School of Doctoral Studies in Biological Sciences
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Spatiotemporal distribution and shoaling behaviour of fish

Ph.D. Thesis

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Annotation

The dissertation thesis is focused on pelagic fish distribution in the large freshwater bodies and the main factors affecting it. Paper 1 describes fish behaviour in a mouth of a midwater trawl during different day time periods as fish activity may importantly affect abundance estimates of the sampled fish stock. Acoustically recorded avoidance behaviour in a vertical direction is described. The second part of the thesis refers to the diel distribution and behaviour of the pelagic fry communities with a particular focus on the vertically migrating bathypelagic percid fry that occupy open water during early ontogeny. Paper 2 shows that the vertically migrating community can create a dominant part of fry assemblages in the reservoir, which is in contrast to many previous observations of an usually prevailing non-migrating epipelagic community. At their day refuge, bathypelagic percid fry (BPF) created dense shoals whose physical parameters are described. Paper 3 for the first time demonstrates that vertical shifts of BPF were under direct light control, hence were not a genetically fixed behaviour. A unique large-scale field experiment with the simultaneously operating up-looking and down looking transducers was carried out under artificially controlled light regime. Moreover effect of predation as the main ultimate cause of vertical shifts is discussed.

The introductory part of the thesis opens with the current possibilities of assessing distribution and behaviour of fish in the open water. Benefits of shoaling/schooling behaviour during defence against predators, foraging and learning abilities of fish are mentioned and some implications of fish behaviour on the fish capture process are pointed out. The second chapter deals with the diel shifts between habitats that belong among the most common activities of fish. However, distribution of fish varies also over the long temporal scale and currently has been strongly affected by changing climate. Therefore, the main affects of climate change on the world´s fish populations are introduced using examples from both freshwater and marine environment.

Declaration

[English]

I declare that this dissertation thesis was fully worked out by myself using only the cited literature. I also declare that in accordance with the Czech legal code § 47b law No. 111/1998 in valid version I consent to the publication of my dissertation in an edition made by removing marked parts archived by Faculty of Science in an electronic way in the public access section of the STAG database run by the University of South Bohemia in České Budějovice on its web pages.

[Czech]

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List of papers

The thesis is based on following papers

Paper 1

Fish behaviour in response to a midwater trawl footrope in temperate reservoirs.

Sajdlová Z., Draštík V., Jůza T., Říha M., Frouzová J., Čech M., Vašek M., Muška M., Blabolil P., Tušer M., Kratochvíl, M. Peterka J., Mrkvička T., Balk H. & J. Kubečka (2015)

Fisheries Research, 172, 105–113; DOI: 10.1016/j.fishres.2015.06.025

IF= 2.23 (2015)

Paper 2

Bathypelagic percid fry, a strongly predominating fry community in a deep European reservoir.

Sajdlová Z., Jůza T., Frouzová J., Seďa J. & M. Čech

Hydrobiologia, 787, 341–352 (2017); DOI: 10.1007/s10750-016-2978-1

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Paper 3

Are diel vertical migrations of European perch (*Perca fluviatilis* L.) early juveniles under direct control of light intensity? Evidence from a large field experiment.

Sajdlová Z., Frouzová J., Draštík V., Jůza T., Peterka J., Prchalová M., Říha M., Vašek M., Kubečka J. & M. Čech

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Declaration of originality

The co-authors fully acknowledge that Zuzana Sajdlová is the first author of all papers presented. Most of the data processing as well as most of the statistical analyses were performed by Zuzana Sajdlová. She also made a major contribution to writing the manuscripts. All papers contain original results. All co-authors consent to the publication of the papers in the dissertation of Zuzana Sajdlová and four authors hereby support this statement with their signature.

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Content

Introduction

Studying fish in their natural environment requires a lot of effort since they can be rarely followed without being disturbed and also because they shift on long distances and occupy various inshore and off-shore habitats over the diel, seasonal and interannual periods (Axenrot et al., 2004; Brönmark et al., 2008, 2013; Ahrenstorff et al., 2011). Behaviour of fish plays an important role during the fish stock surveys but reaching fish, especially in a deep and poorly accessible pelagic habitat, can be arduous and active sampling devices are needed (Misund, 1994; Lucas & Baras, 2000). Trawls have been deployed for more than 70 years (Kristjonsson, 1971) by marine fisheries but they have become common also during investigations of the large land-locked water bodies (Říha et al., 2012; Williams et al., 2013). Trawling requires lot of space and cannot be carried out in the deepest parts of the water bodies where sloppy bottom with obstacles can cause trawls´ damage (Dahm, 1980; Graham et al., 2004). Where use of trawls is limited, however, hydroacoustic devices proved to be effective tools that can (except to many other things) control depth of a trawl and monitor fish behaviour relative to it (Rakowitz et al., 2012). The main positive about the hydroacoustic devices is that they are not limited by light (unlike the optical systems), which is important during underwater surveys because fish behaviour varies under high and low light intensities and may affect trawl catchability (Glass & Wardle, 1989; Misund, 1997). Another positive about the echosounders is that they operate in non-invasive manner and provide accurate information about depth and acoustic size of the single fish targets (particularly split-beam echosounders) (Čech & Kubečka, 2002; Taylor & Maxwell, 2007; Busch & Mehner, 2009) and also about abundance and biomass of fish aggregations (Fässler & Gorska, 2008; Draštík et al., 2009; Slotte et al., 2015).

Evaluating species composition of the sampled fish stock is usually based on the net catches but current effort is to develop acoustic methods that would enable distinguishing among different fish species. This might be problematic if fish occur in dense shoals, fortunately, back-scattering properties of some species, e.g. Atlantic mackerel (*Scomber scombrus* L.) or herring

(*Clupea harengus* L.) are frequency-dependent so that echosounders simultaneously operating at the high and low frequencies can distinguish between the species (Misund, 1997). Another possibility is to look for species-specific target strength (TS, in dB) - length regressions of fishes which can be useful during size estimation in looser fish aggregations in shallow waters (e.g., Godlewska, 2004; Frouzová et al. 2005). However, the measurements are often affected by changing fish orientation relative to transducer (Čech & Kubečka, 2002; McQuinn & Winger, 2003; Ona, 2003) and, in the deep waters, also by changing volume of a fishes´ swim bladder, so that a relatively wide range of TS within species can be observed (Ona, 2003; Fässler & Gorska, 2008). Thus, probably the most reliable approach is to utilize echosounders operating at high frequencies, i.e. acoustic cameras - DIDSON (Tušer et al., 2013) and side scan sonars operating frequency >500 kHz that can provide high-resolution data where single fish targets can be identified into species (Handegard & Williams, 2008; Rudstam et al. 2012).

The conventional fishing vessels are equipped with the vertically and horizontally beaming echosounders operating at frequencies from 20 to 200 kHz where the low frequencies, at which the data resolution is usually poor, are used to detect distant targets whereas higher frequencies (>120 kHz) can provide detailed information about fish targets (Misund, 1997; Simmonds & MacLennan, 2005). Trawls that are towed hundreds of meters behind the fishing vessels are provided with their own trawl eyes controlling depth and the horizontal opening of the trawl. Sometimes, bottom trawls or dredges are monitored by side scan sonar recording details about the terrain of the sea bottom in their path (Lucchetti & Sala, 2012). Besides the fishing operations, fish can be studied using echosounders carried by the towed underwater vehicles (Fernandes et al., 2003) or echosounders mounted to the moored or drifting buoys (Handegard et al., 2003). Moreover, the stationary up-looking transducers for evaluating fish occurrence in surface pelagic layers can be deployed (Graham et al., 2004; Scalabrin et al., 2009; Jarolím et al., 2010). Finally, acoustics can provide valuable information on the individual, population and the species level and belong among the most promising non-invasive tools suitable for studying spatial and temporal distribution of fish as well as their migratory, foraging, defensive and shoaling behaviour.

Benefits of shoaling behaviour

Forming shoals or organized schools is the most obvious behaviour in fishes. Permanent shoals are common in species spending their life time in shoals whereas facultative shoals are created only during certain life period (Pitcher, 1993; Helfman et al., 2009). With a few exceptions, shoaling is affected by light that attenuates with depth and limits visual detection abilities of fish (Pitcher et al., 1976; Glass et al., 1986). Under low light intensities fish cannot properly maintain visual contact with their conspecifics in shoal/school, thus create denser aggregations at day time than at night (Robinson et al., 1995; Guillard et al., 2004;). Light also importantly affects visual detection abilities of fish during prey capture. High light intensities enhance optical contrast of prey towards the bright surface or the dark bottom which allows fish to more effectively recognize transparent prey items (e.g. zooplankton) in open water (Čech & Kubečka, 2002). By swimming in groups, fish can find optimal forage densities in considerably shorter time period than in the smaller groups (Pitcher et al., 1982).

Shoaling/schooling has several functions (Pitcher, 1993). It is beneficial during cooperative feeding, as was observed in the fast swimming pelagic piscivorous fishes, carangids (Carangidae), tunas (Scombridae), cod or saithe (Gadidae) that can create specialized hunting formations to enhance prey capture. Cooperative feeding occurred at day time when single predatory fish would be scarcely successful in attacks on their visually orienting prey fish (Partridge, 1982; Schmitt & Strand, 1982). Moreover, shoaling plays important role during defensive behaviour as fish in shoals have a lower probability of being captured by predators than single swimming individuals (Helfman et al., 2009). Defensive schooling is well developed in pelagic planktivorous species. For instance, Pitcher et al. (1996) observed 15 different schooling events in herring schools that were changing density, shape (e.g. ball, vacuole, hourglass, bend, split and fountain) and depth within short time periods. Antipredator behaviour is highly plastic, adapted to a type of attack (Nøttestad et al., 1996, 2002). Seithe (*Pollachius virens* L.), for instance, use hunting tactic of fast raids, which are more devastating for herring as more of them are killed than during attacks by Atlantic cod (*Gadus morhua* L.), focusing on single herring. Comparably, more harmful are attacks by cooperatively hunting marine mammals that attack fish from below, split them into small units and force them towards the surface where fish are stunned and eaten (Nøttestad & Axelsen, 1999). In contrast, seabirds, Atlantic puffins (*Frathercula arctica* L.), hunt non-cooperatively and during their attacks in surface layers, herring have better chance to escape (Axelsen et al., 2001; Nøttestad, 1998).

Avoidance behaviour of fish is important for trawl and acoustic surveys as it may bias abundance estimates of the investigated fish stocks (Ona et al., 2007). Avoidance to vessels depends on type of vessel and originates from vibrations of a vessel´s hull moving through water and also noise from engines (Mitson, 1993). A wide spectrum of behaviours from none to strong responses was described. Draštík & Kubečka (2005) found that in clear water of the lake Wallersee (Austria) fish escaped approaching boat while no obvious responses were observed in fish from the eutrophic Czech reservoirs. However, in marine environment where water transparency is usually high, Gerlotto & Fréon (1992) and Gerlotto et al. (2004) observed poor vertical avoidance in Round sardinella (*Sardinalla aurita* (Valenciennes, 1847)) and anchovy (*Engraulis ringens* (Jenyns, 1842)) that responded to approaching vessel by shallow dives within upper 10–20 m of water column. Skaret et al. (2005) suggested that the priority of fish at the spawning/feeding grounds can overrule their defensive behaviour which agrees with a generally poor response of herring at the spawning grounds and their strong avoidance at the wintering grounds (Misund, 1994).

Various behaviours can be observed relative to trawls that are constructed so that they provide optical stimuli from otter boards, bridles, warps or netting and attract fish to the trawl mouth (Kim & Wardle, 1998; Glass & Wardle, 1989). For instance, Rakowitz et al. (2012)

revealed eleven different swimming modes of fish in the trawl mouth. During the active avoidance, fish swum under the footrope or escaped from the trawl by fast swimming in ahead and away from the trawl. The most fish, however, behaved passively, and those occuring in the trawl path, were captured. Different behaviour was observed in fast swimming pelagic fishes at day time when fish could keep long reaction distances, most of them avoiding trawl or swimming fast in the direction of tow for several minutes (He, 1993; He & Wardle, 1988). At night, however, reaction distances sharply decreased and trawl catches were significantly higher (Godø et al., 2004; Misund, 1999; Jůza et al., 2012, 2013). Specific behaviour to trawls can be observed in demersal non-schooling species, e.g. flatfish - sole (Soleidae), plaice (Pleuronectidae) or flounder (Bothidae) that, even under sufficient light intensities, keep short reaction distances which arises from characteristic antipredator strategy of these fishes. They wait until predator (trawl) gets into their close proximity and then perform fast "fleeing" manoeuvres (Albert et al., 2003; Ryer, 2008; Winger et al., 2010). Hence, species-specific behaviour and time of a day should be taken on account during fishing operations.

Last but not least, shoaling behaviour is beneficial during social learning in fish which should be considered in heavily fished areas where repeated encounters with the fishing gear may lead fish to increased avoidance behaviour (Walsh et al., 2004). For instance, Pyanov (1993) studied learning abilities of common bream (*Abramis brama* L.) that avoided trawls more than 20 days after a single encounter and the highest probability of avoidance was found in large adult individuals, which is obviously correlated to greater experience of these individuals. Furthermore, the greater the number of demonstrators (experienced individuals) in group, the higher probability that observers (naïve fish) learn to avoid fishing gear next time (Brown & Laland, 2003). Similarly, in migratory schooling species where presence of experienced individuals was greater than 4 %, learning abilities of young (naïve) individuals increased rapidly (Fréon et al., 1993; Huse et al., 2010). However, because social learning is more effective in permanent groups than in randomly mixed shoals created during fish capture, it seems not very likely that catch ability of trawls would be severely impacted.

Diel, seasonal and interannual distribution of fish

Dealing with different environmental and biological conditions often leads fish to switching between habitats. Diel shifts are common activity of fish described in a wide range of species and life stages (Axelsen et al., 2001; Kahilainen et al., 2004; Jůza et al., 2009) and their often mentioned ultimate cause is searching optimal forage densities (Olsson et al., 2006), maximizing energetic gains (Neverman & Wurtsbaugh, 1994; Mehner et al., 2010) and avoiding predators (Kahilainen et al., 2009). For instance, Bohl (1979) and Brodersen et al. (2008) registered foraging inshore off-shore migrations in juvenile cyprinids. Muška et al. (2013) observed partial diel horizontal migrations in adult fish communities performed in order to optimize between feeding and avoiding predators. Comparably, Robinson et al. (1995) detected diel horizontal migrations off the west coast of Baja California (Mexico) when anchovy (*Engraulis mordax* (Girard, 1854)) stayed inshore at night and at dawn they moved into deeper water layers offshore, following their prey, euphausiids (Euphausiidae). In water bodies where the littoral zone is scarce or surface pelagic layers are occupied by predators, fish may utilize deep water as a temporary refuge and perform vertical shifts (Gliwicz & Jachner, 1992; Hardiman et al., 2004). For instance, Scheuerell & Schindler (2003) evidenced that sockeye salmon (*Oncorhynchus nerka* (Walbaum, 1792)) are capable of utilizing even minimal light intensities to forage in deep layers where they could escape their predators for which the same light intensities were too low to orient. Probst & Eckmann (2009) found that deep water serves as important refuge for juvenile burbot (*Lota lota* L.) and, correspondingly, Benoit et al. (2010) evidenced deep day distribution of polar cod (*Boreogadus saida* ((Lepechin 1774)) in the Barents Sea that avoided their predators, ringed seals (*Phoca hispida* ((Schreber 1775)). Predation seems to be the main cause of diel vertical shifts also in pelagic perch (*Perca fluviatilis*

L.) fry that can create numerous assemblages in open water and can create two spatially and temporarily distinct communities (Čech et al., 2005, 2017; Kratochvíl et al., 2008; Kuchta et al., 2009; Petrtýl et al., 2015). The epipelagic (non-migrating) perch/percid community can find optimal temperature conditions and optimal forage densities entire diel period but they must face high predation risk at the bright surface pelagic layers as was supported by Eklöv & Persson (1995) who found that if the suitable refuges are lacking, juvenile fish are easy target of predators. Similarly, Vejřík et al. (2016b) observed that adult perch and also cyprinids belong among predators of juvenile percids in surface pelagic layers. Different, energetically less convenient strategy was chosen by the bathypelagic (migrating) percid fry community that undergoes vertical shifts into deep layers (Čech et al., 2005; 2017). Compared to adult fish preferring warm epipelagic layers, juvenile fish can temporarily bear considerably lower temperature range (Hardiman et al., 2004; Vašek et al., 2004; Prchalová et al., 2008, 2009) and lower concentration of dissolved oxygen (<2.5 mg l^{-1}). Thus, occupying deep layers might be useful in spatial segregation from predators in surface layers (Wang & Eckmann, 1994; Jackson et al. 2001; Vejřík et al., 2016a).

Up to now, the diel activity of fish was mentioned but distribution and behaviour of fish may vary also within long temporal scale, being affected by seasonally and interannually changing environmental conditions. For instance, Baldwin et al. (2002) observed that cutthroat trout (*Oncorhynchus clarki* (Richardson, 1836)) were more pelagic in autumn, utilizing wider range of a water column than in summer when their vertical shifts were limited by temperature stratification. Similarly, Ahrenstorff et al. (2011) found variability in vertical distribution of Lake trout (*Salvelinus namaycush* (Walbaum, 1792)) from the Lake Superior (Canada, USA), and Busch & Mehner (2009) observed seasonal vertical migrations in perch from the Lake Stechlin (Germany), whose shifts into deeper layers in winter were affected by low temperature preference. Marked interannual changes of occurrence and distribution were found also in the bathypelagic communities that, in some years, occupy only the restricted parts of the reservoir whereas in other years they are found in most of the longitudinal profile (Čech et al., 2005; 2007a,b; 2017; Jůza et al., 2010, 2012). Such variability could be explained by changing hydrological conditions in the reservoirs (early summer flood events, income of humic water from the watershed) but there is also strong variability in occurrence between different water bodies which remains poorly understood (Čech et al., 2007a, b; 2017; Sajdlová et al., 2017).

There is ample evidence that long temporal distribution of fishes from equator to poles has been strongly affected by changes in atmospheric and oceanic circulation (Parsons & Leer, 2001; Alheit et al., 2005, 2014). Climate changes are associated with rising global temperature and multi-decadal oscillations of the warm and cold periods and in aquatic ecosystems they manifest by prolonged thermal stratification (Williamson et al., 2009), enhanced eutrophication, intensive seasonal fluctuations of water level (Ficke et al., 2007; Jeppesen et al., 2009). Organisms with limited movement abilities deal with unfavourable conditions either by adaptation or extinction whereas mobile species respond more dynamically, by spatial shifts when entire population or species move their distribution range (Perry et al., 2005; Stenevik & Sundby, 2007; Jeppesen et al., 2010).

In the lakes and reservoirs, latitudinal shifts are less obvious than in the marine environment due to geographical barriers but some general trends in long temporal distribution can be observed (Lehtonen, 1996; Jeppesen et al., 2010). For instance, Malmquist et al. (2004) suggested that cold-water stenothermal species (salmonids) shift polewards or where shifting is not possible, they become locally extinct while eurythermal species, percids (Percidae), cyprinids (Cyprinidae) or centrarchids (Centrarchidae) tend to adapt to new thermal regimes (Jeppesen et al., 2010). Similar trends were registered in marine environment where Perry et al. (2005) observed that several species from the North Sea (e.g. Atlantic cod, blue whiting (*Micromesistius poutassou* (Risso, 1827)), anglerfish (*Lophius piscatorius* L.)) have shifted their geographical range >2 km year^{-1} farther north, being replaced by warm-water species. Climate-related shifts may be positive for new-coming species when free niches arise but the negative aspect resides in intraspecific competition for space and food sources as was evidenced in the Mediterranean Sea where rising sea temperature caused that many non-native species, coming from the warm Red Sea, moved farther north which negatively affected biodiversity of residential species (Bianchi & Morri, 2000; Bariche et al., 2004; Lejeusne et al., 2010).

