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Impact of flood on distribution of bathypelagic perch fry layer along the longitudinal profile of large canyon-shaped reservoir

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Previous studies have shown that under normal spring conditions, the layer of bathypelagic perch *Perca fluviatilis* fry (BPF) is equally distributed along most of the longitudinal profile of reservoirs. In the first half of June 2004, local flooding entering the large canyon-shaped Orlík Reservoir (Czech Republic) completely flushed out the existing fry community from the 31 km long riverine part of the reservoir. The pelagic zone in this reach was then recolonized by cyprinid (mainly roach *Rutilus rutilus* and bream *Abramis brama*) fry being of either littoral or riverine origin. Subsequently, the BPF layer was recorded only in the 22 km long lacustrine part of the reservoir. In the upper reach of this part where, due to the sudden increase in volume, the water current slowed down rapidly and fry originating from both riverine and central parts of the reservoir gathered in high numbers, two distinct BPF layers were observed. During mid-day, the upper BPF layer, created predominantly by shoaling fishes (abundance >126 000 individuals ha^{-1}), occurred between 6 and 10 m. A second, lower BPF layer, created by non-shoaling fishes exclusively (30 000 individuals ha^{-1}), was recorded between 12 and 17 m depth. Both upper and lower BPF layer were composed of perch (69·6 and 66·8% in abundance respectively) and zander *Sander lucioperca* (29·8 and 28·6% in abundance respectively). In the lower BPF layer, ruffe *Gymnocephalus cernuus* also contributed considerably to the fry assemblage (4·0% in abundance). Perch from the upper BPF layer (mean 25·1 mm total length, L_T) did not differ in size from perch from the lower BPF layer (mean 25·0 mm L_T). Similarly, zander from the upper BPF layer (mean 27·2 mm L_T) were almost the same size as those from the lower BPF layer (mean 26·9 mm L_T). Perch from both BPF layers, however, were noticeably smaller than zander. The results from acoustic survey and complementary net catches suggest that no epipelagic perch fry were found in the reservoir where thermal stratification had been destroyed by flooding and windy weather.

Key words: cyprinids; echosounder; Orlík Reservoir; *Perca fluviatilis*; *Sander lucioperca*; shoaling.

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INTRODUCTION

Early in their life history, young perch *Perca fluviatilis* L. and yellow perch *Perca flavescens* (Mitchill) undertake an obligate migration from their near-shore hatching sites into the pelagic area (Guma'a, 1978; Coles, 1981; Whiteside *et al.*, 1985; Craig, 1987; Post & McQueen, 1988; Treasurer, 1988; Wang & Eckmann, 1994; Urho, 1996). During the pelagic stage of life, two perch fry abundance maxima have been observed in water column. In addition to the surface-confined or epipelagic perch fry (EPF) reported by many authors (Coles, 1981; Whiteside *et al.*, 1985; Post & McQueen, 1988; Treasurer, 1988; Wang & Eckmann, 1994; Matěna, 1995; Urho, 1996; Wanzenböck *et al.*, 1997) at least in some deep stratified reservoirs, a deep water or bathypelagic perch fry (BPF) were also recorded (Kubečka & Slad, 1990; Čech *et al.*, 2005, 2007; Čech & Kubečka, 2006). There is recent evidence that the BPF may be similarly present also in deep stratified lakes (Guillard *et al.*, 2004; R. Eckmann & N. Probst, pers. data). The EPF seem to remain pelagic until fin development, the timing of which varies with temperature from June to mid-July, and then move inshore to the littoral area (Guma'a, 1978; Coles, 1981). On the other hand, the BPF remain in deep open water up to autumn (Čech & Kubečka, 2006).

The BPF community is present as a several metres thick scattering layer, which can be followed by an echosounder (Čech *et al.*, 2005). In normal conditions, the BPF layer is distributed equally along most of the longitudinal profile of both large and small canyon-shaped reservoirs (Čech & Kubečka, 2006; Čech *et al.*, 2007). It has been suggested from preliminary data (Čech & Kubečka, 2006), however, that flooding is one of the factors that could have a significant structuring effect on the distribution of the BPF layer in such an artificial water body.

