	−50 (56·4 mm)[‡]
Number of tracked YOY fish	15 988	20 126

[†] Direct ichthyoplankton catches of larvae and juvenile perch during 29–30 May 2002 from Slapy Reservoir (Čech *et al.*, 2005).

[‡] Direct ichthyoplankton catches of larvae and juvenile perch in June from Římov (Matěna, 1995; Macháček & Matěna, 1997; Wanzenböck *et al.*, 1997), Slapy (Čech *et al.*, 2005) and Orlík Reservoir (Čech *et al.*, in press).

detected fry and setting of the size limits was done using the perch fry TS to total length, L_T, relationship for their dorsal aspect (Frouzová & Kubečka, 2004).

In May, the L_T, of perch larvae and juveniles caught in the pelagic zone of Slapy Reservoir ranged from 8·3 to 23·6 mm (Čech *et al.*, 2005). For the post-processing procedure, the TS threshold was set at −70 dB (6·2 mm L_T), to avoid acoustic underestimation of perch fry abundance caused by inclination of fish larvae while maintaining constant depth (Frank, 1967; Ross *et al.*, 1977), or tilting of the fish body during diel vertical migrations and ascent and descent in the water column (Čech & Kubečka, 2002; Čech *et al.*, 2005). To exclude infrequently occurring larger fish, targets > −57 dB (26·0 mm L_T) were manually erased from the analysis, using the erase function of Sonar5 (Balk & Lindem, 2005).

In Orlík Reservoir, the noise threshold was set at −65 dB (*i.e.* 10·7 mm L_T) to detect all BPF, which could be expected at a particular time, considering previous results of direct ichthyoplankton catches of larvae and juvenile perch in June from various Czech reservoirs of similar trophic status (Matěna, 1995; Macháček & Matěna, 1997; Wanzenböck *et al.*, 1997; Čech *et al.*, 2005, 2007). The same references were used for setting the maximum TS threshold (−50 dB, *i.e.* 56·4 mm L_T) in order to exclude infrequently occurring larger fish (Table I). Targets larger than the maximum TS threshold were again manually erased from the analysis. The remaining configuration of the automatic tracking facility is given in Table I. The data were analysed using linear regression.

RESULTS

SLAPY RESERVOIR

During the late May sampling in Slapy Reservoir, the BPF layer was recorded from the dam (river km 92) for 29 km upstream to the locality Zvírotice

(r. km 121) and then it completely vanished from the water column [it was absent from the remaining 13 km of the reservoir up to the inflow; Fig. 2(a)]. The layer was composed of a more or less dense mass of perch larvae and juveniles with no apparent shoaling activity. Over 4 m thick, the BPF layer, staying predominantly in the depths between 8 and 13 m, was relatively compact along most of its longitudinal profile, except for the two most upstream transects where it apparently disintegrated [Fig. 2(b)]. The abundance of BPF increased significantly from the dam to Zvírotice (regression analysis, $r^2 = 0{\cdot}53$, $F_{1,28}$, $P < 0{\cdot}001$; Fig. 3) being, on average, almost 31 000 individuals ha^{-1}. Although the average L_T of BPF showed the same trend and increased upstream (from 8·8 to 12·5 mm; regression analysis, $r^2 = 0{\cdot}86$, $F_{1,22}$, $P < 0{\cdot}001$; Fig. 4), in the last six transects (r. km 116–121) there was an apparent overall decline in fish size and average L_T then decreased sharply to Zvírotice (from 11·2 to 9·1 mm; $r^2 = 0{\cdot}97$, $F_{1,4}$, $P < 0{\cdot}001$; Fig. 4). Other variables describing the BPF layer in Slapy Reservoir in late May 2002 are given in Table II.