The most obvious climate-related shifts were registered in highly mobile pelagic planktivorous fishes that have been important targets of fisheries (Holst et al., 2002; Schröder, 2013) and create large populations with a rapid turnover of generations. For instance, when cold productive southerly currents flowing along the western coast of Africa (Benguela) and South-America (Humboldt) are weak, sardine (*Sardinops sagax* (Jenyns, 1842)) preferring warm water are abundant whereas cold-water anchovy (*Engraulius encrasicolus* L.) with poor swimming abilities shift below thermocline or they look for temporary cold water pockets close to shore (Chavez et al., 2003; Checkley et al., 2017). In these refuges, however, anchovy cannot find optimal life conditions and their abundance declines since below the thermocline are low forage densities and inshore, anchovy have to face strong predation (Alheit & Niquen, 2004; Lehodey et al. 2006; Lindegren et al., 2013). On contrary, the largest fish stock from the North Atlantic Ocean, Norwegian spring spawning herring (NSS) obviously favour years when along the Norwegian coast flows strong, warm westerly current from the Atlantic Ocean (Toresen & Østvedt, 2000; Engelhard & Heino, 2006). The warm current positively affects physical conditions of adult herring during winter period (Fig. 1, 2) when they do not feed and in warm water (>6.5°C) can safe more energy for spring spawning migration (Røttingen, 1992; Skagseth et al., 2015). Moreover, during warm periods, onset of spawning is earlier which positively affect survival of herring larvae. Petitgas (2010) found that earlier hatched larvae can more effectively avoid spatial overleap with their predators and, as evidenced by Skagseth et al. (2015), larvae are faster carried into the nursery grounds where fry can find optimal forage densities (Olsen et al. 2009). In result, during warm periods, more young-of-the-year herring can survive which supports stronger future recruitment.

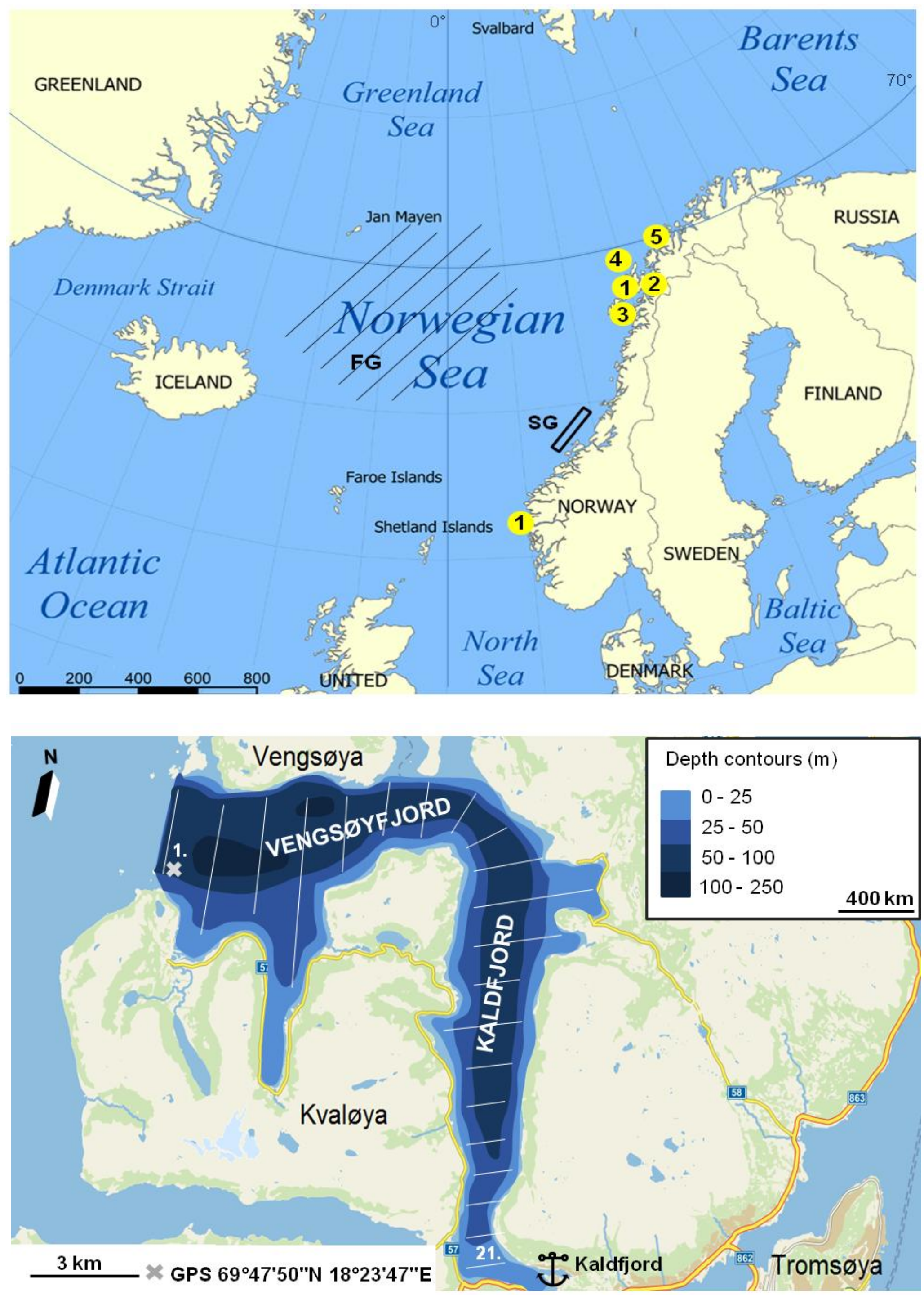

Fig. 1a) Before spawning, NSS herring seek suitable refuges where the adult population (3.5 millions of tons; the last estimate provided by Slotte et al., 2015) over-winters. Location of wintering grounds has been changing markedly and in the last 58 years they can be found in Norwegian fjords: 1) Møre and Lofoten Isls: 1970–1986, 2) Ofotfjord-Tysfjord: 1987–1994, 3) Vestfjord: 1995–2001, 4) North of Vesterlölen Isls.: 2002–2005, 5) Andøya Isl.-Troms-Finnmarken: from 2006. Besides, the location of the recent spawning grounds (SG – black rectangle) and feeding grounds (FG – black lines) are shown (Røttingen, 1992; Foote et al., 1997; Huse et al., 2010); **b)** A detail of the investigated locality in northern Troms that created a sub-area (~80 km^2) of the wintering ground. The white lines indicate individual transects (N=21) of navigation along which herring were acoustically detected by the SIMRAD EK 60 scientific echosounder (f=70 kHz) (K. Ø. Gjelland & Z. Sajdlová, unpub. data).

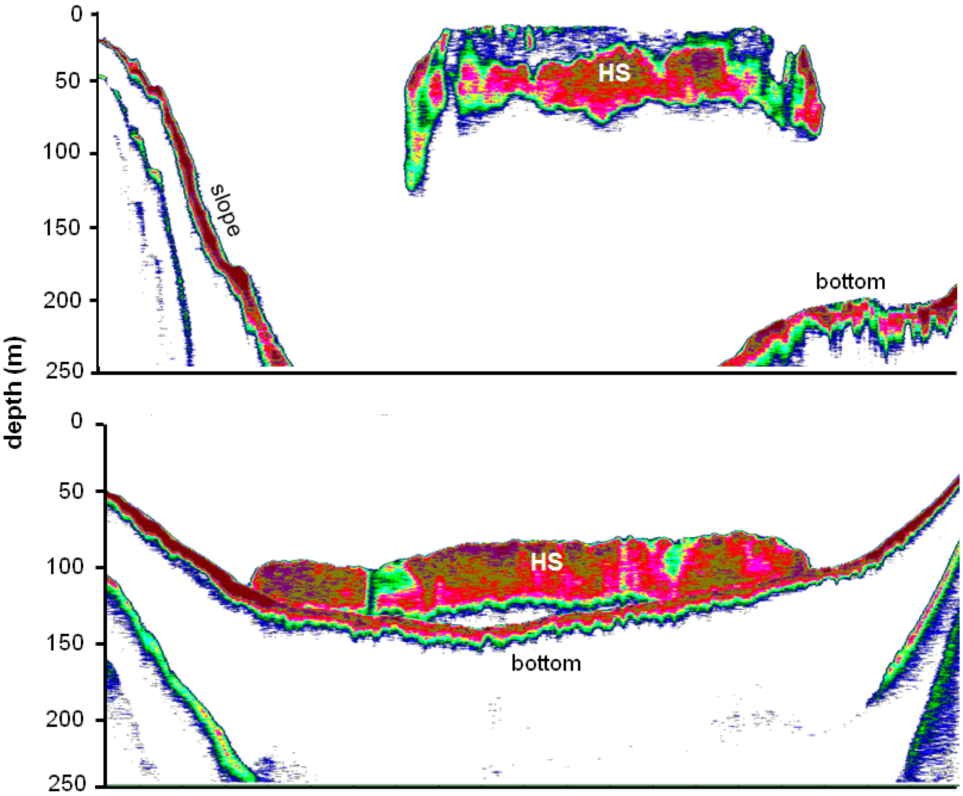

Fig. 2 Overwintering herring create large, acoustically well-detectable schools that extend over the large areas of fjords and are common target for predatory fishes, sea birds and marine mammals (text Table 1, Fig. 3). The example of the two of 117 herring schools (HS) that were recorded during the two consecutive seasons from November to January (2014–2016). The schools reached average height of 68 m (SD ± 40 m) and length of 1002 m (SD ± 932 m) in a course of navigation.

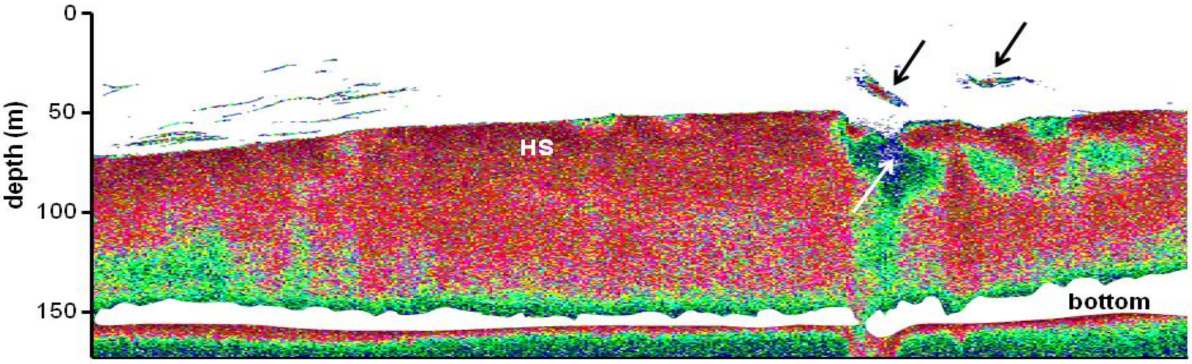

Fig. 3 Predator attack on a herring school (HS) in Kaldfjord recorded on 17 December 2014 (11:40 hr). The black arrows indicate predators, probably the large saithe (*Pollachius virens*, L.). Note the white arrow indicating a typical gap in school during attack. Note also another fish school on the left side of the echogram picture swimming above HS. These fish could be identified as single swimming herring based on a target strength that is close to that of herring (TS=-37 dB; Ona, 2003). But leaving school in a presence of predators does not fit to the antipredatory behaviour of herring so that these targets probably belong to some other schooling species, possibly young (age 2^+) gadoids, cod or pollock (*Pollachius virens* L.). Young gadoids create pelagic schools and because their diet includes mostly crustaceans and smaller fish (capelin, *Mallotus villosus* (O. F. Müller, 1776)), they seem to pose a little threat to herring (Dalpadado & Bogstad, 2004).

Table 1

Do prey abundance and migration distances affect behaviour of the large marine predators?

Killer whales (*Orcinus orca* L.) have been regularly sighted at the wintering grounds of herring for decades (Similä et al., 1996; Nøttestad, 1998). But recently, also large baleen whales, especially humpback whales (*Megaptera novaengliae* (Borowski, 1781)) were observed in the fjords of northern Norway during winter. This is, to our best knowledge, the first evidence of such behaviour since humpback whales from the North Atlantic Ocean (NAO) usually spend winter at the breeding grounds in the Caribbean* and Cape Verde Islands from where whales migrate to the summer feeding grounds located at the western (e.g. Gulf of Maine, Newfoundland, West Greenland) and eastern NAO (Iceland, Jan Mayen Island, Norwegian and the Barents Sea). There is a strong fidelity to these areas since whales return to the feeding grounds were they were firstly taken by their mothers (Clapham, 2009).

The breeding grounds at the Caribbean are shared but only a small portion of whales from the eastern NAO arrives there and only a minority breeds at the Cape Verde Islands. This leads to assumption that the other unknown breeding ground(s) exist. Stevick et al. (2003) found that timing of migration is influenced by the origin of a feeding ground and that there is a strong correlation between the latitude and time of arrival to the breeding grounds. Whales from the eastern NAO have to reach significantly greater distances and arrive later to the breeding grounds than the whales from western NAO. It might lead to assumption that not all the whales regularly migrate which was supported by historical records of Ingebrigsten (1929) who reported humpback whales at the feeding grounds in the Barents Sea for most of the year.

The second possible explanation of why whales may postpone or skip reproduction, are feeding opportunities. Humpback whales have a diverse diet varying slightly across the feeding grounds and besides herring, humpback whales from the eastern NAO feed mostly on capelin (Fleming & Jackson, 2011). Christensen et al. (1992) evidenced that if abundant and nutrient-rich food source is available for most of the year, whales may prefer to prolong feeding period which agrees with the recent observation from 2015–2016 when several hundreds of cooperatively feeding whales (3–8 individuals per group) occurred in the fjords of the Kvaløya Island (Fig. 1) obviously thriving from huge prey abundance (Sajdlová, 2016).

***** Currently including islands off the northern coast of the Greater Antilles (Turks and Caicos Isls.) and Bahamas.

Aims of the study

The dissertation thesis is focused on pelagic distribution and behaviour of fish in the large temperate water bodies studied by the trawls and hydroacoustics. The first part of the thesis describes diel pattern of vertical distribution of fish and their behaviour relative to midwater trawl (Paper 1). The second and the third paper deal with diel distribution and behaviour in pelagic percid fry communities (Paper 2, 3). The specific objectives of the three papers are summarized below.

Paper 1 The main objective was to describe diel patterns of vertical distribution of fish in the two canyon-shaped reservoirs at day and night. Moreover, acoustically recorded behaviour of fish near the footrope of a midwater trawl was described. The paper documents the number of fish that performed avoidance behaviour and evaluates catchability of trawls.

Paper 2 The main objective was to show that bathypelagic percid fry can dominate the whole fry community of the reservoir. Bathypelagic percid fry community in the Vír Reservoir, its species composition, abundance and size distribution in the context of the vertical and horizontal spatial patterns of the whole fry community were investigated.

Paper 3 The main objective was to demonstrate that diel vertical migrations of perch (*Perca fluviatilis* L.) fry were directly controlled by the light intensity. A unique large-scale field experiment with an artificially manipulated light intensity was undertaken in a thermally stratified, canyon-shaped reservoir. The behaviour of perch fry during the whole experiment was acoustically monitored using the semi-mobile down-looking transducer and stationary up-looking transducer.

Results

This dissertation thesis includes three original papers published in international impacted scientific journals - Fisheries Research, Hydrobiologia and Freshwater Biology.

Paper 1

This study addresses fish behaviour at the mouth of a midwater trawl in two temperate reservoirs. Fish distribution and behaviour were monitored using a SIMRAD EK60 (38 kHz) split-beam echosounder with the transducer deployed at the water surface, attached to the surface trawl headrope. We were able to describe day and night patterns of vertical distribution of fish in the reservoirs, describe fish behaviour near the footrope (i.e. vertical swimming velocity, fish tortuosity, vertical direction of swimming), and find the proportion of fish performing avoidance reactions. Significant differences were found between day and night distributions and behaviours. In total, only 35 of the 1514 acoustically recorded fish performed apparent avoidance behaviour. Twenty-seven avoidance reactions were observed in the day (6.3 % of total fish) while eight were observed at night (0.7 % of total fish). Fish were more active in the daytime, while tending to stay still in the water column with no observable reactions at night. We found significant dependence between the size of fish directly avoiding the trawl and their swimming velocities. The greatest echogram slope values belonged to those fish with a strong avoidance reaction. When the footrope was perceived, the fish reacted from approximately 1 m vertical distances and escaped up to 5 m below the footrope (usually 1–2.5 m). Light, water transparency and temperature stratification were the dominant factors influencing vertical distribution and fish avoidance behaviour.

Paper 2

The distribution, species composition, abundance and shoaling behaviour of young-of-year fish were studied in the canyon-shaped Vír Reservoir (Czech Republic) in mid-June 2010. Using the

SIMRAD EK60 echosounder (frequency 120 kHz), fry were acoustically sampled along the longitudinal profile of the reservoir. A framed trawl was used simultaneously to collect fry in the open water. Apparent differences were found in the density of fry between the epipelagic, littoral and bathypelagic zones. Bathypelagic fry strongly predominated in the total fry community creating 95.3% while epipelagic and littoral fry contributed only 4.7 %. The bathypelagic fry were represented by perch *Perca fluviatilis* (84.8 %), zander *Sander lucioperca* (14.9 %) and ruffe *Gymnocephalus cernua* (0.15 %) and were observed all along the longitudinal profile of the reservoir creating a distinct layer on the echogram. The layer, composed of shoaling and non-shoaling fry individuals, reached its greatest depth in the Bay part of the reservoir (7.5–14.5 m) and it was rising in the water column towards the tributary. The situation that the bathypelagic percid fry predominate in the reservoir is absolutely unique and it is completely different from published observations from other canyon-shaped reservoirs where epipelagic percid fry prevailed.

Paper 3

Diel vertical migrations (DVMs) belong among the most pronounced movements in the aquatic environment. A general pattern of DVMs has been well-described, particularly in European perch (*Perca fluviatilis*), but whether the migrations are directly controlled by light and what is the ultimate cause of the diel vertical shifts, remains poorly understood. Undertaking a large-scale field experiment in a thermally stratified, canyon-shaped reservoir, we demonstrated for the first time that DVMs of a bathypelagic early juveniles community, dominated by European perch larvae and juveniles prior the metamorphosis, were under direct control of the light intensity, i.e. they did not operate as a genetically fixed behaviour. Prior to the experiment, the depth distribution of the bathypelagic perch early juveniles was strongly correlated with the light intensity on the water surface ($p<0.001$). The community underwent regular DVMs between the epilimnion (depth <2.0 m) and hypolimnion (depth >3.0 m) reaching a maximum amplitude of

13 m. Hydroacoustic recordings by the echosounder SIMRAD EK 60 (120 and 400 kHz) showed that during the experiment, when the surface was covered with a large black non-transparent foil (2500 m^2; simulated conditions of complete and constant darkness), the regular vertical movement of the bathypelagic perch early juveniles was interrupted and the community occupied the epilimnion constantly for 24 hr. Immediately after the foil was removed at midday, the bathypelagic perch early juveniles were exposed to a steep increase of light intensity (from <1 LUX to >100 × 10^3 LUX) and they escaped into the hypolimnion where they were safe from visual predation which took place in the bright surface layers (epilimnion particularly). Our findings imply that occupying a deep, dark refuge in the daytime is essential for survival of perch in their early life stage.

General discussion, conclusions and perspectives

Fish from the Želivka and the Římov Reservoirs responded to approaching trawl actively at day time, escaping several meters below the footrope whereas at night they behaved passively and most of them did not show any obvious response (Sajdlová et al., 2015). Robinson et al. (1995) also observed significantly greater avoidance rate at day time when most of anchovy schools escaped from trawl. Similarly, Glass & Wardle (1989) and Olla et al. (2000) found light to be the main factor affecting trawl catchability. In total, however, only 2 % of fish from the Želivka and the Římov Reservoirs performed active avoidance behaviour so that trawl catchability seemed not to be severely impacted (Sajdlová et al., 2015). However, behaviour to trawl was recorded solely in the vertical direction and only within a restricted space of the trawl mouth so that the total number of fish escaped from the trawl might have been underestimated when we consider that fish can avoid trawls also in the horizontal direction or pass through the netting of the side panels (Williams et al., 2013; Rakowitz et al., 2012). Nonetheless, day time surveys should not be avoided as many fishes perform diel migrations between inshore and off-shore habitats and can be lacking in open water at night (Draštík et al., 2009; Muška et al., 2013).