The present study was focused on the distribution of the BPF layer within the large canyon-shaped Orlík Reservoir (area of 2733 ha, length of main stream 55 km, volume of 717×10^6 m^3, maximum depth of 72 m; Straškraba *et al.*, 1973), which was hit by local spring flood. The effect of this unique, large-scale, natural intervention on the reservoir's existing fry community was investigated in detail.

MATERIALS AND METHODS

Acoustic and complementary net data were collected using SIMRAD EY 500 split-beam echosounder, SIMRAD ES120-7G transducer and conical ichthyoplankton net in three 14 h sampling surveys (daytime, 0600–2000 hours) during 15–17 June 2004 as described by Čech *et al.* (2005). Sampling took place at five sites along the longitudinal profile of Orlík Reservoir representing (A) the riverine part of the reservoir, (B) the part above the confluence with the reservoir's major side tributary, the Otava River, (C) the part below this confluence and (E) the lacustrine part of the reservoir. Sampling at a fifth site (D), close to the Žd'ákovský Bridge was instigated following a unique record of two bathypelagic layers of perch fry (Fig. 1). Besides simultaneous acoustic and net sampling, the whole reservoir (the Vltava River arm up to the tributary, the Otava River arm up to the tributary and the lacustrine part from the confluence down to the dam) was scanned acoustically. To detect all young-of-the-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 −70 dB (Čech *et al.*, 2005; Čech & Kubečka, 2006).