ORLÍK RESERVOIR

During the late June sampling in Orlík Reservoir, the BPF layer was recorded from the dam (r. km 145) for 52 km upstream [Fig. 5(a)]. The layer only vanished in a very short reach from river km 197 to the inflow. Shoals predominated in the BPF layer along most of its longitudinal profile. The

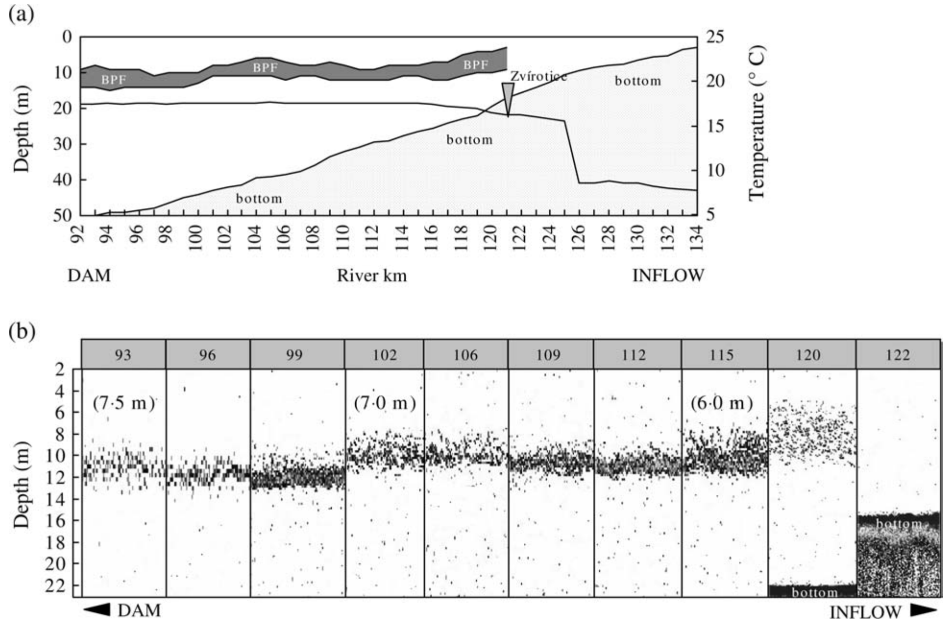

FIG. 2. (a) The shape and thickness of the bathypelagic perch fry layer and its position in the water column along the longitudinal profile of Slapy Reservoir in late May 2002. Surface temperature (——) was continuously measured during acoustic sampling. (b) Sequence of raw 20 LogR TVG echograms (Simmonds & MacLennan, 2005) illustrating the nature of the BPF layer in individual transects along the longitudinal profile of Slapy Reservoir in late May 2002. Numbers indicate river km (for location see Fig. 1). Numbers in parenthesis show water transparency (depth of Secchi disc).

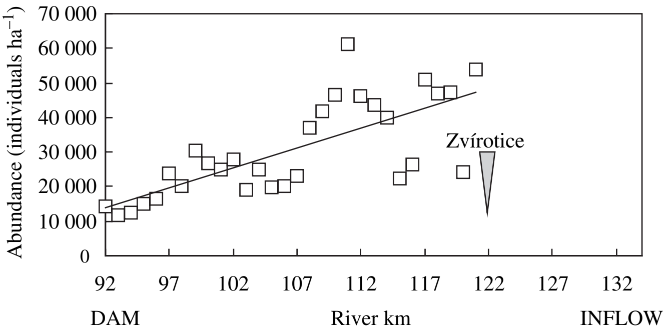

FIG. 3. Abundance of bathypelagic perch fry (BPF) in individual transects (1 km each) along the longitudinal profile of Slapy Reservoir in late May 2002. From Zvírotice (r. km 121) upstream no BPF layer was recorded. The curve was fitted by $y = 1140x - 90\ 780$.

whole layer apparently rose in the water column from the dam (where it was at depths between 16 and 21 m) towards the inflow (where it was at depths between 4 and 5 m), presumably following the decreasing water transparency [Fig. 5(b)]. The abundance of BPF revealed obvious patchiness without any clear trend, being on average over 26 000 individuals ha^{-1} (Fig. 6). Average L_T of BPF, however, increased dramatically from the dam to the inflow (from 24·6 to 44·0 mm; regression analysis, $r^2 = 0{\cdot}89$, $F_{1,51}$, $P < 0{\cdot}001$; Fig. 7). Similarly, with increasing size of the fish, shoaling activity also increased significantly toward the inflow (regression analysis, $r^2 = 0{\cdot}48$, $F_{1,51}$, $P < 0{\cdot}001$; Fig. 8). In agreement with this, the thickness of the BPF layer decreased notably toward the inflow (regression analysis, $y = -0{\cdot}08x + 5{\cdot}70$, $r^2 = 0{\cdot}61$, $F_{1,51}$, $P < 0{\cdot}001$), which fact, however, could be partly biased by the limited water depth in the uppermost, riverine part of the reservoir [Fig. 5(a), (b)]. Other variables describing the BPF layer in Orlík Reservoir in late June 1997 are given in Table II.