Besides time of a day period, trawl catchability can be significantly influenced by swimming speed of fish avoiding trawl gear, as larger individuals are capable of reaching higher velocities (Čech & Kubečka, 2002) and have greater swimming endurance than the small fish as found by He (1993) and by Scruton et al. (1998) who observed that the large lake sturgeon (*Acipenser fulvesens* (Rafinesque, 1817)) were capable of swimming 50 min at speed 0.9 $m.s^{-1}$ whereas intermediate individuals could maintain this speed only a few seconds. Also during our study largest individuals reached the highest velocities. However the velocities were much lower than the speed limits reached during horizontal swimming when fish approach the trawl (He & Wardle, 1988).

The trawl catch from the Želivka and the Římov Reservoirs were dominated by planktivorous species - common bream, roach (*Rutilus rutilus* L.) and bleak (*Alburnus alburnus* L.) (Sajdlová et al., 2015) that belong among the most abundant species of the Czech eutrophic water bodies (Blabolil et al., 2017). Planktivorous species can increase eutrophy by reduction of filter-feeding zooplankton which may negatively affect water quality in water bodies. Hence, regulating size of the populations of planktivorous fishes is required (Mehner et al., 2004). If natural regulation i.e. by predators cannot be done, fish stocks must be controlled artificially as in the case of the Římov Reservoir where intensive surface-water trawling was conducted to reduce over-abundant cyprinid population in 2010 and where similar investigations are planned for near future (ERDF/ESF Biomanipulation project for years 2018–2022).

A pattern of pelagic distribution of fish showed that they occupied greater depth at day time than at night when most of them were dwelling in the warm epipelagic layers which seems to be a common distribution observed also by Prchalová et al. (2008) or Draštík et al. (2009). Even more distinct difference in vertical occurrence was observed in the migrating communities of bathypelagic percid fry that occupied deep (up to 13 m) layers at day and returned into surface layers at the dusk. In the Vír Reservoir, bathypelagic percid fry predominated in the fry community of the reservoir (Sajdlová et al., 2017) which contrasts with previous observations where non-migrating epipelagic fry communities were more abundant (Post & McQueen, 1988; Čech et al., 2005). However, when fish can find optimal life conditions, i.e. when temperature is within their optima and food density is sufficient, fish may prefer utilizing deep water. In the Vír Reservoir, during summer temperature was high enough (>11.9 °C) in most of the water column to allow fry occurrence in deep layers where they could feed on abundant zooplankton (*Daphnia*). In concordance to Čech et al. (2007a), bathypelagic percid fry were following trophic gradient when larger fry individuals were observed more upstream than the smaller fry and were distributed among the most of the longitudinal profile of the reservoir (Sajdlová et al., 2017).

According to Gliwicz & Jachner (1992) diel shifts are genetically fixed behaviour caused as a result of ghost of predation in the past. On contrary, studies by Gjelland et al. (2009); Kahilainen et al. (2009) or Benoit et al. (2010) evidenced that the vertical shifts were externally controlled by light. Under constant light intensity, i.e. under polar night or day regime, vertical shifts were stopped which is in concordance to observations conducted under artificially modified light intensities (Sajdlová et al., 2018). When the constant dark period was set and the water surface was covered by the non-transparent black foil, bathypelagic community stopped the vertical shift and occupied epipelagic layers 24 h. However, when the foil was removed under high day light intensities and the surface become fully illuminated percid fry escaped immediately into the hypolimnetic layers (Sajdlová et al., 2018). At this time, intensive shoaling behaviour could be observed as sufficient day light intensities enabled individuals in shoals to keep visual contact with their conspecifics. Setup of shoaling, however, begins at the certain age so that the bathypelagic layers are usually created by both, shoaling (older) and non shoaling (younger) fry individuals (Čech & Kubečka, 2006).

The most probable ultimate cause of vertical shifts of bathypelagic percid fry is predator avoidance as was suggested by Čech et al. (2005), Čech & Kubečka (2006) and later evidenced by Čech (2007, pers. obs.) or Vejřík et al. (2016b) who found adult perch, bream and roach as the main predators of pelagic percid fry in surface pelagic layers. However, more detailed information about the interactions between the fry and their predators in the different environments are mostly lacking. As shown on the examples of marine pelagic schooling species attacked by different kinds of predators, prey responses can be highly plastic, dependent on type of attack (Nøttestad et al., 1996; Nøttestad & Axelsen, 1999). Thus, different responses can be expected in the percid fry attacked by adult cyprinids and percids since both, perch and bream utilize different hunting tactics. Cyprinids focus on single prey items - zooplankton (Wanzenböck & Schiemer, 1989) that they gain during the up and down (sinusoidal) swimming when high light contrast enables detection of transparent prey towards the bright surface layers whereas percids do not perform sinusoidal swimming and are used to capture fast moving prey (Čech & Kubečka, 2002, Jarolím et al., 2010). Moreover, as observed by Partridge et al. (1982) or Čech et al. (2017), avoidance behaviour is highly affected by time of a day period and also by type of the environment. Thus, in the deep stratified water bodies, vertically migrating community escapes into hypolimnion whereas in shallow non-stratified water bodies, percid fry hide near the bottom (cf. also Kratochvíl et al., 2010).

The diel pattern of distribution and shoaling behaviour in the bathypelagic percid fry from the reservoirs of the Vltava Cascade, the Římov and the Vír Reservoirs was well described but the interannual variability of pelagic percid fry occurrence between different water bodies and between different years has been poorly understood. Since the trawl and hydroacoustic data from many consecutive years are available it would be interesting to examine the long temporal variability in percid fry distribution with respect to environmental and biological factors, i.e. hydrological conditions in the reservoir, income of humic water from the watershed, temperature conditions, availability of suitable spawning grounds and predator abundance a activity.

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Research papers

Paper I.

Fish behaviour in response to a midwater trawl footrope in temperate reservoirs.

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Fish behaviour in response to a midwater trawl footrope in temperate reservoirs

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ABSTRACT

This study addresses fish behaviour at the mouth of a midwater trawl in two temperate reservoirs. Fish distribution and behaviour were monitored using a SIMRAD EK60 (38 kHz) split-beam echosounder with the transducer deployed at the water surface, attached to the surface trawl headrope. We were able to describe day and night patterns of vertical distribution of fish in the reservoirs, describe fish behaviour near the footrope (i.e. vertical swimming velocity, fish tortuosity, vertical direction of swimming), and find the proportion of fish performing avoidance reactions. Significant differences were found between day and night distributions and behaviours. In total, only 35 of the 1514 acoustically recorded fish performed apparent avoidance behaviour. Twenty-seven avoidance reactions were observed in the day (6.3-% of total fish) while eight were observed at night (0.7-% of total fish). Fish were more active in the daytime, while tending to stay still in the water column with no observable reactions at night. We found significant dependence between the size of fish directly avoiding the trawl and their swimming velocities. The greatest echogram slope values belonged to those fish with a strong avoidance reaction. When the footrope was perceived, the fish reacted from approximately 1 m vertical distances and escaped up to 5 m below the footrope (usually 1–2.5 m). Light, water transparency and temperature stratification were the dominant factors influencing vertical distribution and fish avoidance behaviour.

1. Introduction

Many authors have studied how fish behave in response to active fishing gear, particularly for commercially important marine species (Engås and Godø, 1989; Godø and Walsh, 1992; Misund et al., 1999; Kim and Wardle, 2003; Ona and Godø, 1990; Wardle, 1986). However, observations are quite rare in freshwater ecosystems (Rakowitz et al., 2012; Schmidt, 2009) where fish reactions are poorly understood. Detailed knowledge of fish reactions to trawls and understanding fish behaviour in general is important for maximizing efficiency of sampling gear and obtaining more precise estimates of fish abundance (Kubečka et al., 2009). There are many advantages of using trawls as survey gears, including large sampling capacity (Hayes et al., 1996; Kubečka et al., 2009; Winger et al., 2010), as they can cover large areas of open water that are usually difficult to reach using other sampling methods.

It is known that fish behaviour near trawls is species-specific (Piasente et al., 2004) and influenced by biotic and abiotic factors such as water temperature or transparency (Kim and Wardle, 1998; Winger et al., 2010). Fish behaviour in the trawl mouth is highly dependent on light intensity where high light intensities enable fish to maintain visual contact with both the net and other fish, and stay in more coherent groups (Gerlotto, 1996). However, in low light intensity conditions, shoaling behaviour is reduced as fish are more dispersed in the water column and they cannot keep visual contact with their conspecifics. As a result, fish behaviour changes trawl efficiency, which can vary between day and night periods (Rakowitz et al., 2012).

Fish escape from the trawl mouth in different directions. While some studies of European freshwater bodies evaluated lateral

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avoidance reactions (Rakowitz et al., 2012), reactions in the vertical plane (below the trawl) have not been evaluated. Such knowledge is very important for trawl catchability.

Quantification of fish behavior near trawls is a complex task in conditions of low light transparency. In such conditions optical systems are inadequate for fish monitoring, while echosounders have proven to be effective devices. A vertical echosounder is commonly employed in combination with trawls in marine surveys (Graham et al., 2004; Misund, 1997), however observations from freshwater are relatively rare (Emmrich et al., 2010; Schmidt et al., 2005). The split-beam type, used in this study, is equipped with a four-quadrant transducer face that enables us to determine three-dimensional position of targets in the acoustical beam by comparing echo signals in each quadrant (Simmonds and MacLennan, 2005).

The objectives of this study were a) to describe day and night pattern of vertical distribution of fish in the reservoirs so as to allow studying fish reactions to the trawl b) to describe fish behaviour near the footrope of a midwater trawl, andc) to document the proportion of fish with avoidance reactions. The main goal was to evaluate catchability of freshwater trawl for efficient fish stock sampling in the open water.

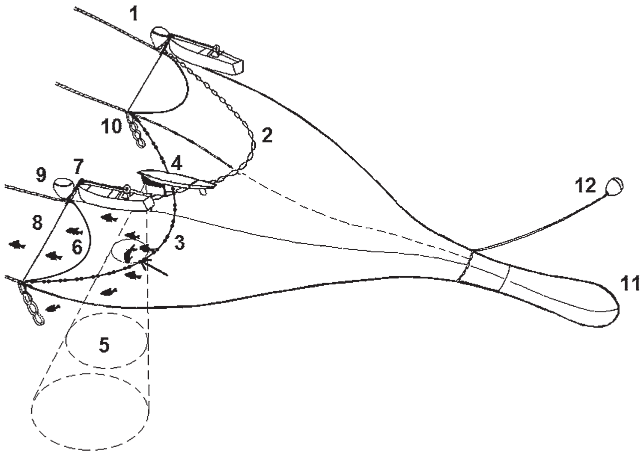

Fig. 1. Scheme of a midwater trawl used during the experiments; 1–bridles, 2–headrope, 3–footrope, 4–floater carrying transducer, 5–acoustical beam, 6–fish in the trawl mouth (black arrow is showing an example of avoidance reaction below the footrope), 7–supporting boat, 8–iron warp regulating depth of the footrope, 9–headrope buoy, 10–weights (chains or concrete-iron blocks), 11–codend, 12–codend buoy.

2. Materials and methods

2.1. Study areas

The survey was conducted in the Želivka Reservoir (2009) and the Římov Reservoir (2009 and 2011) in the Czech Republic during the month of August. The Želivka Reservoir is located in the Central Bohemia (49°43′32′íN; 15°05′20′íE) and has a surface area of 1430 ha, a mean depth of 17 m and a volume of 250 mil. m^3. The Římov Reservoir is located in the South Bohemia (48°51′00′íN; 14°29′30′íE), and has a surface area of 210 ha, a mean depth of 16 m and a volume of 33 mil. m^3. Both reservoirs are used for drinking water storage and are canyon-shaped, with thermal and oxygen stratification during summer. The summer thermocline usually extends 2–3 m in depth in the Římov Reservoir and 5 m in depth in the Želivka Reservoir. The most common species in both reservoirs are Cyprininds and Percids, specifically common bream (*Abramis brama*), roach (*Rutillus rutillus*), bleak (*Alburnus alburnus*), perch (*Perca fluviatilis*), pikeperch (*Sander lucioperca*) and ruffe (*Gymnocephalus cernuus*) (Prchalová et al., 2009; Říha et al., 2012). These species do not have high commercial value in the Czech reservoirs but their abundance may have great effect on water quality.

2.2. Sampling and analyses

A midwater pair trawl (Říha et al., 2012) with a full body length (mouth-codend) of 48 m, a vertical mouth opening of about 8 m, and an effective horizontal mouth opening of up to 13.5 m, with mesh sizes (knot to knot) of 80, 40, and 20 mm in the main body and 10 mm at the codend, was used for the study. The trawl was pulled by the two survey vessels with engine power of 60HP and 210HP. The trawl headrope was always on the surface (Fig. 1). In the Želivka Reservoir the footrope depth was 7–7.3 m during tows. In the Římov Reservoir the footrope depth was up to 8.5 m (2009) and 6 m (2011). Two small supporting boats were used to control the depth of the footrope and to monitor the GPS position of the trawl mouth. The main charateristics of survey hauls is shown in Table 1.

Fish behaviour at the trawl mouth was monitored with a SIMRAD EK 60 split-beam echosounder, operating at a frequency of 38 kHz. The transducer SIMRAD ES 38 – 12, with a 12 degree nominal beam angle was fixed to the windsurf floater attached to the headrope and used to observe fish within the trawl mouth (Fig. 1). The ping rate of the echosounder was between 4.5 and 8 pings per second and the near field was approximately 2 m (Simmonds and MacLennan, 2005). Fish tracks of this range were not included in the analysis.

Both the echosounder and computer were placed aboard the supporting boat. The system calibration was done according to Foote et al. (1987). The lowest size threshold for targets in the acoustic data was set at -54 dB. Smaller targets were unreliable for the acoustical analysis. There was no upper size threshold as no other large objects were expected in the open water. Fish acoustic sizes are shown in target strength - TS (dB) scale. For acoustic sizing only the straight parts of fish tracks without slope were used (normal position of fish with respect to vertical acoustic beam). Sloped tracks that changed time scale and represented diving or rising fish were not suitable for acoustic sizing.

Sonar 5 software (Balk, 2007) was used to analyze acoustical data. A method of target manual tracking, which combines single target detections (SED) of fish into tracks, was used. It is based on the identification of hits obtained from a single object. At least three consecutive echoes were set to make one track. The tracks consist of several single detections shown as points per ping on a two-dimensional echogram. The Y-axis of the echogram shows the depth and the *X*-axis shows time or ping number. Information such as depth, target strength, three-dimensional position (x, y, z coordinates), echo length, etc. were stored with each fish track in a Fishbaskets database in *Sonar 5* and exported for further processing. Ambient water temperature was measured by an YSI 556 MPS probe at several localities in both reservoirs and water transparency was measured by a Secchi disk (Fig. 2).

A vertical track slope, calculated for all fish tracks, was used in two ways in this study: a) as a measure of vertical direction of swimming and b) to compute swimming velocities of fish in the vertical plane. The vertical track slope is defined as the average change in range per ping during a trace ($\Delta R/\Delta n$) (Draštík and Kubečka, 2005). The track slope demonstrated whether fish descended (positive slope), ascended (negative slope) or stayed at the same depth (close to zero slope). Slope in the range of ±1 cm/ping was considered as no slope, meaning that the fish did not ascend or descend. This is common fish behaviour at night and in deeper water during the day in reservoirs (Jarolím et al., 2010). To compute the vertical swim-

Table 1
General characteristics of hauls performed in reservoirs.

	Total number of DAY hauls	Total number of NIGHT hauls	Total time (h) of trawling	Mean towing velocity (km.h^{-1})	Mean tow duration (min)	Total sampled area (ha)
Želivka 2009	9	7	10.02	4	37.4	70.3
Římov 2009	6	9	4.35	4.5	18	26.5
Římov 2011	23	19	5.13	4	10	38.5
Σ	38	35	19.5	–	–	135.3

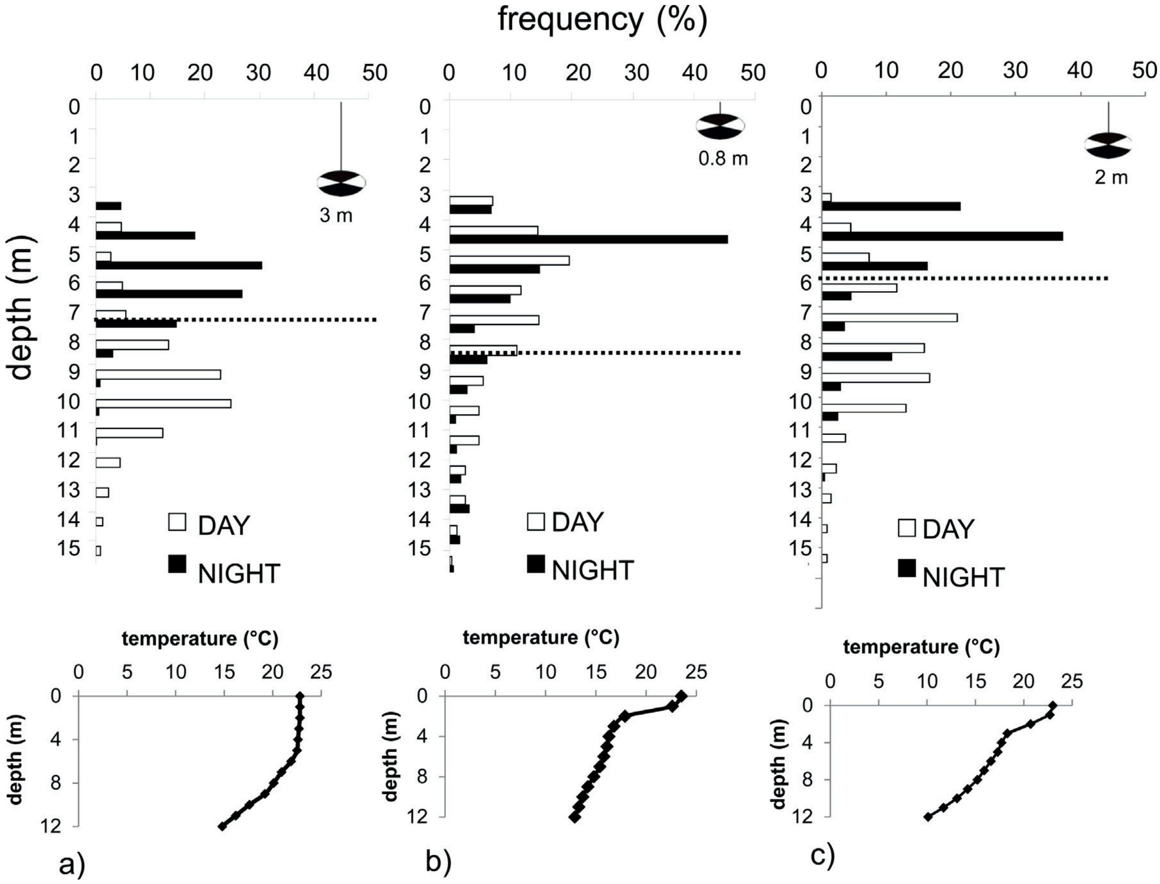

Fig. 2. Histogram of depth distribution for both years shown separately a) the Želivka Reservoir (2009); b) the Římov Reservoir (2009) and c) the Římov Reservoir (2011). The black dotted line shows the position of the footrope. Secchi discs show medium transparency depths (m) during the seasons. Temperature stratification for the reservoirs is shown below.

ming velocity of fish, vertical range (ΔR) was divided by the time during which fish were recorded in the acoustical beam. Swimming velocity means vertical swimming velocity (depth change) throughout the paper.