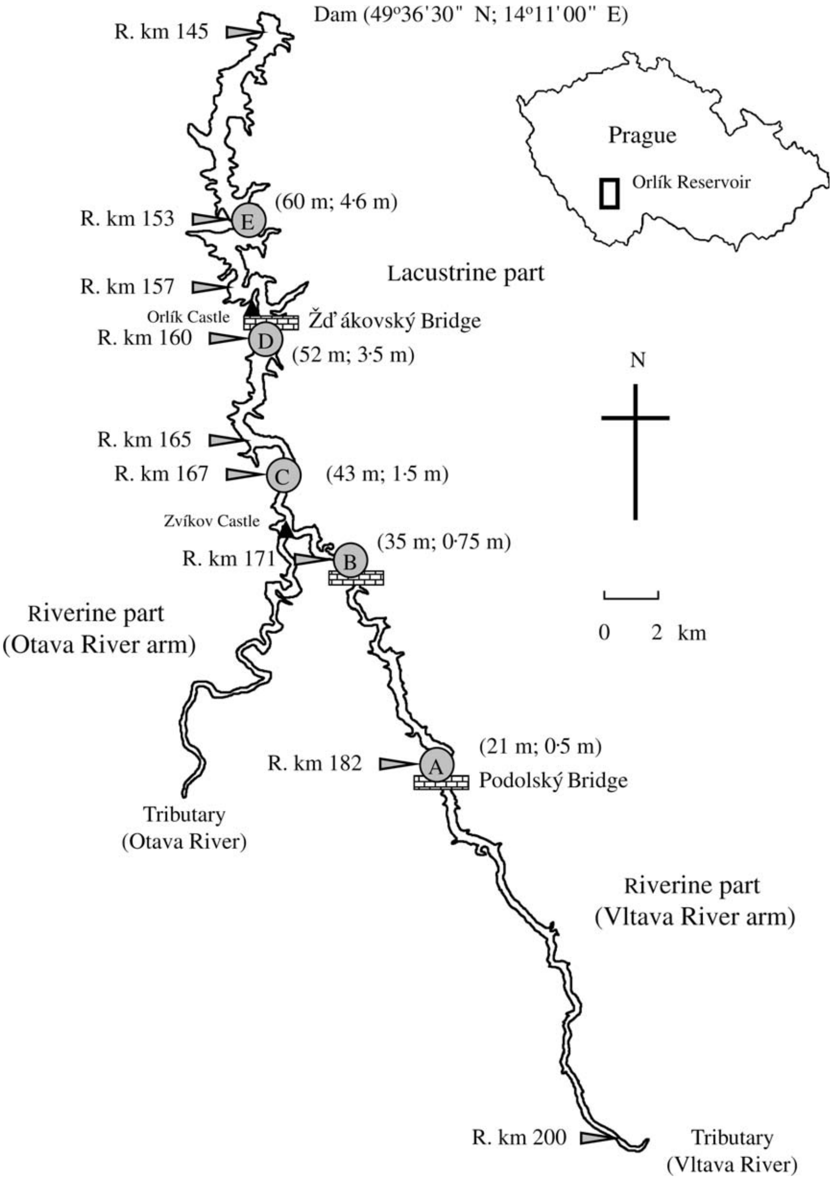

FIG. 1. A map of Orlík Reservoir and its location in the Czech Republic. The relative position of sites where ichthyoplankton samples were taken and stratification variables (temperature and dissolved oxygen) were measured is shown. A, Podolský Bridge (riverine part of the reservoir); B, above the confluence with the Otava River; C, below the confluence; D, Žd'ákovský Bridge; E, main lacustrine part of the reservoir. Maximum depths (first number) and current transparency (depth of Secchi disc) are given in parentheses for each sampling site. R. km, river km, *i.e.* distance from the mouth of the Vltava River into the Elbe River.

The acoustic data were analysed in detail using the automatic tracking facilities of the post-processing software, Sonar5, developed at the University of Oslo (Balk & Lindem, 2005) by the method of Čech *et al.* (2005, 2007). Samples obtained from ichthyoplankton catches (32 hauls, 30 300 m^3 of water filtered, 15 844 YOY fishes caught) were preserved immediately in the field using 6–10% formaldehyde. All fish larvae and juveniles were determined to species according to the keys of Koblickaya (1981), measured (total length, L_T) and grouped into 1 mm L_T classes. Although perch fry predominated in both recorded BPF layers, direct sampling revealed, that unlike the community in Slapy Reservoir (Čech *et al.*, 2005), the community in Orlík Reservoir also contained a considerable proportion of zander *Sander lucioperca* (L.). Thus for Orlík Reservoir, the BPF layer should more accurately be taken to mean the bathypelagic percid fry layer.

During the sampling period in mid-June, perch and zander fry caught in the pelagic zone of Orlík Reservoir ranged from 14 to 39 mm L_T. For the post-processing procedure, the TS threshold was set at −64 dB [12·0 mm L_T; length calculated from TS according to the equation of Frouzová & Kubečka (2004) for the dorsal aspect of perch fry], to avoid acoustic under-estimation of perch fry abundance caused by inclination of fish fry 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 fishes, targets >−53 dB (40·5 mm L_T) were manually erased from the analysis, using the erase function of Sonar5 (Balk & Lindem, 2005). Higher quality of acoustic recordings compared to those gathered in previous studies (Čech *et al.*, 2005; Čech & Kubečka, 2006) made it possible to tighten up other configurations of the automatic tracking facilities as follows: the minimal number of detections to track a fish (minimum track length, *i.e.* hits in beam) was set to four and both the maximal number of missing pings per track (maximum ping gap) and maximal range between detections (gating range) were set to 0. As a result, acoustic noise could be further eliminated and estimates of L_T frequency distribution and of fry abundance were improved. Despite of this, >70 000 fish fry were tracked.

The data were analysed using linear regression and *t*-tests. Where necessary, ANOVA for unequal *n* was used instead of the *t*-test.

RESULTS

During the first half of June 2004 Orlík Reservoir was ‘hit’ by a local flood [Fig. 2(a)], which completely flushed the old reservoir water out of the 31 km long riverine part of the reservoir (the Vltava River arm) [Fig. 2(b), (c)]. Strong winds and the passage of floodwater, moreover, destratified the water column along most of the longitudinal profile of the entire reservoir.

Following the flood, the pelagic fry assemblage of the riverine part of the reservoir (the Vltava River arm) was strongly dominated by cyprinids (132 individuals 1000 m^{-3}, 95·9% in abundance; Fig. 3). Fishes were equally present throughout the upper 4 m of the water column, in turbid floodwater of very low transparency. No BPF layer was recorded. A similar situation was observed above the confluence with the Otava River. Cyprinids [mainly roach *Rutilus rutilus* (L.) and bream *Abramis brama* (L.)] were again highly dominant in the pelagic fry assemblage (98 individuals 1000 m^{-3}, 82·4% in abundance; Fig. 3). Probably due to a slightly improved transparency, most fishes were caught deeper in water column, between 4 and 6 m below the water surface while surface layers were only sporadically occupied. No BPF layer was recorded and acoustic scanning of the whole of the Otava River arm of Orlík Reservoir gave the same result.