In both reservoirs, the I_A calculated for the whole BPF layer [tendency to flock in a dense layer in case of Slapy, *cf.* Fig. 2(b); ability to create distinct shoals in case of Orlík, *cf.* Fig. 5(b)] increased significantly with increasing size of fish (regression analysis, $r^2 = 0{\cdot}32$, $F_{1,81}$, $P < 0{\cdot}001$; Fig. 9).

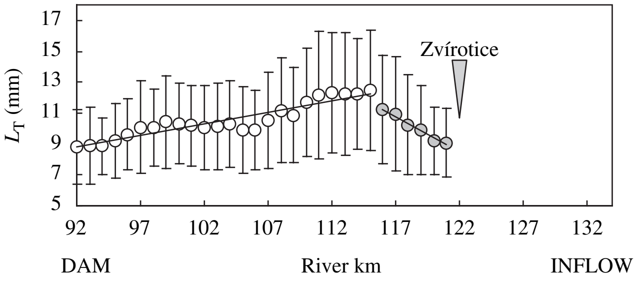

FIG. 4. Mean ± S.D. total length of bathypelagic perch fry (BPF) in individual transects (1 km each) along the longitudinal profile of Slapy Reservoir in late May 2002. From Zvírotice (r. km 121) upstream no BPF layer was recorded. The curves were fitted by $y = 0{\cdot}15x - 5{\cdot}06$ (○) and $y = -0{\cdot}46x + 64{\cdot}74$ (●).

TABLE II. Mean, S.D., maximal and minimal values for individual variables describing bathypelagic perch fry (BPF) layer in Slapy Reservoir in late May 2002 (30 transects 1 km each) and Orlík Reservoir in late June 1997 (53 transects 1 km each)

		Slapy Reservoir	Orlík Reservoir
Average depth of main layer (m)	Mean	10·2	10·1
	Maximum	12·5	18·5
	Minimum	6·5	4·5
	S.D.	1·5	3·5
s_v of main layer (m^2 m^{-3})	Mean	5·6E-07	6·2E-06
	Maximum	5·7E-06	2·7E-05
	Minimum	7·4E-08	1·3E-07
	S.D.	1·0E-06	6·0E-06
Abundance of main layer (individuals m^{-3})	Mean	1·1	1·9
	Maximum	2·6	8·1
	Minimum	0·4	0·1
	S.D.	0·6	1·7
Per cent of multiple targets in the whole BPF layer (aggregation index)	Mean	47·4	66·5
	Maximum	84·8	96·6
	Minimum	1·6	6·6
	S.D.	23·7	21·7
Thickness of whole BPF layer (m)	Mean	4·4	3·5
	Maximum	6	7
	Minimum	3	1
	S.D.	1·2	1·6
BPF abundance (individuals ha^{-1})	Mean	30 626	26 054
	Maximum	61 123	89 111
	Minimum	11 699	2197
	S.D.	13 794	18 610

DISCUSSION

As in the case of Římov Reservoir (Čech & Kubečka, 2006), in this study also the BPF layer was recorded during both sampling surveys. While in Orlík Reservoir the layer was present along nearly the whole longitudinal profile of the reservoir [except in the uppermost 3 km reach where, according to Straškraba (1998), the flow obviously prevents full development of the pelagic community], in Slapy Reservoir the layer was absent from the whole upper third of the reservoir. The reason for this was that the hypolimnetic water discharged from Orlík Reservoir (situated upstream) was of extremely low temperature [7·7–8·5° C; Fig. 2(a)]. This temperature represents the usual lower limit for initiation of perch spawning (Frank, 1967; Craig, 1974; Prokeš, 1985; Treasurer, 1988; Sandström *et al.*, 1997) and for that reason also prevents the eventual invasion of the existing fry community in Slapy Reservoir by perch originating in Orlík Reservoir.