Recorded tracks were grouped according to whether they crossed the footrope or not. Sloped fish crossing the footrope were descending, and escaping towards deeper water (positive slope). These were classified as "E" - escaping fish. The beginning of the escape response was identified on the SED echogram when part of a fish track occurred above the footrope or at the position of the footrope while the other part of the same track was observed below the footrope. The first echo in the track is considered the start of the response while the last echo is considered the end of the response. To standardize the rate of avoidance reactions in both reservoirs, a relative unit, expressed as the number of avoidance reactions per one hour of trawling (NAPTH) was introduced.

The fish that did not cross the footrope were recorded as either above the footrope (A) or under the footrope (U) with respect to their initial position. The trawl footrope was used as a marker to classify the vertical position of fish on the echogram. Fish above the footrope (A) included fish in the trawl path, which occurred from a 2 m depth (the boundary of the near field of the transducer) to 6–8.5 m deep (the ranges of footrope depths in the Římov Reservoir) and up to 7.3 m (in the Želivka Reservoir). These fish apparently did not escape the trawl and were likely captured at the codend. U category fish stayed deeper than the position of the footrope and were not captured.

Measuring tortuosity is a way to evaluate the complexity of a fish's movement. Tortuosity is a ratio of the length of the straight line between the first and last echo to the length of the total track of the fish (Rakowitz et al., 2012). Relationships between tortuosity (a dependent variable) and the footrope position (factor against which the dependent variable was tested) were evaluated. In this case, all three dimensions (*x*–along ship, *y*–athwartship, *z*–depth) were considered for calculation. Fish that were swimming in a straight line had tortuosity values close to "1" and fish with more complex trajectories had tortuosity values close to "0". We assumed that fish with more complex motion would have stronger reactions to approaching trawl gear (i.e. perform avoidance behaviour) compared to those which did not respond.

Table 2
Number of avoidance reactions with respect to time of trawling (acoustics sampling).

	Želivka 2009			Římov 2009 and 2011		
Period of day	Number of all acoustically recorded fish	Total number of avoidance reactions	NAPHT*	Number of all acoustically recorded fish	Total number of avoidance reactions	NAPHT*
Day	316	21 (6.6%)	3.91	108	6 (5.6%)	1.12
Night	807	4 (0.5%)	0.86	283	4 (1.4%)	0.96

*Number of avoidance reactions per one hour of trawling.
**Numbers in brackets show percentage of avoiding fish at day and night.

2.3. Statistical analysis

The statistical tests were based on all acoustically recorded fish. We tested the following 5 relationships as part of the study:

1) Fish vertical distribution was tested with respect to time of a day period to find whether the vertical distribution of fish is affected by the diel period.

2) Vertical track slope was evaluated against the position of fish with respect to the footrope at the start of a track, fish size and velocity. We also compared slope values of A and U fish.

3) Fish response (escaping) activity (categories A, U and E) was tested against the fish size (TS) and time of a day period. It is hypothesized that more avoidance activities would occur during the day and in larger individuals.

4) Tortuosity was tested against fish size and position relative to the footrope. It is hypothesized that tortuosity would be affected by the fish size and position relative to the footrope. Tortuosity between the fish above the footrope (A) and escaping individuals (E) was evaluated to see if fish performed any complex behaviour in a trawl path, prior to avoiding the footrope.

5) Vertical swimming velocity was tested in relation to vertical track slope, fish size and position with respect to the footrope. It was hypothesized that fish crossing the footrope would be fastest individuals. In addition, dependence between the size of the escaping fish and their velocities were evaluated.

Generalized linear models (GLM) were applied to tests 1, 2 and 5, using data with continuous dependent predictors (i.e., vertical distribution of fish and vertical track slope). The Logit model was applied to tests 3 and 4, using data with categorical dependent predictors (i.e. fish response activity and fish tortuosity). Tortuosity values 0–0.4 were treated as ”tortuous movement” (category avoiding fish) while tortuosity values 0.5–1 were treated as ”straight movement” (category non-avoiding fish). The Kruskall-Wallis test was used to compare vertical slopes for A and U categories of fish. Statistics and models are summarized in Table 3. Statistical software (StatSoft and Inc. (2011)) was used for the statistical analysis.

3. Results

3.1. Distribution of fish

Distinct day and night vertical distribution and size composition patterns were observed in the Želivka and the Římov Reservoirs (Fig. 2, Table 3, line 1). At night fish tended to migrate towards the surface and were more likely to be in the trawl path.

The most dominant species caught in trawls in both reservoirs were cyprinids: bream, roach and bleak. Asp (*Aspius aspius*), pikeperch (*Sander lucioperca*) and catfish (*Silurus glanis*) were also caught. In the Želivka Reservoir we observed a distinct pattern in day/night size composition revealed by both direct trawl catches and acoustical observations (Fig. 5). During the day large bream occupied open water while at night, bleak, small roach, and bream predominated. Direct trawl catches also revealed a certain proportion of large bream in open water at night (Fig. 4). In the Římov Reservoir, a similar shift in size composition between day and night was observed. There was a greater range of sizes of fish in the Římov Reservoir than in the Želivka Reservoir. Comparison between acoustic sizes (sonar measurements) and directly measured fish sizes (trawl catches) showed similar trends (Fig. 5).

Table 3
Summary of statistical results.

Želivka

No. of tested relationship (2.3.)	Dependent variable	Method	Explanatory variables				
			Diel period	Acoustic size	Vertical swimming velocity	Track slope	fish A,U, E
1)	depth	GLM	$p = 0.000$				
2)	track slope	GLM		$p = 0.005$	$p = 0.000$		$p = 0.000$
3)	fish activity	Logit Model	$p = 0.000$	$p = 0.000$			
4)	fish tortuosity	Logit Model		$p = 0.041$			$p = 0.000$
	fish tortuosity	Logit Model					$p = 0.000$*
5)	velocity	GLM	$p = 0.040$	$p = 0.656$		$p = 0.000$	
	velocity	GLM		$p = 0.04$**			

Římov

No. of tested relationship (2.3.)	Dependent variable	Method	Explanatory variable				
			Diel period	Acoustic size	Vertical swimming velocity	Track slope	Fish A,U, E
1)	depth	GLM	$p = 0.000$				
2)	track slope	GLM		$p = 0.03$	$p = 0.000$		$p = 0.000$
3)	fish activity	Logit Model	$p = 0.94$	$p = 0.001$			
4)	fish tortuosity	Logit Model		$p = 0.78$			$p = 0.022$
	fish tortuosity	Logit Model					$p = 0.79$*
5)	velocity	GLM	$p = 0.018$	$p = 0.14$		$p = 0.000$	
	velocity	GLM		$p = 0.50$**			

* Tested only for A and E fish categories.
** Tested only for fish E category.

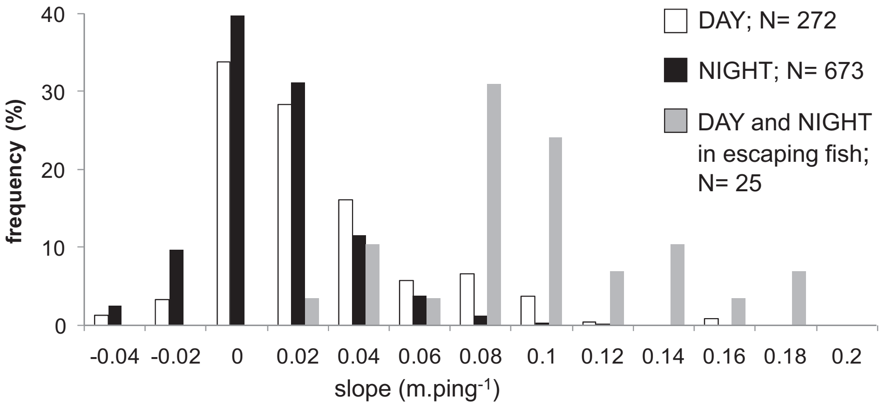

Fig. 3. Histogram for fish slope – example from the Želivka Reservoir. It is apparent that the most positive slope values belong to the directly avoiding individuals (E fish).

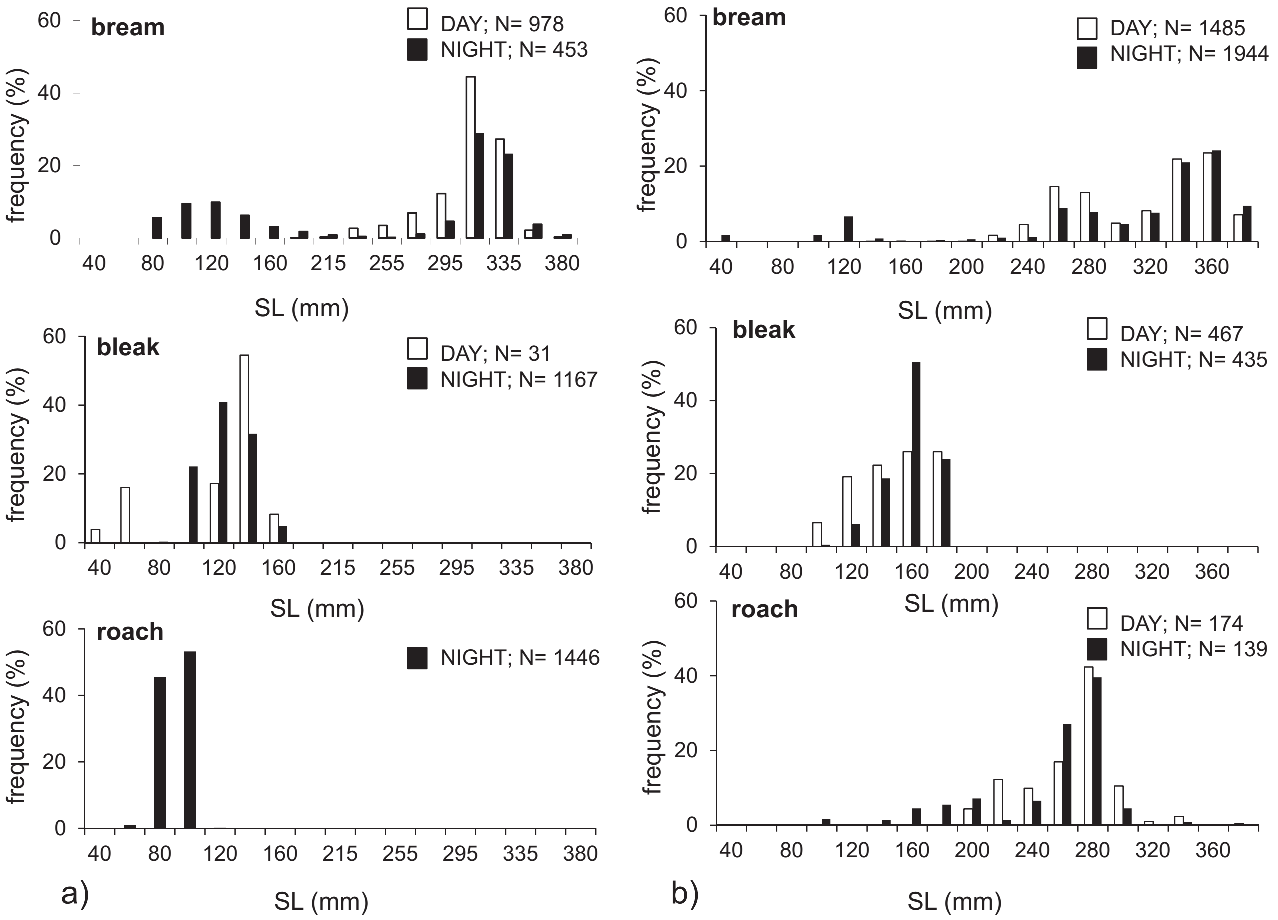

Fig. 4. (a) Size distribution of single species caught in the trawl: bream, bleak and roach in the Želivka Reservoir. b) Size distribution of single species caught in the trawl: bream, bleak and roach in the Římov Reservoir (data from 2009 and 2011 pooled together).

3.2. Track slope and fish avoidance behavior

Slope in relation to the footrope position, fish size and vertical velocity was evaluated. All factors influenced slope in the multifactorial test design in both reservoirs. Most observations were close to zero slope (Fig. 3), indicating weak or no reaction. The largest values of positive slope belonged to the fish directly escaping the footrope (Fig. 3). Fish with negative slope were also present.

Fish size, vertical swimming velocity and the position with respect to the footrope affected slope significantly in both reservoirs (Table 3, line 2). The slope between fish above and below the footrope was significantly different in the Želivka Reservoir ($p < 0.001$) and the Římov Reservoir ($p = 0.02$) (Kruskall-Wallis test). There were higher values of positive slope in U category.

Twenty seven avoidance reactions were recorded on the echogram during day trawling in both reservoirs (Table 2) where fish perceived the gear well and dove up to 5 m below it to escape (usual escape range was 1–2.5 m, Fig. 6). The frequency of day observations was higher in the Želivka Reservoir than in the Římov Reservoir but only small differences were obtained from night observations in both reservoirs (Table 2). The vertical distance from which fish started to clearly avoid the approaching footrope was

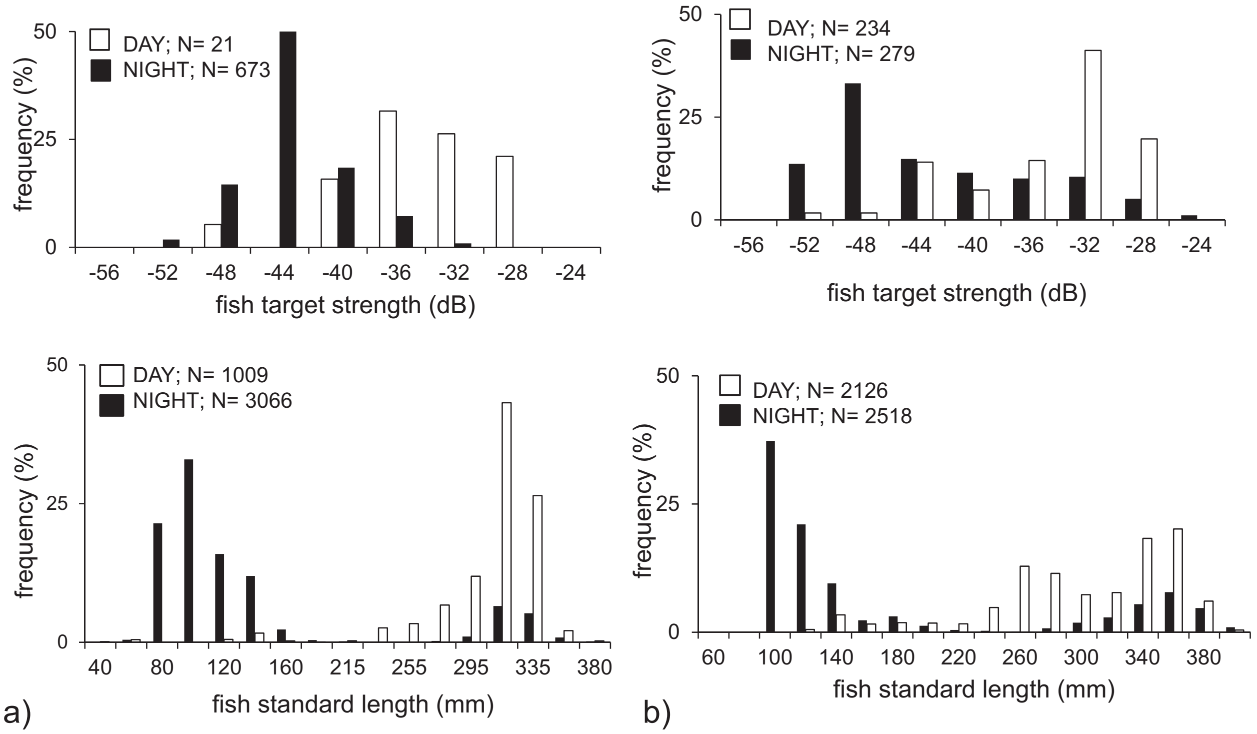

Fig. 5. (a) Histogram for size distribution of fish – the Želivka Reservoir showing only fish above the footrope; UPPER picture: acoustics results, LOWER picture: direct trawl catches. b) Histogram for size distribution of fish – the Římov Reservoir (data from 2009 and 2011 pooled together) showing only fish above the footrope; UPPER picture: acoustics results, LOWER picture: direct trawl catches.

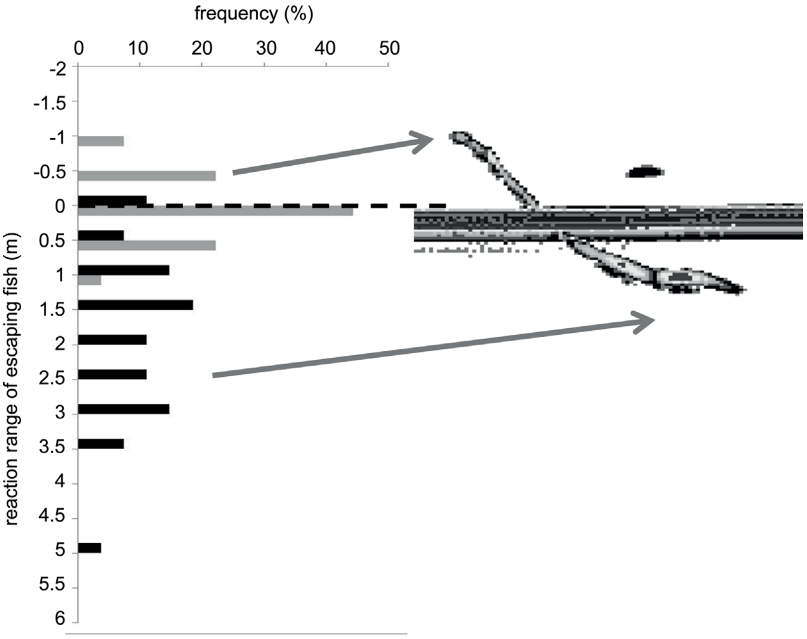

Fig. 6. Vertical reaction distances of fish (day situation in the Želivka Reservoir). The gray columns stand for the distance from the footrope in which fish obviously started to react. The black columns stand for the distance which fish reached after their escape. The mean depth of the footrope observed during avoidance reactions was about 7.6 m and it was set at zero for better comparability of all records. The footrope is shown as a dashed black line. The right side picture shows an echogram of typical escaping fish crossing the footrope of the trawl (thick horizontal line). This particular fish started to react when it was 1 m above the footrope and it reached more than 1 m below the footrope at the end of record.

about 1 m (in both directions of reaction range). The depth position of fish at the start and the end of avoidance reaction are shown in 6 .

The effect on escaping activity was evaluated for time of day and fish size (Table 3, line 3). Different results were obtained for the diel period factor in both reservoirs. In the Želivka Reservoir time of day affected escaping activity while not so in the Římov Reservoir. Fish size had a positive effect on the escaping activity in both reservoirs. In general 5.6–6.6% of fish were escaping during the day while only 0.5–1.4-% were escaping during the night.

Avoidance behaviour in both reservoirs was influenced by the abiotic conditions. In the Želivka Reservoir, water column was less thermally stratified and higher water transparency was measured

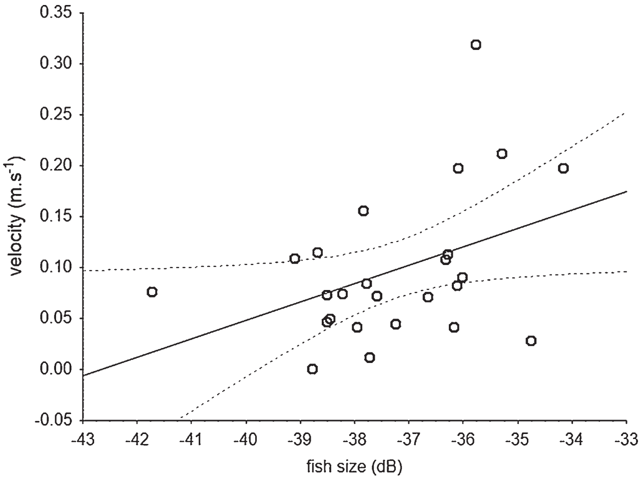

Fig. 7. Relationship between the fish size and fish vertical velocity of 25 fish directly avoiding the footrope in the Želivka Reservoir (day time). Depen dences between the fish size and velocity were found in both reservoirs, but only Želivka was found significant (regression equation: fish velocity = 0.77 + 0.0181*x; dashed line depicts 0.95 conf.int).

than in the Římov Reservoir (Fig. 2) which contributed to higher rate of avoidance reactions in the Želivka Reservoir. Observed fish behaviour was also affected by the effective diameter of the acoustical beam that was approximately 1.7 m at the depth of the footrope and therefore only 13% of the footrope length was sampled.