In contrast, percids were unambiguously dominant in the pelagic fry assemblage of the lacustrine part of the reservoir (94·6–100% in abundance; Fig. 3).

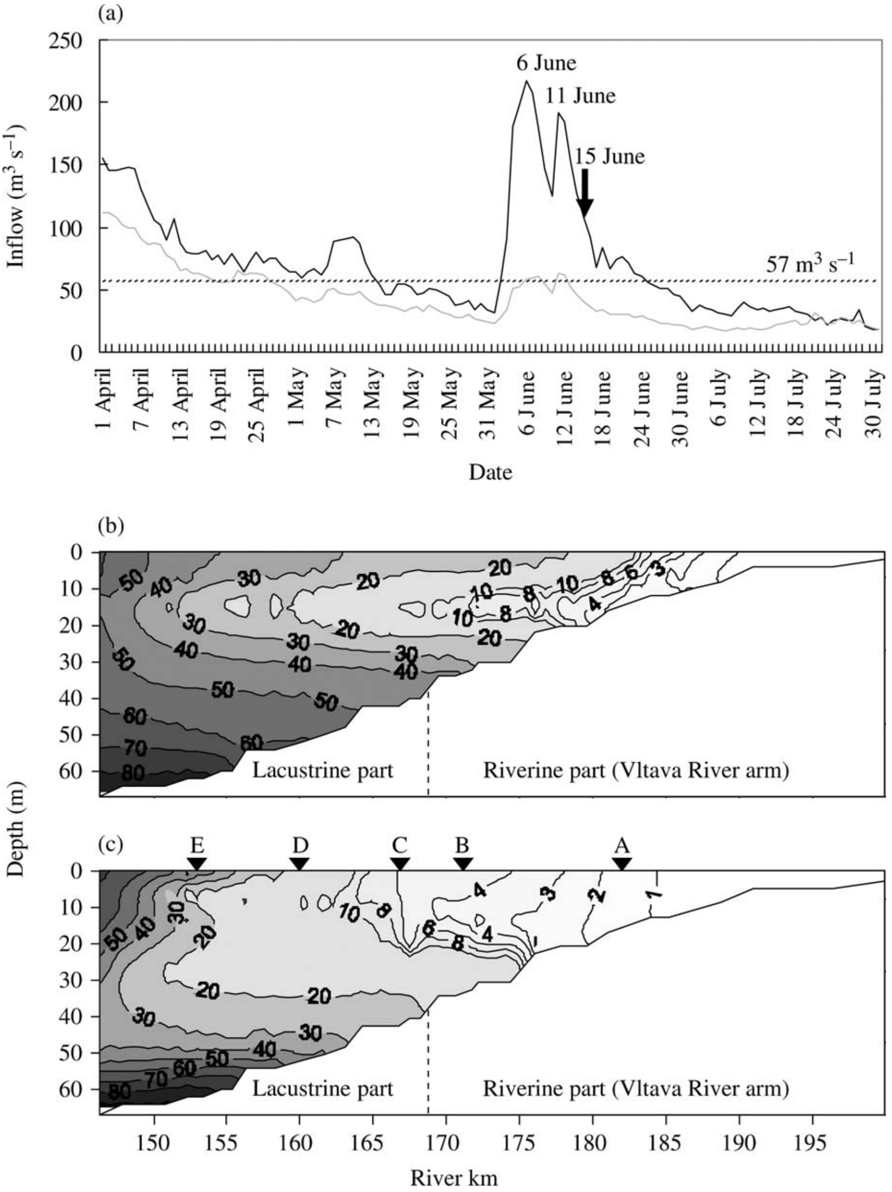

FIG. 2. Course of local flood entering the upper part of Orlík Reservoir (the Vltava River arm) during the first half of June 2004. (a) Comparison of mean daily inflow in spring and early summer 2004 (——), mean daily inflow calculated for the same period from years 2000–2004 (▬) and mean annual inflow (----) into the Vltava River arm of Orlík Reservoir. High inflow values in early April are due to ice melting (Czech Hydrometeorological Institute, unpubl. data). Arrow indicates the first day of acoustic and ichthyoplankton sampling. (b) Age of water (days) on the cross-section of the whole Orlík Reservoir immediately before the flood (1 June, 1200 hours). (c) Age of water on the cross-section of the whole Orlík Reservoir during the first day of sampling (15 June, 1200 hours). Age of water was simulated by the two-dimensional mathematical model CE-QUAL-W2 (Cole & Wells, 2003). Points A–E indicate position of sampling sites (see Fig. 1). Dotted line shows the confluence with the Otava River.

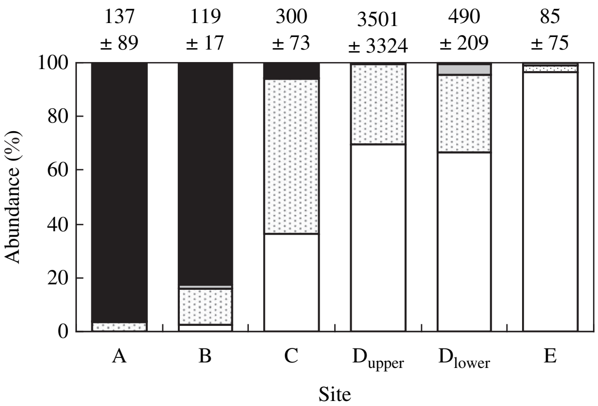

FIG. 3. Composition of the fry assemblage [cyprinids (■), ruffe (▨), zander (░) and perch (□)] in the pelagic zone of Orlík Reservoir in mid-June 2004 during daytime (0600–2000 hours; Čech *et al.*, 2005) estimated with the ichthyoplankton net. Numbers above each column show pelagic fry mean ± S.D. individuals 1000 m^{-3}). A, Podolský bridge (riverine part of the reservoir); B, above the confluence with the Otava River; C, below the confluence; D_{upper}, Žd'ákovský Bridge, upper bathypelagic perch fry (BPF) layer (7–9 m below the water surface exclusively); D_{lower}, Žd'ákovský Bridge, lower BPF layer (13–15 m below the water surface exclusively); E, main lacustrine part of the reservoir.