An interesting phenomenon, recorded in both reservoirs, was the gradual increase in the L_T of BPF toward the inflow. The main reason for this seems

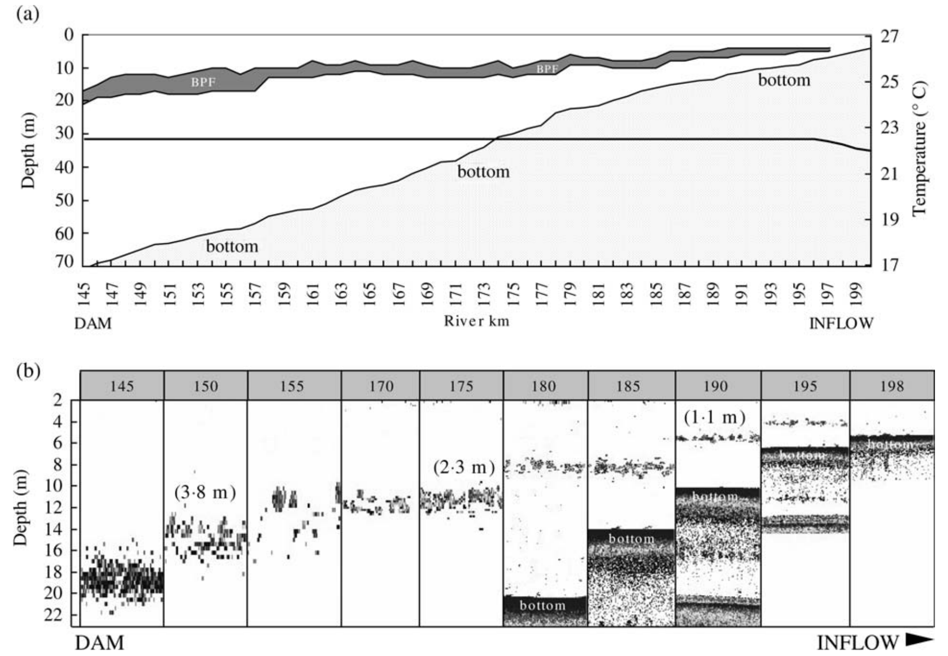

FIG. 5. (a) The shape and thickness of the bathypelagic perch fry (BPF) layer and its position in the water column along the longitudinal profile of Orlík Reservoir in late June 1997. Surface temperature (——) was continuously measured during acoustic sampling. (b) Sequence of raw 20 LogR TVG echograms illustrating the nature of the BPF layer in individual transects along the longitudinal profile of Orlík Reservoir in late June 1997. Numbers indicate river km (for location see Fig. 1). Numbers in parenthesis show water transparency (depth of Secchi disc). Clear descent of the BPF layer at r. km 145 was due to a 'deepening of epilimnion' a result of discharging of hypolimnetic water by a lower dam outlet situated at a depth *c*. 48 m.

to be strong oligotrophication along the longitudinal profile of these large canyon-shaped reservoirs ('eutrophic' at the inflow *v*. 'oligotrophic' at the dam) documented for Slapy reservoir by Hrbáček *et al.* (1966) and Procházková *et al.* (1973) and for Orlík Reservoir by Hejzlar & Vyhnálek (1998). The same trophic gradient was recorded for Římov Reservoir (Hejzlar & Vyhnálek, 1998) and similarly, in this reservoir larger perch individuals were caught in the fry trawl in its riverine part compared to near the dam (Vašek *et al.*, 2006). In contrast, in the littoral zone of Římov Reservoir the trend was completely opposite, with larger perch fry individuals occurring near the dam and smaller ones close to the inflow (Vašek *et al.*, 2006). The reason for such an interesting pattern is competition for food generated by both juvenile and adult fishes of various species, which in the littoral zone dramatically increased towards the inflow. This trend, implying higher zooplankton densities in upstream parts of the reservoir (*i.e.* following the trophic gradient) is, however, less apparent in the pelagic zone (Vašek *et al.*, 2004, 2006).