3.3. *Fish tortuosity*

The location of fish with respect to the footrope proved to affect tortuosity in both reservoirs (Table 3, line 4). Further we examined the difference in the tortuosity of fish in a trawl path (A) and fish directly avoiding the trawl (E). The difference in tortuosity between A and E groups in the Želivka Reservoir was significant ($p > 0.001$). No difference in tortuosity was found between A and E groups in the Římov Reservoir ($p = 0.79$). Fish tortuosity was affected by the fish size only in the Želivka Reservoir where larger individuals possessed more complex trajectories.

3.4. *Vertical swimming velocity*

Fish velocities in a vertical plane ranged between 0 and 0.33 m.s^{-1}. The highest values belonged to the fish directly avoiding the footrope (E). Diel period and the track slope affected fish velocity in both reservoirs (Table 3, line 5). Dependence between the size of fish that directly avoided footrope and their velocities was found only in the Želivka Reservoir indicating that larger individuals swam faster (Fig. 7).

4. Discussion

In this study we investigated fish behaviour in the mouth of the midwater trawl regarding fish's vertical swimming velocity, vertical track slope, fish size and position relative to the footrope. The rate of avoidance reactions in the vertical plane and diel pattern of vertical distribution of fish in the reservoirs was also evaluated. The work complements observations of Rakowitz et al. (2012) who described avoidance behaviour in the lateral direction.

Fish day and night vertical distribution was influenced by abiotic factors as found by the different depth distributions in both reservoirs. During the night, fish moved upwards and were found in shallower layers in both reservoirs which resulted in higher susceptibility to the trawl. During the day, fish were found in larger numbers below the footrope in the Želivka Reservoir while in the Římov Reservoir, difference in day/night pattern of fish distribution was less striking. In both reservoirs the absolute density of large fish in the open water declined slightly due to partial inshore migration (Muška et al., 2013; Říha et al., 2015). The difference in day distribution of fish between reservoirs was likely caused by differing water transparency and temperature conditions. Prchalová et al. (2008, 2009) found these abiotic factors as the main drivers of vertical distributions of fish in these reservoirs. We also obtained differences in day and night size distributions from acoustical and trawl catch data. Both methods showed that predominantly large fish inhabited open water during the day while small fish dominated at night in this zone. The trawl catches identified adult bream as the dominant species of day catches while bleak and small roach were the dominant night species. Such results are in agreement with other studies from these reservoirs dealing with diel changes of fish habitat utilization (Muška et al., 2013; Říha et al., 2015). Larger proportions of small fish could contribute to a lower share of avoidance reactions at night as small fish are very passive at night (Říha et al., 2012).

The study confirmed that vertical avoidance behaviour can be studied using the vertical track slope, as was found by Draštík and Kubečka (2005) in horizontal sonar observations. In both reservoirs, there were many daytime observations of the highest positive slope values due to higher proportions of escaping fish. The escapement was always directed below the footrope and thus avoiding individuals were not caught in the trawl. Escaping fish dove up to 5 m below the trawl. Downward movement during avoidance reactions has been previously observed and appears to be a common response (Suuronen et al., 1997; Williams et al., 2013). The vertical distance from which fish started to avoid the trawl was about 1 m which agrees with reaction distance found for freshwater fish (Pyanov, 1993).

In total, 35 of the 1514 acoustically recorded fish performed apparent avoidance behaviour and time of day effects avoidance behaviour importantly. Twenty-seven avoidance reactions were observed during the day in both reservoirs (6.3 % of total fish) while eight were observed at night (0.7% of total fish). A similar pattern of avoidance behaviour with respect to day period was found by Suuronen et al. (1997) in Baltic herring (*Clupea harengus*). Far fewer avoidance observations were obtained at night when visibility was low and motionless fish seemed to “burst” dive when disturbed by contact with the footrope. Low ambient visibility makes it difficult for fish to orient themselves with respect to the fishing gear (Olla et al., 2000; Kim and Wardle, 1998; Williams et al., 2013). Night trawling results are likely to be much less influenced by fish avoidance under the footrope in pelagic trawls. However, both marine and freshwater trawling considerably underestimates abundance of small fish at night because they obviously escape through the netting of the side panels (Říha et al., 2012; Williams et al., 2013). Therefore, experiments with side pocket-nets that catch fish escaping through the side panels would be a useful tool (Ingólfsson and Jørgensen, 2006; Suuronen et al., 1997; Williams et al., 2011).

Important factor influencing avoidance behaviour was the fish size. Larger fish swam faster during avoidance reactions in the Želivka Reservoir and we assume that the strongest avoidance was performed by large bream that created 79 % of the species composition in both reservoirs and that are known to perform stronger avoidance to fishing gear than other species (Pyanov, 1993; Říha et al., 2008). In addition, large silver carp were occasionally observed to avoid the trawl in the Želivka Reservoir (pers.obs.).

Many authors have studied the relationship between fish size and velocity (Čech and Kubečka, 2002; Breen et al., 2004; Main and Sangster, 1983; Videler and He, 2010). Rakowitz et al. (2012) reported that fish avoided the trawl gear in horizontal directions at velocities up to 2 m.s^{-1} while we registered much lower velocities (up to 0.33 m.s^{-1}) during our study. However, it must be considered that our intention was to detect vertical avoidance velocities which can be slower than lateral ones. A potential reason for the difference of velocities might be the difference in optical stimuli given by the side panels of the trawl. Side netting panels might have been more visible for fish in comparison to the footrope which was permanently towed in low visibility layers in the Želivka and the Římov Reservoirs.

The study has also revealed dependence between tortuosity and the position of fish relative to the footrope. In general, more complex behaviour was observed in fish directly avoiding the footrope and the erratic trajectories of such fish could be considered anti-predation tactics (Winger et al., 2010). However, straight and tortuous tracks were sometimes observed in both categories of fish, with and without an obvious reaction to the trawl gear, and tortuous trajectories are not necessarily connected with avoidance behaviour. Fish size was correlated positively with tortuosity only in some cases.

This study had several limitations. The first limitation was the acoustical underestimation of fish close to the water surface. During the survey, especially at night, many fish targets were not available for vertical recording due to the transducer's near field and possible disturbance caused by the gear (i.e. trawl headrope, transducer). However, the fish in transducer's near field are quite far from the footrope and thus unlikely to react to it. Therefore this bias is unlikely to be significant. Another limitation is the restricted acoustically sampled area of the footrope. The effective diameter of the acoustic beam is only 1.7 m at the depth of the footrope, thus we were able to sample only about 13% of the footrope length. Split beam echosounders have generally narrow beam (Simmonds and Mac Lennan, 2005) so studies of this nature will be always under sampling all reactions. An effort was made to sample representative sections of the footrope and to extent the observation time to record an adequate number of fish (1514 individuals).

In summary, the vertical track slope was found to be an important characteristic that can predict potential avoidance reactions and thus effect trawl catchability. Tortuosity was not an important factor influencing trawl catchability but is a useful tool for describing the complexity of fish motion and fish activity. Escaping behaviour in the vertical direction could be potentially important but due to a relatively low proportion of fish avoiding footrope, we assume that such individuals do not greatly affect trawl efficiency in reservoirs. Abiotic factors, especially water transparency, influence vertical distribution of fish and their ability to detect trawls. Water transparency and fish vertical distribution should be taken into account during trawling operations.

The main goal of the study was to evaluate fish behaviour with respect to trawl catchability, which is important for effective sampling of freshwater reservoirs. In this work we studied fish behaviour in the trawl mouth. However, how fish behave inside the trawl remains a question. Furthermore, information about pre-trawl avoidance should be also evaluated. Fish avoidance triggered by the vessel or gear noise was observed in the marine environment (Handegard et al., 2003; Ona et al., 2007) but no studies have been carried out in freshwater reservoirs.

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Paper II.

Bathypelagic percid fry, a strongly predominating fry community in a deep European reservoir.

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PRIMARY RESEARCH PAPER

Bathypelagic percid fry, a strongly predominating fry community in a deep European reservoir

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Abstract The distribution, species composition, abundance and shoaling behaviour of young-of-year fish were studied in the canyon-shaped Vír Reservoir (Czech Republic) in mid-June 2010. Using the SIMRAD EK60 echosounder (frequency 120 kHz), fry were acoustically sampled along the longitudinal profile of the reservoir. A framed trawl was used simultaneously to collect fry in the open water. Apparent differences were found in the density of fry between the epipelagic, littoral and bathypelagic zones. Bathypelagic fry strongly predominated in the total fry community creating 95.3% while epipelagic and littoral fry contributed only 4.7%. The bathypelagic fry were represented by perch *Perca fluviatilis* (84.8%), zander *Sander lucioperca* (14.9%) and ruffe *Gymnocephalus cernua* (0.15%) and were observed all along the longitudinal profile of the reservoir creating a distinct layer on the echogram. The layer, composed of shoaling and non-shoaling fry individuals, reached its greatest depth in the Bay part of the reservoir (7.5–14.5 m) and it was rising in the water column towards the tributary. The situation that the bathypelagic percid fry predominate in the reservoir is absolutely unique and it is completely different from published observations from other canyon-shaped reservoirs where epipelagic percid fry prevailed.

Keywords Echosounder · Fry trawling · *Gymnocephalus cernua* · *Perca fluviatilis* · *Sander lucioperca* · Shoals

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Introduction

Compared to shallow restricted area of a littoral zone, open water creates the main part of many European reservoirs (Čech et al., 2005; Vejřík et al., 2016a). In the littoral, fry have to face a strong competition for space and food and in case of a lack of a structural complexity they are highly vulnerable to predation (Gliwicz & Jachner, 1992; Eklöv, 1997; Lewin et al., 2004). These environmental pressures could be reduced or even minimized by shifting the fry community into the poorly occupied deep pelagic zones (Čech & Kubečka, 2006; Čech et al., 2016; Vejřík et al., 2016b).

In early life history, open water offers a crucial temporary habitat for young-of-the-year percids, such as European perch *Perca fluviatilis* L., ruffe *Gymnocephalus cernua* (L.) and zander *Sander lucioperca* (L.) (Treasurer, 1988; Urho, 1996b; Čech et al., 2005). At the end of the larval phase, a portion of a community moves shoreward, where it is later known as littoral fry. A considerable portion may, however, stay in the open water (Wang & Eckmann, 1994; Uhro, 1996b; Čech & Kubečka 2006; Guillard et al., 2006) and create two spatially and temporarily distinct forms described as shallow-water fry (epipelagic, EPF) and deep-water fry (bathypelagic, BPF) (Čech et al., 2005). Epipelagic percid fry, including the closely related species, yellow perch *Perca flavescens* (Mitchill), have been studied worldwide (e.g. Whiteside et al., 1985; Post & McQueen, 1988; Wang & Eckmann, 1994 etc.) while bathypelagic percid fry are less frequently mentioned (Čech et al., 2005; Čech & Kubečka, 2006; Kratochvíl et al., 2010).

Bathypelagic percid fry, that are known for their diel vertical migration, have been well described in the European temperate reservoirs of the North Sea drainage area (Čech et al., 2005; Čech & Kubečka, 2006; Čech et al., 2007a, b; Kratochvíl et al., 2010; Jůza et al., 2012; Petrtýl et al., 2015). Recently, they were also discovered in the Vír Reservoir (the Black Sea drainage area). Bathypelagic fry usually represent a minority of the total pelagic community (Čech et al., 2005) but in the present study we give evidence that the situation can be completely reversed.

Percids represent the dominant fish species in many reservoirs (Mehner et al., 1998; Čech et al. 2007b; Vašek et al., 2013; Vejřík et al., 2016a) and knowledge about the species ecology in all details might be important for provisioning of clear water and other ecosystem services provided by the reservoir ecosystem. For example, it has been shown recently by Vejřík et al. (2016a, b) that superdominant percid fry community could strongly affect other components of the trophic pyramid in the reservoir, change their behaviour and distribution.

The aim of this study was to show that, conversely to what generally reported in literature, bathypelagic fry can dominate the fry community of reservoirs. In particular, we investigated the predominating bathypelagic percid fry community in the Vír Reservoir, its species composition, abundance and size distribution in the context of the vertical and horizontal spatial patterns of the whole fry community; this is, to our best knowledge, the only description of such a phenomenon so far.

Study area

The study was conducted in the canyon-shaped, eutrophic Vír Reservoir, in the Czech Republic (49°34′19.9″N 16°17′20.7″E) (Fig. 1a). The reservoir was built by damming of the Svratka River in 1957 and serves as a water supply for Brno and its surroundings. The maximum area of the reservoir is 223.6 ha and its length 9.3 km, maximal volume 56 million m^3, maximal depth 64 m, mean depth 25 m and the altitude of the water surface 462 m.a.s.l. The fish community of this eutrophic water body is dominated by cyprinid and percid species.

Net sampling

A framed trawl (mouth opening 2 × 2 m; rectangular mesh size 1 × 1.35 mm), a standard device for sampling of pelagic fry (Jůza et al., 2010, 2012), was used to collect fry in the open water along the longitudinal profile of the reservoir during the daylight period on 15 and 16 June 2010 (Fig. 1b). The uppermost tributary part (from 113.5 km upstream) was not sampled due to overall riverine character, insufficient depth, high turbidity and absence of thermal stratification. This part composed <1% of the reservoir volume (Vejřík et al., 2016a). Forty-five tows were done from the surface up to a depth of 12 m in the pelagic zone of the water body. Twenty-four tows were epipelagic (depth <4 m, i.e. in the epilimnion or epilimnion/metalimnion; 25,040 m^3 of water filtered) and 21 were bathypelagic (depth >4 m, i.e. in the hypolimnion; 21,700 m^3 of water filtered). The trawl was towed approximately 50 m behind the 64 hp research vessel at an average speed of 1.04 ms^{-1} (2.03 kn). The average duration of the haul was 4:21 min. The distance of each tow was measured by Garmin GPSmap 60CSx receiver (Garmin International, Inc., Olathe, KS, USA). The total trawl catch was 23,605 fry individuals (trawl mean 50.5 ind.100 m^{-3}).

To estimate fry abundance in the littoral area, four localities along the longitudinal profile of the reservoir were sampled with a beach seine of 10 × 2 m, with a rectangular mesh size of 1 × 1.35 mm, that was set three times in the different transects of each locality

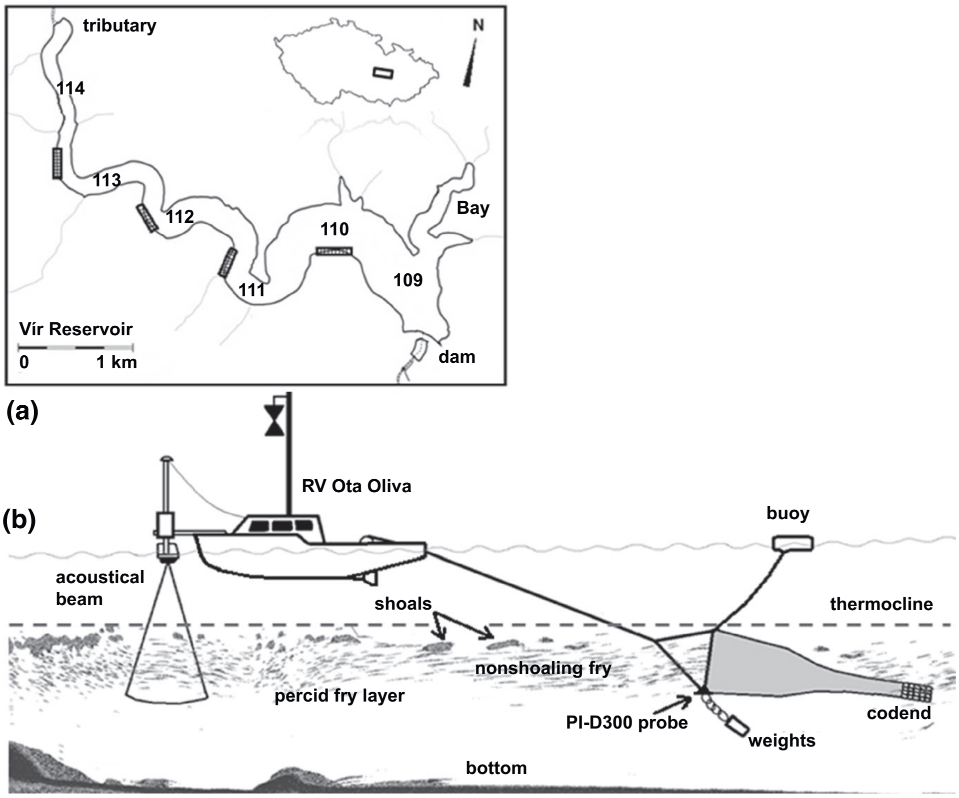

Fig. 1 **a** Map of the Vír Reservoir with kilometres along the river. The *black rectangles* show places where beach-seining was done. **b** Setup of vessel, trawl and echosounder during sampling

($50\ m^3$ filtered per one beach seine haul). The total catch was seven fry individuals (beach seine mean 1.2 ind.100 m^{-3}). In addition, a hand-held push net was used to collect fry individuals in adjacent near-shore areas of the reservoir that were not accessible by a beach seine due to boulders and tree stumps on the bottom (10–20 sampling attempts per locality). Despite a considerable sampling effort no fish were caught in these areas.

All captured fry individuals were immediately preserved in 4% formaldehyde, in the field. In the laboratory, total length (L_T) of each fish was measured to the nearest mm and all individuals were identified to species level (Uhro, 1996a). The bathypelagic, epipelagic and littoral fry trawl catches were expressed as the number of individuals caught per volume effort unit (ind. 100 m^{-3}).

Acoustic sampling

Acoustic sampling was carried out simultaneously with the trawling. A split-beam echosounder SIMRAD EK 60 (120 kHz) with ES120–7C circular transducer was deployed from the aluminium construction of the bow of the vessel. A sonar system calibration was done according to Foote et al. (1987). The acoustic beam, with a 7.1° nominal angle, aimed vertically and monitored the path of the approaching trawl that was towed along a gently curved trajectory to avoid fry avoidance in the sampled area. The average ping rate of the echosounder was 3.5 ping s^{-1} and its pulse length was 0.128 ms^{-1}. Acoustic recordings were subsequently processed in the Sonar5 Pro software (Data Acquisition AS, Oslo, Norway) and fry abundance was counted using the echo-integration method in Sonar 5 described in detail by Čech et al. (2005).

Single fry targets with minimal track length of two consecutive echoes, zero ping-gap and the gating range 0.05 m were automatically tracked for each 5-min echogram using tracking facilities in Sonar 5. Prior to tracking, the echograms were divided into the two groups because shoals and single fish were processed separately. In the first group, only the single fish were preserved. Unwanted echoes from shoals, larger fish or gas bubbles, were manually erased. Simultaneously, a copy of each echogram of the first group was made. In the copies (second group), only the shoals and consecutive shoaling layers were preserved. Shoals were defined as distinct objects, with high scattering properties, clearly separated from each other by a space of water. If more of the shoals were connected together so that they were not recognized as separate objects, they were called shoaling layers.

The tracking was done separately for each one-metre-thick layer of the water column for which abundance was later calculated. The depth range of tracked layers was 2.5–14.5 m below the surface, which is also the depth range of where fry layers occurred. The uppermost 2 m of a water column were not used for the acoustic analysis due to a near-field of the transducer, potential avoidance and disturbance close to the water surface.

In total, 21,032 fry tracks were stored in the echo database (Fishbasket) and later served for a size frequency distribution in the abundance estimation. The lowest threshold for fry target strength (TS) during tracking was −70 dB (5 mm L_T fry), the upper threshold was −54 dB (33 mm L_T fry) which is based both on the size range of the trawl catches and TS-length regression given by Frouzová & Kubečka (2004).