Although no clear pattern was recognized for zander and ruffe *Gymnocephalus cernuus* (L.), the contribution of perch to the pelagic fry assemblage dramatically increased along the longitudinal profile of the reservoir (Fig. 3) (regression analysis: $y = 25{\cdot}89x - 36{\cdot}72$, $r^2 = 0{\cdot}97$, $F_{1,3}$, $P < 0{\cdot}01$) from only 0·2% in the riverine part to 36·4% below the confluence and reaching 96·4% in the main lacustrine part of the reservoir.

Two interesting phenomena were observed in connection with the apparent shift from cyprinid to percid fry community in the lacustrine part of Orlík Reservoir. Firstly, fish fry completely vanished from the upper 4 m of the water column. Secondly, the BPF layer was recorded below the confluence with the Otava River for the first time (Fig. 4). This layer of predominantly shoaling fry was then observed continuously in the remaining 22 km of the lacustrine part of the reservoir. Further downstream, below the confluence, the acoustic record of the BPF layer was complemented by a sparse second layer of fry, in the water column well below the dense upper layer. This layer, which changed very soon into the regular second BPF layer of non-shoaling fry, was well developed within 8 km reach of the lacustrine part of Orlík Reservoir around sampling site D (Žd'ákovský Bridge), but vanished in the vicinity of the dam (Fig. 4). Both layers were evenly spread across the whole transverse profile of the reservoir, with a separating depth of *c.* 2 m between them.