In Slapy Reservoir, in the case of the last six transects of the BPF layer (r. km 116–121; Fig. 4), there was an apparent overall decline in fish size, resulting most probably from later spawning and therefore a later hatching

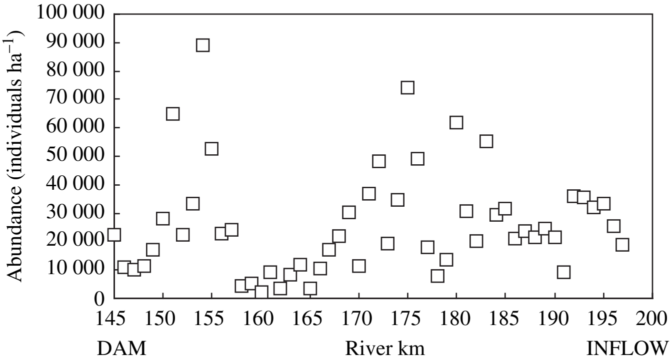

FIG. 6. Abundance of bathypelagic perch fry (BPF) in individual transects (1 km each) along the longitudinal profile of Orlík Reservoir in late June 1997. From r. km 197 upstream no BPF layer was recorded.

period. In Slapy Reservoir, surface water warming progresses from the lower, lacustrine part towards the inflow, *i.e.* it propagates against the cold hypolimnetic water discharged from Orlík Reservoir (Straškraba *et al.*, 1973), which particularly influences the timing of egg strand deposition and was most probably responsible for the smaller size of BPF in most upstream transects. The cold water inflow may also have an effect on zooplankton development (Romare *et al.*, 2005) and thus on food available for the perch fry. The same artificial effect of cold hypolimnetic water on perch reproduction and early life history in general could not be seen in Orlík Reservoir, which is filled with relatively warm, homogeneous water from the small Kořensko Reservoir (theoretical retention time <0·5 day) situated upstream, and fed directly with water from two rivers (Otava River and Lužnice River, the Kořensko Reservoir's major side tributary entering the reservoir close to the dam). Kořensko Reservoir itself is again filled with relatively warm water from the medium-sized Hněvkovice Reservoir situated upstream (the first reservoir in the functional system of the Vltava River cascade reservoirs, poorly stratified, with a theoretical retention time of <10 days) [*cf.* Fig. 1(c)].

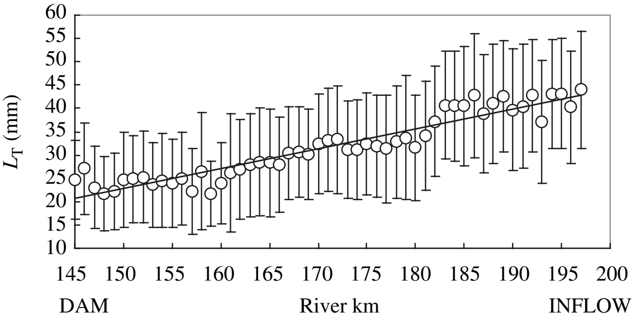

FIG. 7. Mean ± S.D. total length of bathypelagic perch fry (BPF) in individual transects (1 km each) along the longitudinal profile of Orlík Reservoir in late June 1997. From r. km 197 upstream no BPF layer was recorded. The curve was fitted by $y = 0{\cdot}43x - 40{\cdot}97$.

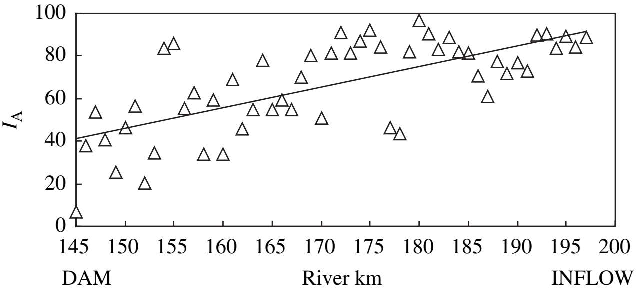

FIG. 8. Aggregation index (I_A) indicating the extent of shoaling of bathypelagic perch fry (BPF) in individual transects (1 km each) along the longitudinal profile of Orlík Reservoir in late June 1997. From r. km 197 upstream no BPF layer was recorded. The curve was fitted by $y = 0{\cdot}97x - 99{\cdot}18$.