In both non-shoaling and shoaling fry layers, abundance estimation was based on the size composition of trawl catches. For this purpose, L_T of 4,348 bathypelagic fry individuals was converted to the dB units (TS) using the above-mentioned TS-length regression. Abundance was counted for single fish baskets made for single trawled transects using Biomass control dialogue in Sonar 5. In addition, the height and length were measured for 204 fry shoals on the SED echogram. The height was measured by tracking the uppermost and lowermost echo of the shoal on the echogram. The alongside dimension of shoals (m) (i.e. length of the shoals in the direction of navigation) was counted from the ping rate (ping s^{-1}) of the echosounder, time (s) during which the shoal was recorded by the echosounder and the vesseĺs velocity (1.04 ms^{-1}).

Zooplankton sampling

Zooplankton sampling in mid-June was investigated concurrently with fry sampling using conical plankton net with a diameter of 0.2 m and mesh size 200 μm. There were nine vertical hauls conducted in five different localities (Bay, 109th, 111th, 112.5th, 113.5th km, Fig. 1a). Except in the 113.th km, where a single haul was done over 0–6 m, two separate hauls (one in the epipelagial and one in the bathypelagial) were done in each locality. In the same way as with the fry, zooplankton was preserved in formaldehyde, identified to species and their abundance was counted. Five zooplankton families of 21 genera were determined using a microscope.

Furthermore, *Daphnia*, as the main prey of percid fry (Kratochvíl et al., 2008, 2010; Vejřík et al., 2016a, b) irrespective of their species composition, were collected for size structure analysis in the 109th km. A closing net was used to sample *Daphnia* in separate depths of the water column on 9th June and 27th July 2010. Size of the carapace was photographed and measured using a microscope.

Limnological characteristics

Principal limnological characteristics were measured in five localities (dam, Bay, 111th, 112.5th, 113.5th km, Fig. 2) along the longitudinal profile of the reservoir. Water transparency was measured using a Secchi disk; temperature and dissolved oxygen were measured with an YSI 556 MPS probe.

Statistical analysis

Analysis of variance for unequal N (ANOVA) was used to compare the sizes of the bathypelagic fry from the locality “Bay” and sizes of fry from the rest of the localities investigated (109th, 110th, 111th, 112.5th, 113.5th km). Fry size was the dependent variable. In the same way, sizes of *Daphnia* (109th km) between early June and late July were compared in order to evaluate the potential predation effect of bathypelagic percid fry. *Daphnia* size was the dependent variable. Linear regression was used to test the dependence of the average size of perch and zander with respect to the sampled localities along the longitudinal profile of the reservoir. Statistical software (Statsoft Inc., 2011) was used to carry out this statistical analysis.

Results

Juvenile fish

Net catches showed that the bathypelagic fish represented 95.3% of the total fry community in the Vír Reservoir. Perch was the major species of the bathypelagic community contributing 84.1% (trawl mean 77.8, SD ± 112.5

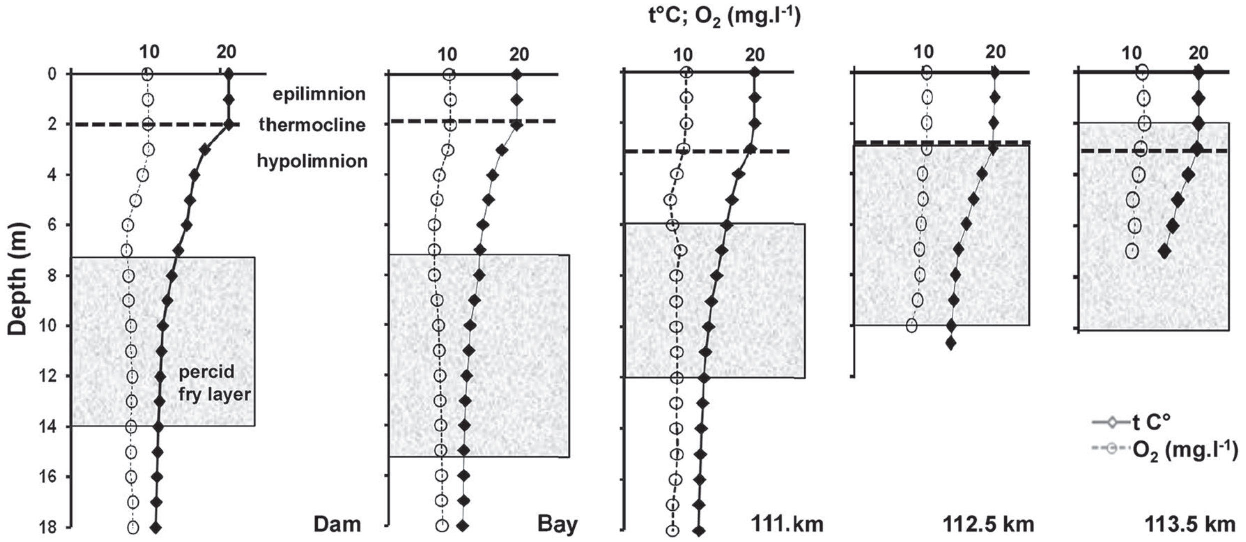

Fig. 2 Temperature and oxygen stratification in the 5 localities of the Vír Reservoir. Secchi thermocline and depth of common fry layer occurrence are also displayed

inds.100 m^{-3}). It was followed by zander at 15.6% (trawl mean 14.4, SD ± 20.5 inds.100 m^{-3}) and ruffe at 0.2% (trawl mean 0.2, SD ± 0.3 inds.100 m^{-3}). In the bathypelagic zone, a small number of cyprinid fry were also found (0.05%, trawl mean 0.05, SD ± 0.2 ind.100 m^{-3}).

In contrast, epipelagic and littoral fry were rather sparse in this water body. The epipelagic fry were composed of perch (95.4%, trawl mean 4.4, SD ± 18.1 inds.100 m^{-3}), zander (3.17%, trawl mean 0.15, SD ± 0.23 inds.100 m^{-3}) and ruffe (0.6%, trawl mean 0.03, SD ± 0.08 inds.100 m^{-3}). A small number of cyprinids were also present (0.74%, trawl mean 0.03, SD ± 0.05 inds.100 m^{-3}). In contrast, littoral fry comprised only 0.2% of the total fish fry community in the reservoir which represents a density of 1.2 inds.100 m^{-3}). The littoral fry were composed of perch (28.5%, seine mean 0.33, SD ± 0.34 inds.100 m^{-3}), cyprinids (28.5%, seine mean 0.33, SD ± 0.28 inds.100 m^{-3}) and pike (42.85%, seine mean 0.5, SD ± 0.62 inds.100 m^{-3}). Fry densities from the bathypelagic, epipelagic and littoral hauls are summarized in Fig. 3.

When we focus on the size distribution of the bathypelagic fry in the trawl catches, perch were the largest, reaching an average size of 20 mm L_T (SD ± 4.3). Zander were smaller, reaching an average size of 17 mm L_T (SD ± 3.7) and in some hauls small ruffe of average size of 6 mm L_T (SD ± 1.06) were also present. An apparent trend was observed in the size composition of bathypelagic fry along the longitudinal profile of the reservoir. Average L_T in both perch and zander increased towards the tributary (perch: $F = 146.42$, $P < 0.001$; zander: $F = 84.8929$, $P < 0.001$) (Fig. 4) and the largest fry were observed in the Bay locality compared to the rest of the reservoir (ANOVA, $F = 1.16$, $P = 0.03$).

Acoustic data showed that the bathypelagic fry created a dense scattering layer (Fig. 1b). This layer was composed of both shoaling and non-shoaling individuals and reached an average acoustic density of 500 ind.100 m^{-3} (SD ± 1072). Non-shoaling fry reached an average acoustic density of 33 ind.100 m^{-3} (SD ± 29.9), while most of the fry layer consisted of shoals of average acoustic density 1250 ind.100 m^{-3} (SD ± 1443). The shoals were predominately situated in the upper part of the fry layer. As for the main parameters of the acoustically detected shoals ($N = 141$), their average height was 0.6 m (SD ± 0.59) (Fig. 5a) and their average length was 0.8 m (SD ± 1.33) (Fig. 5b).

Regarding the distribution of bathypelagic fry along the longitudinal profile of the reservoir, the bathypelagic fry layer was spread along the whole longitudinal profile and it reached the highest acoustic density (900 ind.100 m^{-3}, SD ± 323.5) in the 112.5th km. Except for 112.5th km, the highest abundance was found in the Bay locality, near the left inlet to the reservoir, close to the dam. The lowest acoustic density of the fry layer, where no shoals were observed, was recorded at the 111th km (17 ind.100 m^{-3}, SD ± 8.89) (Table 1).

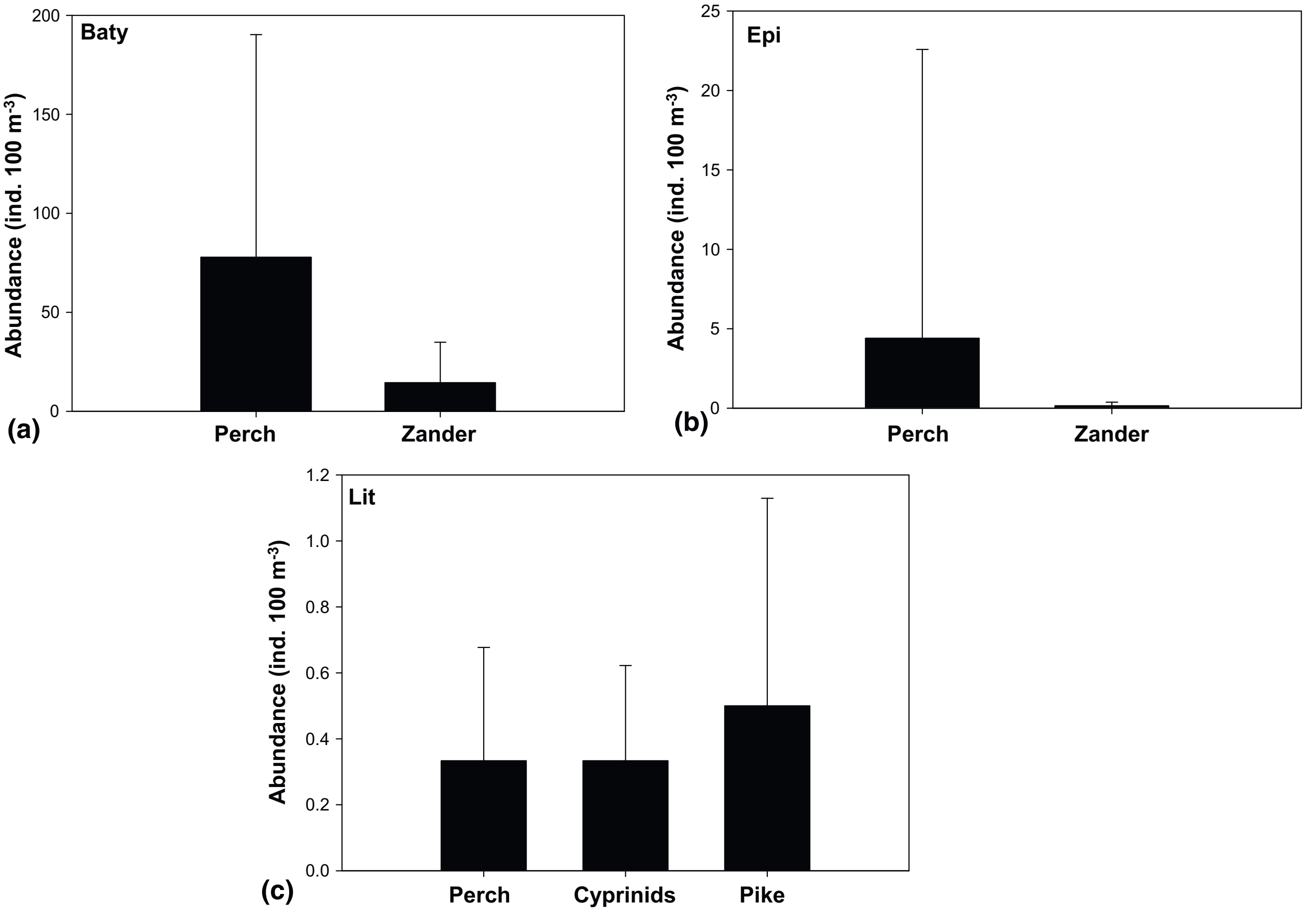

Fig. 3 Abundance (mean ± SD) of fry from the Vír Reservoir in **a** 21 bathypelagic hauls, **b** 24 epipelagic hauls and **c** 12 littoral beach seine hauls. The ruffe is not depicted due to the very low number of individuals

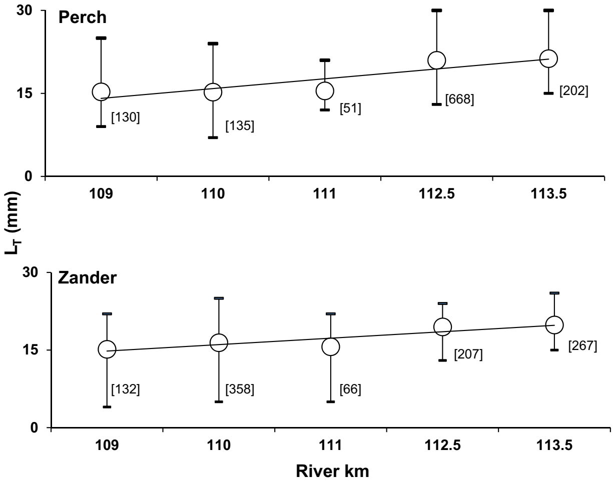

Fig. 4 Total length (min., mean, max.) of **a** bathypelagic perch and **b** zander in different localities along the longitudinal profile of the Vír Reservoir. The *numbers in brackets* are numbers of fish for which L_T was measured. The total length (mean ± SD) of epipelagic ($N = 209$) and bathypelagic fry ($N = 2903$). *Regression line for perch* size (mm) = −80.9604 + 0.9664x., *Regression line for zander* size (mm) = −69.7388 + 0.8492*x

As for the vertical pattern of their distribution, the bathypelagic fry layer was rising in the water column from the dam towards the tributary as the fry were following sharply decreasing water transparency (from 3.4 m in the Bay and dam to 1.4 m at 113.5th km). In the upper part of the reservoir (113.5th km), abundant shoals of percid fry were present both in the hypolimnion and also around the thermocline (Table 1). In contrast, the fry layer reached the deepest depth in the Bay (14.5 m) where the largest water transparency was measured. In this locality, the longest and highest shoals, that sometimes created consecutive layers, were also observed (Table 1).

Zooplankton

Apart from *Synchaeta* (Rotifera), the family Daphnidae were the most abundant zooplankton taxon in the Vír Reservoir in mid-June, contributing 41% to the

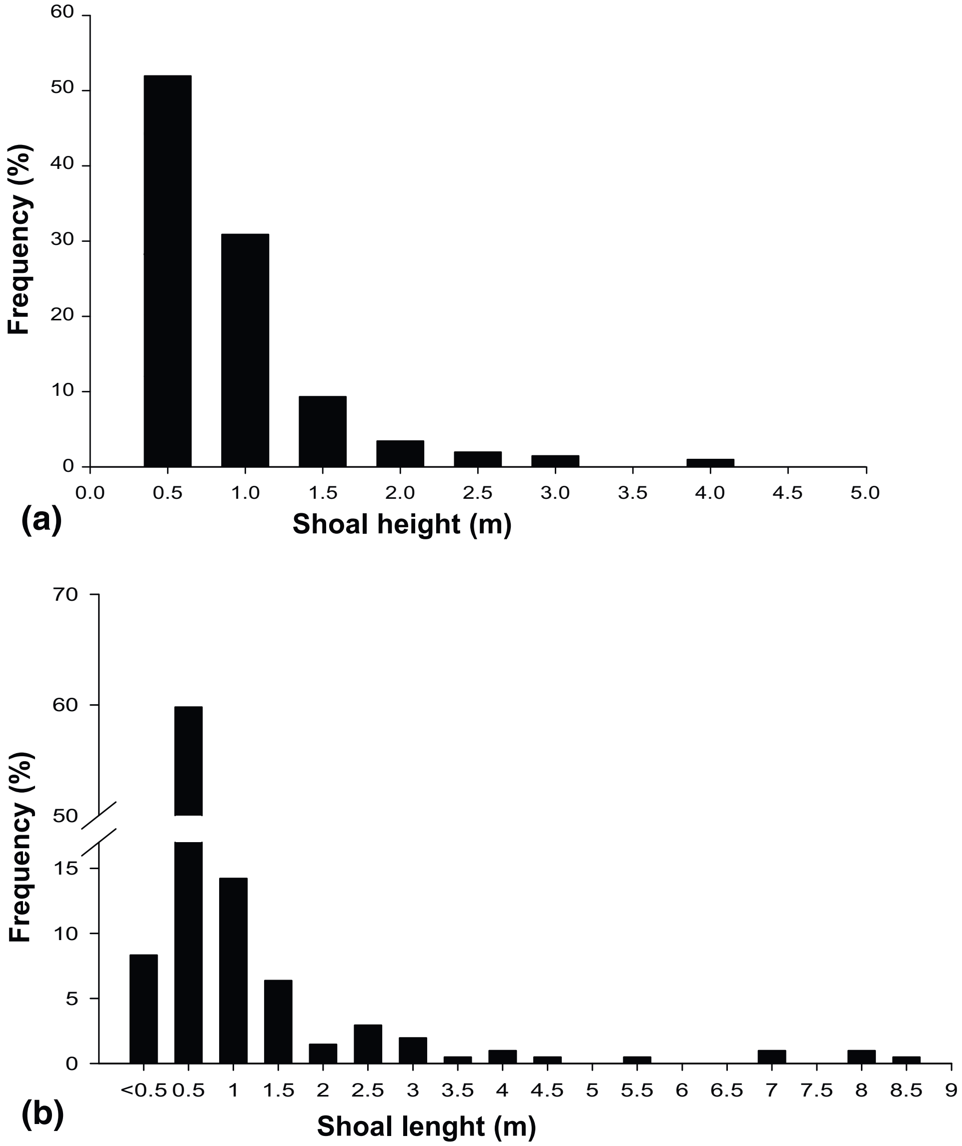

Fig. 5 **a** Height (m) and **b** alongship dimension (m) of the acoustically detected percid fry shoals ($N = 141$) in the Vír Reservoir observed from 8:36 to 14:22 h during 15 June 2010 and 16 June 2010

total zooplankton abundance. Daphnidae were followed by the families Cyclopidae (29% of zooplankton abundance) and Diaptomidae (16% of abundance). The highest abundance of epipelagic zooplankton was observed in the 109th km area, while highest abundance of bathypelagic zooplankton occurred in the 111th km area (Fig. 6).

When we focus solely on *Daphnia*, the most striking difference was found when sizes of *Daphnia* from the mid-water column between early June (9.6.) and late July (27.7.) were compared. *Daphnia* occupying 2.5–11 m depths in early June (Fig. 7a) reached a mean size of 1.04 mm (Fig. 7c). In late July, *Daphnia* occupied depths 6–15 m (Fig. 7b) and were markedly smaller (mean size 0.5 mm) (ANOVA, $F = 263.6$, $P < 0.001$) (Fig. 7d). The less striking but significant difference was found when the sizes of *Daphnia* from the upper water column were compared between both months. The *Daphnia* that occupied depths between 0 and 2 m (Fig. 7a) reached a mean size of 0.75 mm in early June (Fig. 7c). In late July, they extended to 5 m (Fig. 7b) and reached a mean size of 0.54 mm (ANOVA, $F = 7.16$, $P = 0.007$) (Fig. 7d). In late July, some *Daphnia* were also found in the deep bathypelagial (18–55 m) (Fig. 7b) but since these individuals occurred deeper than the bathypelagic fry layer, they were outside the main fish interest.