During mid-day (1000–1400 hours; Čech *et al.*, 2005), the upper BPF layer was between 6 and 10 m, while the lower BPF layer was between 12 and 17 m below the water surface. The lower BPF layer was significantly thicker than the upper BPF layer (*t*-test, d.f. = 36, $P < 0{\cdot}001$; Table I), however, much greater abundance of fry was recorded acoustically in the upper BPF layer (mean ± S.E. 126 538 ± 14 109 individuals ha^{-1}) compared to the lower

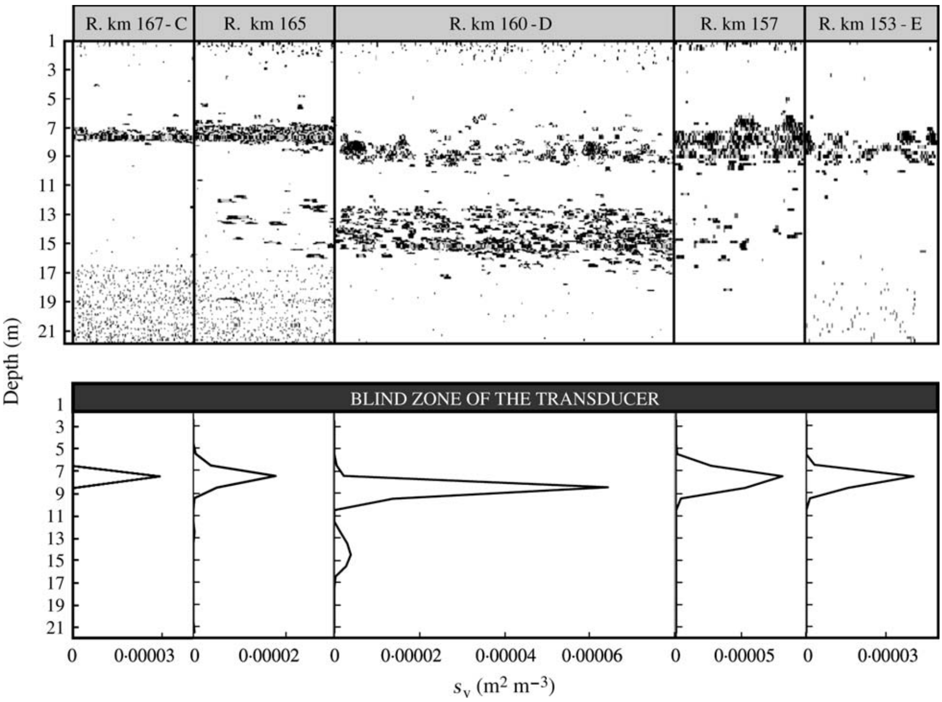

FIG. 4. Sequence of raw 20 LogR TVG echograms (Simmonds & MacLennan, 2005) and corresponding acoustic biomass diagrams illustrating presence of one bathypelagic perch fry (BPF) layer and formation of a second BPF layer along the longitudinal profile of lacustrine part of Orlík Reservoir in mid-June 2004 (time 1526, 1539, 1630, 1710, 1721 hours). The upper BPF layer created by shoaling fry individuals in particular was firstly recorded at r. km 167 (sampling site C, below the confluence with the Otava River) and was continuously present in water column for another 22 km up to the dam of the reservoir. The lower BPF layer created by non-shoaling fry individuals exclusively was well developed within an *c.* 8 km reach around the sampling site D (Žd'ákovský Bridge). It arose immediately at r. km 165 and vanished from the water column suddenly at r. km 157 (see Fig. 1).

BPF layer (mean ± S.E. 29 935 ± 1663 individuals ha^{-1}; *t*-test, d.f. = 36, $P <$ 0·001; Table I). This was confirmed by direct catches in which the abundance of fry in the upper BPF layer exceeded the abundance of fry in the lower BPF layer by more than seven times. Similarly, the abundance of fry in the main layer of the upper BPF layer (6·8 individuals m^{-3}) was significantly higher than that in the main layer of the lower BPF layer (1·0 individuals m^{-3}; *t*-test, d.f. = 36, $P <$ 0·001; Table I). Other variables describing both BPF layers are given in Table I.

Both upper and lower BPF layer were composed mainly of perch (2435 and 327 individuals 1000 m^{-3}, and 69·6 and 66·8% in abundance respectively) and zander (1043 and 140 individuals 1000 m^{-3} respectively, 29·8 and 28·6% in abundance respectively). The lower BPF layer also included a notable complement of ruffe (20 individuals 1000 m^{-3}, 4·0% in abundance; Fig. 3).