Another interesting phenomenon was the increase in abundance of BPF towards the inflow, which was clearly apparent in the case of Slapy Reservoir, where, according to fish size (Čech *et al.*, 2005), the BPF community was monitored closely after hatching and ensuing migration from littoral to the open water, however, much less apparent in the case of Orlík Reservoir, where the BPF community was monitored much later after hatching. Such an increase of fry abundance towards the inflow was also recorded in Římov Reservoir (Vašek *et al.*, 2006). Most probably this increase could be simply explained by the ratio between the area of littoral zone (perch spawning and hatching habitat) and the area of the pelagic zone (perch fry nursery habitat), which, due to the shape of Slapy Reservoir, increased upstream (J. Hejzlar, unpubl. data). In contrast, in Orlík Reservoir, the pattern of BPF abundance is not easy to interpret. The above mentioned effect of reservoir morphology could be masked in Orlík by: (1) less appropriate conditions for perch spawning due to the steep rocky banks in several sections of the reservoir (the most likely reason for the observed patchiness), (2) a gradual shift of perch fry from the

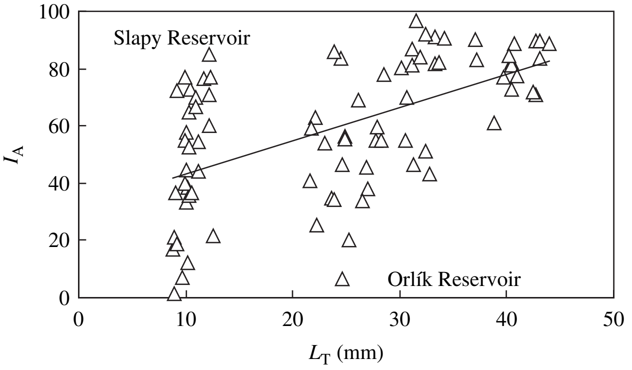

FIG. 9. The relationship between average total length of bathypelagic perch fry (BPF) in individual transects (1 km each) and the aggregation index (I_A) calculated for the whole BPF layer. This relationship was highly significant for both the separate, late May (Slapy) and late June (Orlík) data, as well as for the pooled data (reservoirs in the cascade). The curve was fitted by $y = 1{\cdot}15x + 31{\cdot}82$.

pelagic zone into the littoral area (Coles, 1981; Treasurer, 1988; Wang & Eckmann, 1994), (3) a shift of part of the BPF community from the bathypelagic to an epipelagic habitat induced by the decline of zooplankton below the thermocline (M. Kratochvíl & J. Peterka, unpubl. data) or (4) various types of mortality (Craig, 1987; Kubečka, 1991; Sandström *et al.*, 1997). Although it is unlikely that this exception from the general trend was caused by flood (Čech *et al.*, in press), the gradual drift of the BPF community further downstream could not be excluded.

In agreement with previous studies (Čech *et al.*, 2005; Čech & Kubečka, 2006) there was no shoaling activity of the BPF (average L_T 10·4 mm) observed during the late May sampling in Slapy Reservoir, however, a strong tendency for BPF (average L_T 31·8 mm) to create shoals was recorded during the late June sampling in Orlík Reservoir. This is consistent with the ontogenetic threshold connected with development of the lateral line system (Cahn *et al.*, 1968), which in perch represents a length of *c.* 14 mm (Disler & Smirnov, 1977) leading presumably to better orientation in space and easier communication with conspecifics. A completely new finding is that the tendency to flock in a dense layer, and later to create distinct shoals, continuously increased with size of BPF.

Undoubtedly, aggregating or shoaling behaviour is well developed in perch. Whether this behaviour, especially in the case of BPF, however, really serves as a protection against predators, mainly inter-cohort cannibals (Wang & Eckmann, 1994) or whether, as suggested by Čech & Kubečka (2006), it is a result of a social need (shoaling serves to reduce social deprivation and so the energetic budget of individual fish) still remained unclear. Up to now, the only evidence there is (Čech *et al.*, 2005) that BPF shoals form well after sunrise and break up well before sunset.

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