Table 1 Bathypelagic fry layer along the longitudinal profile of the Vír Reservoir

DAM ← → INFLOW

			BAY			109			110	111			112.5			113.5
t°C[a]			12.9			13.9			_	13.9			19.3			20.3
$S_{ec}D$[b]			3.4			3.4			_	3.1			2.3			1.4
$D_{m.f.\ a.}$[c]			9.5			7.5			7.5	8.5			3.5			2.5
Shoals N[d]			25			7			1	0			67			31
Avg. abundance[e]			744			237			63	17			373			37
Ds.n.f.*																
2.5															21	21
3.5												900	900		14	14
4.5												700	700	28	5	17
5.5											28	600	314	29	3	16
6.5										12	59	300	180	52	3	28
7.5		400	400		1000	1000	10	300	155	22	110	700	405	116	7	62
8.5	38	2700	1369	5	600	303	32	200	116	30	87		87	111		111
9.5	17	4800	2409	18	600	309	38		38	22	27		27	30		30
10.5	51	2500	1276	25		25	29		29	12						
11.5	72	800	436	15		15	12		12	6						
12.5	45		45	7		7	29		29							
13.5	13		13	1		1										
14.5	6		6													

Grey columns mean acoustic abundance of the non-shoaling fry layer, black columns mean acoustic abundance of the shoaling fry layer. Transparent columns show average acoustic abundances of fry layer. The abundances are expressed as ind.100 m^{-3}

[a] Temperature in the depth of maximal abundance of fry layer (measured in five localities)

[b] $S_{ec}D$ is water transparency (m) measured by a Secchi disk in five localities.

[c] $D_{m.f.a.}$ is the depth (m) of maximal abundance of fry layer. *$D_{s.n.f.}$ is the depth (m) of shoaling and non-shoaling fry layer (numbers in the left most column)

[d] Number of acoustically detected shoals in each locality

[e] Avg. abundance means average abundance of the bathypelagic percid fry in each locality

Discussion

The day survey conducted in the Vír Reservoir in 2010 gave evidence that bathypelagic fry dominated the fry community in the reservoir comprising 95.3%. Epipelagic fry, in contrast, represented only 4.5%. Such finding is rare because bathypelagic fry have represented a minority of the fry community so far (5–28%) (Čech et al., 2005) and sometimes were completely lacking in the water body (Uhro, 1996b; Probst & Eckmann, 2009; Jůza et al., 2010). In agreement with Čech et al. (2005) and Jůza et al. (2012), perch was the major species of the bathypelagic community constituting 84.1% (Fig. 3).

Reasons for such behaviour can be diverse. It is often mentioned that fry occupy deeper, poorly lighted environments in daytime, being less vulnerable to attacks by visually orientated predators (Gliwitz & Jachner, 1992; Staby et al., 2013; Čech et al., 2016). This hypothesis is further supported by shoaling behaviour which is also considered an antipredator strategy (Pitcher & Parrish, 1993). The shoals in the Vír Reservoir were predominately situated in the upper part of the fry layer which agrees with Čech et al. (2005, 2007b) who observed a similar pattern in the reservoirs of the Vltava river cascade. There were many relatively small shoals in mid-June in the Vír Reservoir, reaching an average height of 0.5 m and length of 0.81 m, being smaller than shoals observed by Probst & Eckmann (2009) in Lake Constance. Nevertheless, in the Bay locality and in the upper part of the Vír Reservoir (114.5 km) shoals created massive consecutive layers that were up to 4 m in height and their length exceeded 8 m. Moreover, the hypothesis of this being antipredator strategy is supported by observations of Vejřík et al. (2016b) who found that in

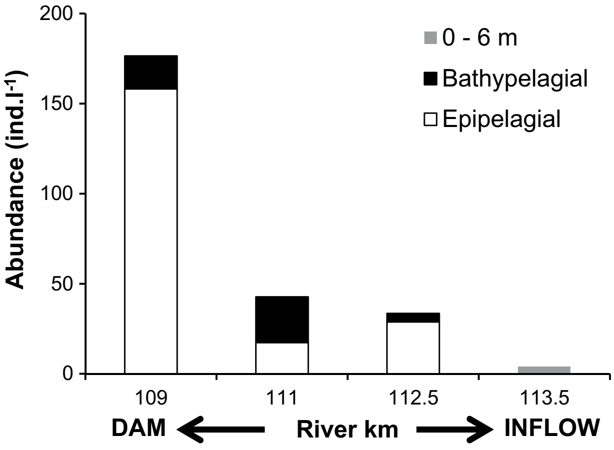

Fig. 6 Abundance of zooplankton (*Daphnia*, *Cyclops, Eudiaptomus* and *Bosmina*) along the longitudinal profile of the Vír Reservoir

the Vír Reservoir, percid fry represented a considerable portion of the diet of adult common bream *Abramis brama* (L.) and common carp *Cyprinus carpio* L. that were present in upper open water and therefore could contribute to the fry avoidance into greater depths.

In the canyon-shaped reservoirs and deep lakes, vertical and horizontal spatial distribution of fish is driven through gradients of abiotic factors, such as light intensity (Appenzeller & Leggett, 1995; Čech et al., 2005), temperature and dissolved oxygen (Baldwin et al., 2002; Vašek et al., 2004). Vertical gradients are usually steeper than horizontal gradients. In the Vír Reservoir, the water column was relatively well stratified thermally in mid-June and the temperature gradient

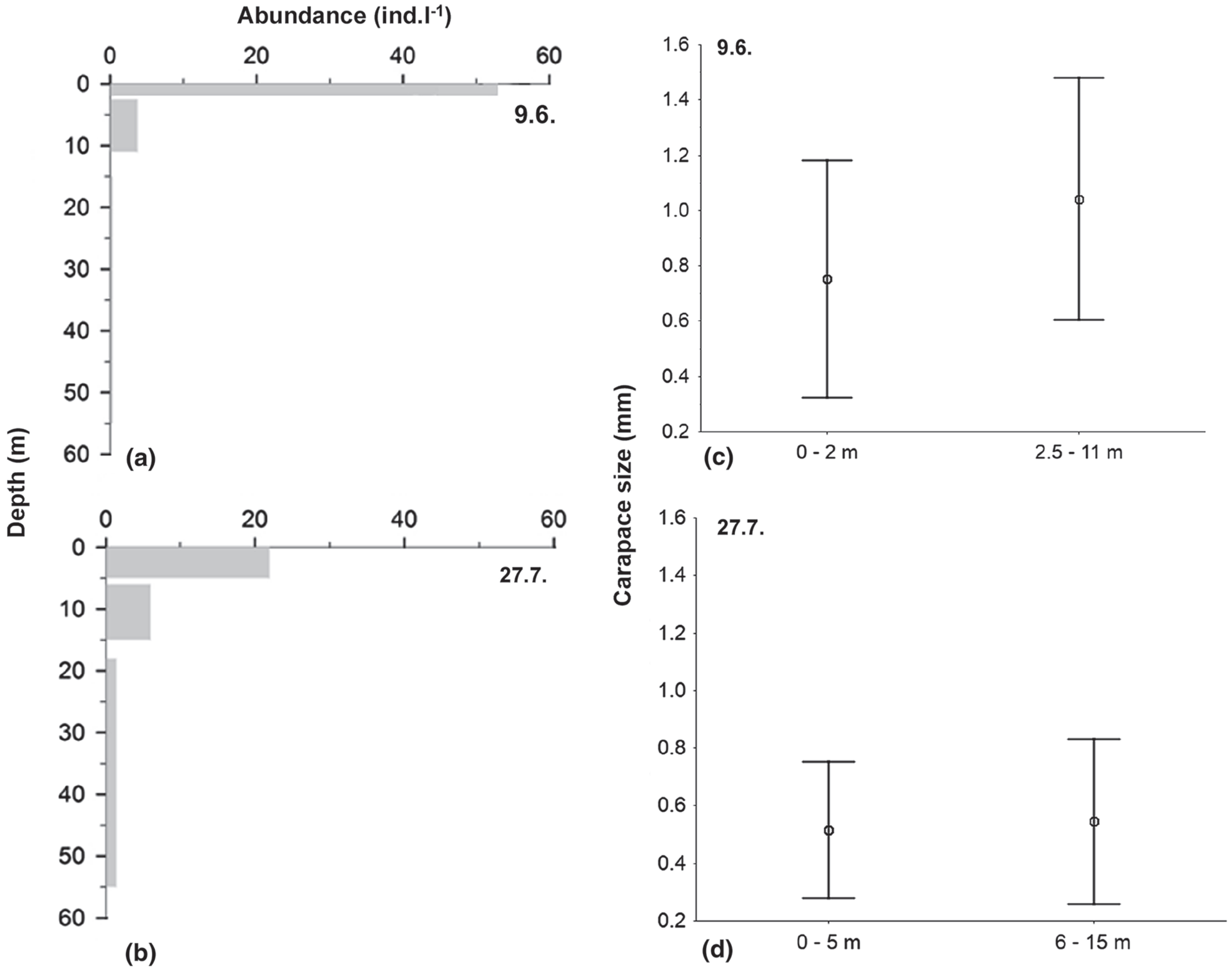

Fig. 7 **a** Abundances (*left*) and **c** carapace sizes (mean ± SD; *right*) of *Daphnia* from the dam part of the Vír Reservoir on 9 June 2010. **b** Abundances (*left*) and **d** carapace sizes (mean ± SD; *right*) of *Daphnia* from the dam part of the Vír Reservoir on 27 July 2010

between the surface and 15 m depth represented ±8°C. In the canyon-shaped reservoirs, cold hypolimnetic and poorly oxygenated water often prevents fry from occupying greater depths which was not the case in the Vír Reservoir where temperature and oxygen concentration in the bathypelagic zone was high enough (it did not decline below 11.9°C and 8 mg.l^{-1}) to still be within the optimal life range of percid fry (Brown et al., 2009). Temperature conditions do not seem to have a marked effect on bathypelagic percid fry distribution in the Vír Reservoir.

The high abundance of fry in the deep open water in the Vír Reservoir can be explained by the availability of zooplankton. The family Daphnidae created the most abundant and frequently consumed zooplankton taxon (Vejřík et al., 2016a). They were followed by Cyclopidae and Diaptomidae that also belong among potential prey of the bathypelagic percid fry (Kratochvíl et al., 2008, 2010). Based on the vertical distribution of the bathypelagic fry layer in the dam area (the highest abundance was observed at 7.5 m), it seems that fry had an opportunity to feed on zooplankton in daytime below or close to the thermocline. Only daytime data were available for the acoustic analysis but a vertical shift of the fry layer towards the water surface (indicating diel vertical migrations described by Čech et al., 2005) was clearly apparent in the late afternoon hours (Z. Sajdlová, pers. observation) so that night occurrence in shallow water layers could be expected. Bathypelagic fry also ascend to the surface each time when clouds covered the sun (M. Čech, pers. observation) and they were present shallower in the water column in parts with low transparency (113.5th km; this study).

To support our assumption about the intensive predation pressure caused by the bathypelagic percid fry, we focused on differences in sizes of *Daphnia* from early June and late July. It is known that zooplankton deal with fish predation by decreasing their body size (Macháček, 1991). Smaller zooplankton are less detectable by visually orienting fish and thus less susceptible to predation (Lazzaro, 1987; Jarolím et al., 2010). In our study, *Daphnia* body size was observed to decrease towards late July in consequence of predation imposed by extremely abundant bathypelagic fry (cf. also Vejřík et al., 2016a). In *Daphnia* that occupied depths of 2.5–11 m in early June, the mean size of a carapace declined from 1.04 to 0.5 mm in late July.

The acoustic survey has revealed that bathypelagic fry created a densely scattered layer consisting of both shoaling and non-shoaling individuals. The fry layer in the Vír Reservoir reached the highest density observed in the Czech canyon-shaped reservoirs. A mean density of 1250 ind.100 m^{-3} seems to be nearly five times higher than that found in the Orlík and Slapy Reservoirs, in the Vltava Cascade (Čech et al., 2007a). Such an extreme fry density could lead to a significant decrease in *Daphnia* size and abundance during the season, moreover, it could lead to a marked changes in the distribution pattern of the main zooplankton species (Vejřík et al., 2016a) and finally to an anomalous predator–prey role exchange between key fish species in the reservoir (Vejřík et al., 2016b).

It should be noted that the acoustic density of the fry layer in our results (Table 1) does not fully match with the trawl results (Fig. 3). These differences might have been caused by (a) the lower trawl catchability of shoals since they are usually composed of older (i.e. larger) fry that have better ability to avoid the trawl (Jůza et al., 2010), (b) by a decrease of the filtering capacity of the trawl caused by both the large zooplankton *Leptodora kindtii* (Focke) and phytoplankton (colonial Cyanobacteria) and (c) also due to a possible distortion (under or overestimation) originating from high target densities that contributed to the total echo energy (Simmonds & McLennan, 2008).

In summary, percid fry, dominated by European perch, preferentially occupied deep open water of the Vír Reservoir in late spring which is considerably different from all the other studies (Čech et al., 2005, 2006, 2007a, b; Vašek et al., 2006; Jůza et al., 2010, 2012). The acoustic survey revealed that fry created a dense scattering layer which was composed mostly of dense shoals. These shoals were predominately situated in the upper part of the layer. The vertical distribution of the fry layer was influenced by availability of zooplankton in both the epi/metalimnion and hypolimnion, by a relatively warm, deep water column that was safe from predators. Percid fry apparently found the bathypelagic zone to be a favourable day refuge. As it has been recently shown by Vejřík et al. (2016a, b), these hidden percid fry could impose considerable predation pressure on zooplankton, which could finally lead to a dramatic decrease of water quality and to the overall destruction of an usual trophic pyramid in the reservoir.

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Paper III.

Are diel vertical migrations of European perch (*Perca fluviatilis* L.) early juveniles under directcontrol of light intensity? Evidence from a large field experiment.

(original pages 1–10 and Appendixes)

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ORIGINAL ARTICLE

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Are diel vertical migrations of European perch (*Perca fluviatilis* L.) early juveniles under direct control of light intensity? Evidence from a large field experiment

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Abstract

1. Diel vertical migrations (DVMs) belong among the most pronounced movements in the aquatic environment. A general pattern of DVMs has been well described, particularly in European perch (*Perca fluviatilis*), but whether the migrations are directly controlled by light and what is the ultimate cause of the diel vertical shifts, remains poorly understood.
2. Undertaking a large-scale field experiment in a thermally stratified, canyon-shaped reservoir, we demonstrated for the first time that DVMs of a bathypelagic early juveniles community, dominated by European perch larvae and juveniles prior the metamorphosis, were under direct control of the light intensity; that is, they did not operate as a genetically fixed behaviour.
3. Prior to the experiment, the depth distribution of the bathypelagic perch early juveniles was strongly correlated with the light intensity on the water surface ($p < .001$). The community underwent regular DVMs between the epilimnion (depth <2.0 m) and hypolimnion (depth >3.0 m) reaching a maximum amplitude of 13 m.
4. Hydroacoustic recordings by the echosounder SIMRAD EK 60 (120 and 400 kHz) showed that during the experiment, when the surface was covered with a large black non-transparent foil (2500 m^2; simulated conditions of complete and constant darkness), the regular vertical movement of the bathypelagic perch early juveniles was interrupted and the community occupied the epilimnion constantly for 24 hr.
5. Immediately after the foil was removed at midday, the bathypelagic perch early juveniles were exposed to a steep increase in light intensity (from <1 LUX to >100 × 10^3 LUX) and they escaped into the hypolimnion where they were safe from visual predation which took place in the bright surface layers (epilimnion particularly). Our findings imply that occupying a deep, dark refuge in the daytime is essential for the survival of perch in their early life stage.

KEYWORDS
acoustics, antipredatory behaviour, black foil, trawling, water surface illumination

1 | INTRODUCTION

Diel activity of fish is controlled externally, by environmental conditions (e.g. light, temperature), and internally, by biological clocks synchronised to daily rhythms of environmental conditions (Čech et al., 2012; Jackson, Peres-Neto, & Olden, 2001; Reebs, 2002; Zhdanova & Reebs, 2006). Light-induced synchronisation adjusts the period of their clocks to 24 hr and its phase to a value that determines the pattern of diel activity (Doyle & Menaker, 2007). Among the most pronounced diel activity in fishes is shifts between habitats, performed to seek safe temporary refuges (Eggers, 1978; Gliwicz & Jachner, 1992; Hardiman, Johnson, & Martinez, 2004; Rechencq, Sosnovsky, Macchi, Alvear, & Vigliano, 2011) and/or optimal foraging densities (Bohl, 1979; Kratochvíl et al., 2008). In temperate waterbodies with a spatially diverse, well-structured littoral zone fish may perform diel horizontal shifts between open water and the littoral zone (Bohl, 1979; Eklöv, 1997). But in waterbodies where spatial complexity of the inshore habitat is scarce, where fish have to face both inshore and offshore predation and competition for food sources, a possibility is to utilise deeper layers (Hardiman et al., 2004; Mehner, 2012; Vašek, Kubečka, Matěna, & Sed'a, 2006).

General patterns, the amplitude, duration and the main proximate trigger of diel migrations have been well described (Ahrenstorff, Hrabik, Stockwell, Yule, & Sass, 2011; Bohl, 1979; Busch & Mehner, 2009; Rechencq et al., 2011; Ringelberg, 1995). But whether diel migrations are endogenous, genetically fixed behaviour, undergone as a response to a ghost of a predation past or they are a flexible response to abruptly changing environmental conditions (e.g. light intensity), remains unclear. Studies favouring the former assumption suppose that fish continue with migration irrespective of constant light intensity. For instance, Jurvelius and Marjomäki (2008) observed that fish from the Finnish Lake Vuokalanjärvi did not change the pattern of their vertical shifts in winter, during permanent darkness when the surface was snow-covered. Gliwicz and Jachner (1992) showed that diel migrations in a community of juvenile fishes from the Polish Lake Rós did not diminish, in spite of no currently present predation, apparently as a result of predation risk in the past. Comparably, Gaudreau and Boisclair (1998, 2000) who studied fish communities from the Canadian Lakes found that long-term coexistence of predators, such as brook trout (*Salvelinus fontinalis*: Salmonidae (Mitchill, 1814)), and their prey fish, may cause genetically induced diel migrations in prey with a short generation time.

In contrast, other studies have suggested that diel migrations are also a plastic behaviour that ceases under constant light intensity. For instance, Gjelland et al. (2009) observed that during the 24-hr bright period of a midnight sun in the high northern latitude, diel vertical migrations (DVMs) in the whitefish (*Coregonus* spp.) were very restricted but with the prolonging of the night period in late summer, the amplitude of migration was steadily increasing. Similarly, vertical shifts of whitefish (*Coregonus lavaretus*: Salmonidae (L.)) and its predator, brown trout (*Salmo trutta*: Salmonidae (L.)), ceased in the dark period of a polar night and were reinstated with the prolonging of the day period towards the end of winter (Kahilainen, Malinen, & Lehtonen, 2009).

In late spring and early summer, the open water of many deep, thermally stratified European lakes and reservoirs is occupied by young-of-the-year European perch (*Perca fluviatilis*: Percidae, L.), a widely distributed species that accounts for a considerable proportion of pelagic early juveniles communities (Čech, Kubečka, Frouzová, Draštík, Kratochvíl, & Jarošík, 2007; Jůza et al., 2009; Probst, Thomas, & Eckmann, 2009; Vašek et al., 2006; Vejřík, Matějíčková, Jůza et al., 2016; Wang & Appenzeller, 1998). Perch early juveniles (larvae and juveniles till the metamorphosis when fish started to be fully pigmented with individual fins fully developed) were observed to split into vertically separated communities (epipelagic, bathypelagic) in which spatially and temporarily distinct bathypelagic early juveniles migrated vertically as part of their antipredatory behaviour. In daytime, they can be found as a distinct, acoustically scattering layer in the hypolimnion (Čech, Kratochvíl, Kubečka, Draštík, & Matěna, 2005; Čech, Kubečka, Frouzová, Draštík, Kratochvíl, Matěna, et al., 2007; Jůza et al., 2012). At dusk, however, an upward shift into a less hostile environment of warm epilimnion is essential to prevent severe exhaustion of migrating individuals (Čech et al., 2017). The idea that DVMs in bathypelagic perch early juveniles are affected by light intensity has previously been proposed (Čech et al., 2005), but direct evidence has been lacking.