Apart from their different use of space in time, there was, surprisingly, no difference in the recorded sizes of conspecific fish in the two different layers.

TABLE I. Mean ± S.D. values for individual variables describing two bathypelagic perch fry (BPF) layers in Orlík Reservoir in mid-June 2004 (19 transects 0·4 km each from r. km 165 to r. km 157; see Fig. 1)

	Upper BPF layer	Lower BPF layer
Average depth of main layer* (m)	8·6 ± 0·8	14·3 ± 0·7
S_v of main layer ($m^2 m^{-3}$)	2·0E-05 ± 9·0E-06	3·6E-06 ± 8·3E-07
Abundance of main layer (individuals m^{-3})	6·8 ± 3·5	1·0 ± 0·2
Per cent of multiple targets in the whole BPF layer (Aggregation index†)	95·5 ± 3·5	84·5 ± 6·5
Thickness of whole BPF layer‡ (m)	3·7 ± 0·6	4·9 ± 0·6
BPF abundance (individuals ha^{-1})	126 538 ± 61 498	29 935 ± 7248

*Defined by Čech & Kubečka (2006) as the 1m thick layer of the water column with the highest s_v (for definition of s_v see MacLennan *et al.*, 2002).

†Defined by Čech & Kubečka (2006) as the proportion of the acoustic biomass of multiple (overlapping, shoaling) targets in the total s_a (for definition of s_a see MacLennan *et al.*, 2002). Aggregation index = $100(s_a - s_{a\ \mathrm{single}})s_a^{-1}$, where $s_{a\ \mathrm{single}}$ is the area backscattering coefficient of single targets in a particular transect. An aggregation index of 100% means that no single targets were present.

‡Defined by Čech & Kubečka (2006) as all the consecutive 1m thick layers where s_v exceeds 5% of s_a.

Perch from the upper BPF layer ranging from 18 to 32 mm L_T (mean ± S.D. 25·1 ± 1·7 mm) were not significantly different in size to those from the lower BPF layer ranging from 17 to 31 mm L_T (mean ± S.D. 25·0 ± 2·1 mm) (ANOVA, $F_{1,5670}$, $P > 0{\cdot}05$). Similarly, zander from the upper BPF layer ranging from 16 to 39 mm L_T (mean ± S.D. 27·2 ± 3·0 mm) were thus almost the same size as conspecifics from the lower BPF layer ranging from 19 to 37 mm L_T (mean ± S.D. 26·9 ± 3·0 mm) (ANOVA, $F_{1,4015}$, $P > 0{\cdot}05$). In both BPF layers, however, perch were significantly smaller than zander (ANOVA, $F_{1,9687}$, $P < 0{\cdot}001$).

DISCUSSION

Previous studies carried out in Římov Reservoir (Čech & Kubečka, 2006), Slapy Reservoir and Orlík Reservoir (Čech *et al.*, 2007) have shown that in normal spring conditions the BPF layer is equally distributed along most of the longitudinal profile of these canyon-shaped reservoirs. The only exception is very shallow riverine section of the reservoir close to its tributary (Čech & Kubečka, 2006), where the BPF layer is either absent or changed into bottom-dwelling community of fry well hidden to both acoustic and direct sampling techniques. The other possibility is that this upper part of the reservoir is affected by the cold hypolimnetic water released from the reservoir situated upstream in the cascade (Čech *et al.*, 2007).

The floodwaters that swept through the riverine part of Orlík Reservoir (the Vltava River arm and to a lesser extent the Otava River arm) during the first half of June 2004 completely shifted the existing pelagic community of fry, especially perch and zander, from the riverine into the lacustrine part of the reservoir. In the riverine part of the reservoir, the pelagic zone was then recolonized by cyprinid fry, coming most likely from the littoral habitat and entering the open water during periodically reversed diel horizontal migrations (Copp & Jurajda, 1993). The possibility of an allochthonous origin of the new community of fry in the upper part of Orlík Reservoir cannot be also excluded (Peterka *et al.*, 2004).

As a result of the flood, percid communities originating from both riverine parts of Orlík Reservoir appear to have been flushed into the upper reach of the lacustrine part of the reservoir, where, due to the sudden increase in volume, the water current slows down rapidly. Evidence for this assumption lies in the overall abundance of BPF, which in this part of the reservoir (r. km 165–157) was noticeably higher (mean ± S.E. 156 474 ± 14 335 individuals ha^{-1}) than in lower reach of the lacustrine part of the reservoir (mean ± S.E. 52 832 ± 13 027 individuals ha^{-1} within r. km 157–145) (ANOVA, $F_{1,27}$, $P < 0{\cdot}001$). This high concentration of relatively large (Matěna, 1995; Čech *et al.*, 2005) perch and zander fry may also explain the phenomenon of the second BPF layer, which only vanished in the lower reach of the lacustrine part of the reservoir. In contrast, the observed flood event had negligible effect on the distribution of larger fishes compared to other years (J. Kubečka, J. Frouzová, M. Čech, unpubl. data).

Since two bathypelagic fry layers have not been observed previously in any reservoir or lake with percids, the reasons for the phenomenon can only be hypothesized. It could simply be a result of hydrodynamic events. Fishes in different layers may have been individuals carried from different locations in the reservoir by the flood. Apart from their different use of space in time, however, the fry communities in the upper and lower BPF layer were similar, with both layers being composed of fishes of similar sizes, with the same species in approximately the same proportions.

This study aside, the formation of two distinct sound-scattering layers in freshwater systems has also been reported for cucumberfish *Retropinna retropinna* (Richardson) in Lake Rotoiti, Lake Rotoma and Lake Okataina, New Zealand (Rowe, 1994). In these lakes, however, the upper layer was created by juvenile cucumberfish (30–50 mm fork length, L_F) and the lower layer was created by large-sized individuals (50–80 mm L_F). Fish were feeding during the daytime (Rowe, 1994). This is consistent with preliminary results from Orlík Reservoir where during daylight hours both perch and zander were feeding on large *Daphnia* sp. and in case of the lower BPF layer surprisingly also *Bosmina* species. By contrast, in Slapy Reservoir BPF did not feed at all during the daytime, staying hungry in the cold hypolimnion. For fry performing diel vertical migrations, the feeding habitat was the warm epilimnion, which they reached at dusk (M. Kratochvíl & J. Peterka, unpubl. data).

There is, however, a strong discrepancy between the results from Slapy Reservoir and those presented here from Orlík Reservoir. In the former, the water column was highly stratified and the temperature difference between epilimnion and hypolimnion was >10° C (Čech *et al.*, 2005). In the latter, the water column had been destratified by passing floodwater and strong winds and the difference in temperature between the surface waters and the layers of upper and lower BPF layer occurrence was only 2·0 and 3·5° C respectively. The overall destratification of the water column and large waves on the water surface may be major factors contributing to the absence of classical epipelagic percid fry community in the upper 4 m of the water column reported by many authors (Guma'a, 1978; Coles, 1981; Viljanen & Holopainen, 1982; Whiteside *et al.*, 1985; Post & McQueen, 1988; Treasurer, 1988; Wang & Eckmann, 1994; Matěna, 1995; Urho, 1996; Čech *et al.*, 2005). This is also supported by observations from the well-mixed West Blue Lake, Manitoba (Ward & Robinson, 1974), Lake Michigan (Perrone *et al.*, 1983) or Lipno Reservoir, Czech Republic (M. Čech & J. Kubečka, pers. data), where perch fry were extremely rare in catches taken at the surface during daylight hours and most of the community was composed of bottom-dwelling fishes. Summarizing this, in relatively homogeneous water column, deeper layers seem to be preferred greatly over surface layers by perch fry (perhaps percid fry in general). It could be then easily hypothesized that in such a habitat both BPF and bottom-dwelling perch fry are well hidden to visual predators (Levy, 1990). At least, Čech & Kubečka (2006) have shown very low abundance of potential predators around the BPF layer and the same was reported by Eckmann & Imbrock (1996) for the near-bottom habitat.

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