In this study, we hypothesised that if DVMs were under direct light control, then their regular daytime pattern would be interrupted by constant light intensity and reinstated under changing light intensity. To test our hypothesis, we, for the first time, performed a large-scale field experiment to obtain DVMs in bathypelagic perch early juveniles under direct light control. Moreover, undertaking such an experiment in natural conditions might help to solve the persisting problem regarding spatial segregation in pelagic perch early juveniles communities, as the ultimate cause has still remained poorly understood. The epipelagic and bathypelagic perch early juveniles communities were found to be genetically identical (Kalous et al., 2017) and did not differ, for example, in the degree of endoparasite infection (Kuchta et al., 2009). In this way, the large-scaled field experiment, in which the entire pelagic early juveniles community is involved, might be a possible solution as such an experiment would scarcely be feasible in artificial (laboratory) conditions. In this study, the daytime depth distribution and density of pelagic early juveniles were examined under conditions with open and covered surfaces. In addition, predation in the epilimnion versus the hypolimnion, water transparency and temperature were used to explain the main ultimate cause of DVMs in perch early juveniles.

1.1 | Study area

The canyon-shaped Římov Reservoir, in the Czech Republic, is an artificial meso- to eutrophic waterbody located on the Malše River, 170 km south of Prague (Figure 1a). Its length is 9 km, mean depth 16 m, maximum surface area 210 ha, and the volume is 33×10^6 m^3. The reservoir has served as a freshwater store for České Budějovice and adjacent localities (Říha et al., 2012). The local early juveniles communities are dominated by cyprinids but percids, particularly perch and pikeperch (*Sander lucioperca*: Percidae, L.), are also important components (Jůza et al., 2009; Jůza et al., 2010, Jůza et al., 2012). During the daylight hours, the most common piscivorous fish species in the open water of the Římov Reservoir are adult perch and asp (*Aspius aspius*: Cyprinidae (L.)) (Vašek et al., 2004). The experiment was carried out at the mouth of the Strahovská Bay (Figure 1a,b), the largest bay on the left side of the Římov Reservoir,

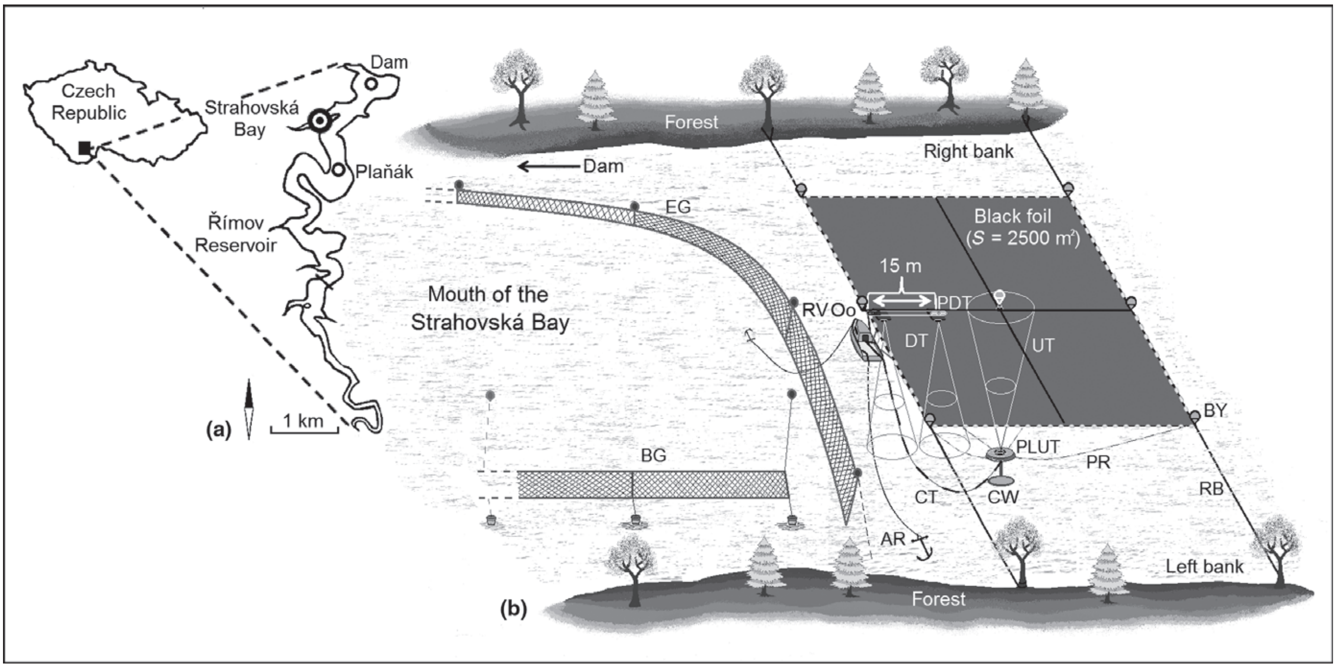

FIGURE 1 (a) A map of the Římov Reservoir and its location in the Czech Republic. The double circle shows the experimental area in the Strahovská Bay. Single circles indicate localities of pelagic early juveniles trawling in the downstream (Dam) and upstream (Plaňák) parts of the reservoir sampled simultaneously with the experimental area on 13 June 2006. (b) General scheme of the experimental area. RV Oo, anchored research vessel Ota Oliva; BY, buoy; RB, rope connecting the foil with the bank; PR, pendant rope of the up-looking transducer ES 120-7G (120 kHz); PLUT, platform carrying the up-looking transducer; CW, counterweight; UT, acoustic beam of the up-looking transducer; DT, acoustic beam of the down-looking transducer ES 400–7C (400 kHz); PDT, platform carrying the down-looking transducer; AR, anchor rope; CT, cable of the transducer; EG, epipelagic gillnets; BG, bathypelagic gillnets

where the maximum depth is 27 m, maximum width 96 m, length 850 m and its area c. 6 ha (48°50′39.7″N, 14°28′48.5″E). The bay has steep rocky banks and is protected from wind by the surrounding forest in most directions (Figure 1b).

2 | METHODS

2.1 | Time schedule of the experiment

The experimental sampling was conducted from 6 to 13 June 2006 and was divided into five sampling periods (Appendix S1). On 6–7 June, pelagic early juveniles consisting of distinct spatially and temporarily segregated epipelagic (non-migrating) and bathypelagic (vertically migrating) communities were acoustically scanned along the longitudinal profile of the Římov Reservoir, including the Strahovská Bay, to confirm the presence of bathypelagic early juveniles (the Initiation period). Pelagic early juveniles trawling was carried out to provide samples for subsequent genetic and parasitological analysis (for details, see Kuchta et al., 2009; Kalous et al., 2017).

On 7–8 June, a square frame of ropes was installed from the boat across the mouth of the Strahovská Bay. To keep the construction properly fixed and spread out, the frame was fastened to the firm vegetation ashore (full-grown trees; Figure 1b, Appendix S2). At the same time, stationary and semi-mobile acoustic equipment (for details, see *Acoustic sampling*) was installed in the experimental area and acoustic recording with the open water surface was conducted for more than 24 hr (the pre-foil period). At midnight on 8–9 June, when the pelagic early juveniles community occupied surface layers, a floating, black polyethylene, non-transparent foil, with an area of 2500 m^2 (square 50 × 50 m), was installed from the boat across the surface at the mouth of the experimental bay (Figure 1b, Appendix S2). To keep the foil properly fixed and spread, it was attached to the above-mentioned frame of ropes (Figure 1b). At the time of high light levels during midday, a SCUBA diver checked that the foil was not damaged during the installation. Then, 32 hr of stationary and semi-mobile acoustic recording was conducted with the water surface covered (the Foil period).

At midday on 11 June, under the high-intensity daylight, the foil was removed from the surface and stationary and semi-mobile acoustic recording that lasted until midday on 12 June was conducted with the water surface open (the post-foil period). In addition to the acoustic sampling, epipelagic gillnets were exposed in the experimental area during the post-foil period (in late afternoon on 11 June and the morning of 12 June). Bathypelagic gillnets were exposed daily throughout all the sampling periods (Appendix S1). Their purpose was to obtain adult fish and potential predators of the pelagic early juveniles, for stomach content analysis. Finally, on 13 June, pelagic early juveniles were sampled with the frame trawl at the three localities along the longitudinal profile of the Římov Reservoir (Figure 1a) to evaluate the species composition of pelagic early juveniles (the Termination period) and to ensure that the distribution of the early juveniles was unchanged in the pre-foil and post-foil periods.

2.2 | Abiotic environmental characteristics

Light intensity on the water surface at the Strahovská Bay was recorded every five minutes using a digital lux meter MDLX. Light penetration below the water surface (light attenuation; in the experimental area and directly below the foil) was measured by a LI-COR LI-1400 underwater light meter working with a spherical quantum underwater sensor LI 193 SA (sensitivity 7 μA per 1000 μmol m^{-2} s^{-1} in water, precision 0.005 μmol m^{-2} s^{-1}; LI-COR, Lincoln, USA). Water transparency was measured using a Secchi disc. The temperature profile in the experimental area was recorded by a calibrated ISY 556 and multi-parameter WTW probes (Figure 2). Stable, calm weather conditions, with a partly cloudy sky and light breeze, prevailed throughout the course of the whole experiment.

2.3 | Net sampling

To check the species composition, the pelagic early juveniles were sampled during midday (10:00–14:00 hr, when the communities of epipelagic and bathypelagic perch early juveniles are spatially well segregated; Čech et al., 2005, 2017) using a framed trawl net (2 × 2 m; rectangular mesh size 1 × 1.35 mm) at the three localities in the reservoir (Figure 1a). The trawl was pulled at a distance of approximately 50 m behind the research vessel Ota Oliva (64 HP) at an average speed of 3 km/h. There were three epipelagic hauls at a depth of 0–2 m with the total volume of water sampled being 3501 m^3 and three bathypelagic hauls at a depth of 10–12 m with the total water volume sampled 2433 m^3. The average tow duration was five minutes, and the distance of each tow was measured by a Garmin GPS map 60CSx receiver (Garmin International, Inc., Olathe, KS, USA). All captured early juveniles were killed by overdosing with MS 222 (1 g/l; left in the solution for 10 min) and immediately preserved in 6%–10% formaldehyde, in the field. They were identified to species level in the laboratory.

Adult fish were sampled using the epipelagic and bathypelagic gillnets (Figure 1b). Epipelagic gillnets (depth range 0–3 m) with rectangular mesh sizes of 29, 35, 43, 55 mm (knot-to-knot; four panels, each 3 m high and 25 m long) were used at the experimental area to capture adult fish in the epilimnion. Similarly, bathypelagic gillnets (depth range 11–14 m; four panels, each 3 × 25 m) of the same mesh sizes were exposed to capture adult fish in the hypolimnion. The adult fish were again killed by overdosing in MS 222 and immediately dissected in the field for their stomach and gut contents. This vertebrate work was approved by the Ethics Committee of the Czech Academy of Sciences. All sampling procedures and experimental manipulations were approved by the Czech Academy of Sciences, Vltava River Authority and the Environmental Department of the Municipal Authority of the Town of České Budějovice. The field study did not involve endangered or protected species.

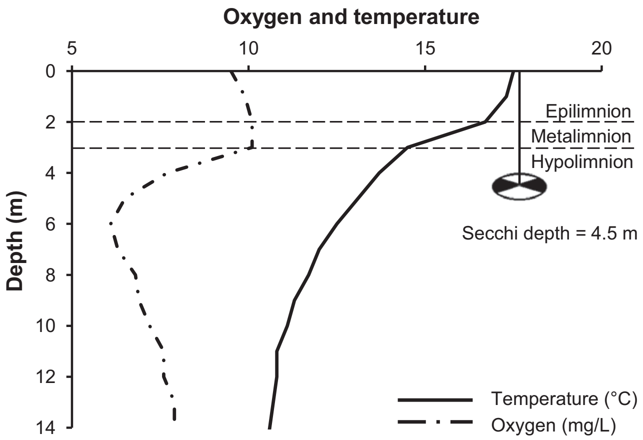

FIGURE 2 A vertical profile of temperature and dissolved oxygen in the experimental area (Strahovská Bay, Římov Reservoir, midday) on 11 June 2006. The depth of the Secchi disc is provided

2.4 | Acoustic sampling

The distribution and behaviour of the pelagic early juveniles associated with both the foil cover and open water surface conditions were recorded by the split-beam scientific echosounders SIMRAD EK 60 (120 kHz and 400 kHz) equipped with two simultaneously operating circular transducers. The acoustic beams of both transducers (nominal angle of 7° each) were pointing up or down vertically. The average ping rate was 10 pings/s, and the pulse length was 0.128 /ms. One of the transducers was stationary ES 120-7G (120 kHz) and was deployed as up-looking (Čech & Kubečka, 2002) at a depth of about 25 m with the beam aiming directly towards the centre of the foil (Figure 1b). The second transducer was a semi-mobile transducer ES 400-7C (400 kHz) deployed as down-looking. It was carried by the block and tackle installed between the centre and the periphery (one halfway to the edge) of the foil so that the transducer could be shifted back and forth at a distance of 15 m (the transducer changed its position in 5-m steps each 20 min; Figure 1b). The down-looking transducer monitored the water column below the foil, including the peripheral space where the foil was bordering on the open surface. The main purpose was to avoid potential variability in the vertical distribution of early juveniles, particularly when the sun was low above the horizon and penetrated the water surface at a low angle.

Calibration of the sonar systems was done according to Foote, Knudsen, Vestnes, MacLennan, and Simmonds (1987). In total, >80 hr of acoustic recordings from the pre-foil, foil and the post-foil sampling periods was stored on the hard disk of a portable computer and processed in the laboratory using Sonar 5 Pro software (Data Acquisition AS, Oslo, Norway). Single fish targets with a minimal track length of three consecutive echoes, zero ping-gap and the vertical gating range of 0.05 m were automatically tracked for each five-minute echogram using tracking facilities in Sonar 5. Unwanted echoes from larger fish and gas bubbles were manually erased. Early juveniles were tracked for single 5 m depth layers from depths of 1 to 16 m. Depths greater than 16 m, where no early juveniles were acoustically detected, were not included in the analysis. In total, 3335 single early juvenile tracks were stored in the echo database in Sonar 5. The lowest threshold for target strength (TS) of early juveniles during tracking was −70 dB (5 mm L_T), and the highest threshold was −50 dB (43 mm L_T). The size range of the early juvenile tracks and TS–length regression given by Frouzová and Kubečka (2004) served for the analysis of abundances using the echo-integration method in Sonar 5 that was described in detail by Čech et al. (2005). To obtain a detailed picture of DVMs of early juveniles and to determine the control role of the light intensity on this behaviour, the water column was further divided into 1 m thick layers down to a depth of 16 m below the water surface. For each of the fifteen 1 m thick layers (1–2, 2–3, . . ., 15–16 m), the abundance of early juveniles was then calculated separately for each five minutes of the acoustic record following the earlier work of Čech, Kubečka, Frouzová, Draštík, Kratochvíl, and Jarošík (2007), Čech, Kubečka, Frouzová, Draštík, Kratochvíl, Matěna et al. (2007), Čech et al. (2005). The depth of the main layer was defined as the 1 m thick layer of the water column with the highest abundance of migrating early juveniles (Čech et al., 2005).

The vertical speed of migrating bathypelagic early juveniles was measured immediately before and after the foil packing in Sonar 5. This measurement was based on the depth of the main layer; the vertical speed of migrating early juveniles was a result of depth (m) reached between the initial time and terminal time (h).

For the purpose of this study, the acoustic recordings of early juveniles density and their depth distribution were divided into four time periods: dawn (3:00 a.m.–5:00 a.m.), day (7:00 a.m.–17:00 p.m.), dusk (19:00 p.m.–21:00 p.m.) and night (23:00 p.m.–01:00 a.m.).

2.5 | Statistical analysis

Statistical comparison of the acoustic daytime densities of the bathypelagic early juveniles in the hypolimnion, between the pre-foil and the foil sampling periods (142 density values from both periods entered the analysis), was done using analysis of variance (one-way ANOVA). In the same manner, daytime densities of bathypelagic early juveniles in the hypolimnion before (8:00–9:30 hr) and immediately after the foil removal (12:30–14:00 hr) were compared (end of the foil period versus beginning of the post-foil period; 14 density values from both periods entered the analysis). Depth of the bathypelagic early juveniles layer (the main layer) with respect to the light intensity was tested using linear regression. R software version 3.2.2. was used for the statistical computing (R Core Team, 2013).

3 | RESULTS

The trawl net survey revealed a homogenous species composition of the pelagic early juveniles community at the Dam (downstream), Strahovská Bay (experimental area) and Plaňák (upstream) localities of the Římov Reservoir where, in total, 3171 individual early juveniles were captured and identified to species (Figure 3). Bathypelagic early juveniles formed 45% of the pelagic early juveniles community and were dominated by perch (97.02%, trawl mean 55.72, *SD* ± 20.97 inds. 100 /m^3). The other, less abundant species, were pikeperch (2.41%, trawl mean 1.38, *SD* ± 1.22 inds. 100 /m^3) and ruffe (*Gymnocephalus cernua*: Percidae, L.) (0.56%, trawl mean 0.32, *SD* ± 0.34 inds. 100 /m^3). Epipelagic early juveniles formed 55% of the pelagic early juveniles community and were dominated by cyprinids (63.63%, trawl mean 31.93, *SD* ± 9.02 inds. 100 /m^3). In addition to the cyprinids, perch (29.14%, trawl mean 14.62, *SD* ± 4.19 inds. 100 /m^3), ruffe (6.49%, trawl mean 3.26, *SD* ± 1.49 inds. 100 / m^3) and pikeperch (0.74%, trawl mean 0.37, *SD* ± 0.35 inds. 100 / m^3) were also present in the epipelagic hauls.

The acoustic results showed that in the daytime, during the pre-foil sampling period, early juveniles reached their highest acoustic density in the hypolimnion at an average depth of 11.5 m, but the deepest occurrence of early juveniles was at 13 m (Figure 4a). The depth distribution of migrating bathypelagic perch early juveniles was strongly correlated with the light intensity on the water surface ($F_{1,20}$ = 495.5, p < .001, Figure 5; water transparency 4.5 m). The light intensity fluctuated markedly during the course of the day because of the prevailing semi-cloudy weather to which early juveniles responded by a clear change in their depth distribution (Figure 6). At dusk, when the light

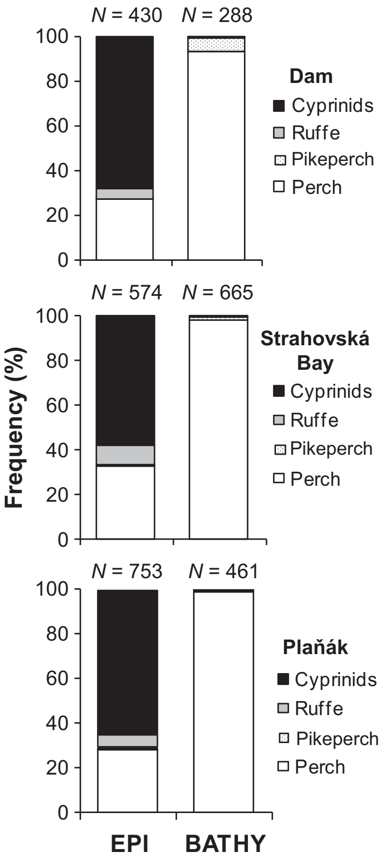

FIGURE 3 Species composition of the communities of the epipelagic (EPI) and bathypelagic (BATHY) early juveniles in the Dam (downstream), Strahovská Bay (experimental area) and Plaňák (upstream) localities in the Římov Reservoir on 13 June 2006. Numbers of individuals caught in each locality are provided above each bar. Note that the bathypelagic community was strongly dominated by perch while in the epipelagic community cyprinids predominated

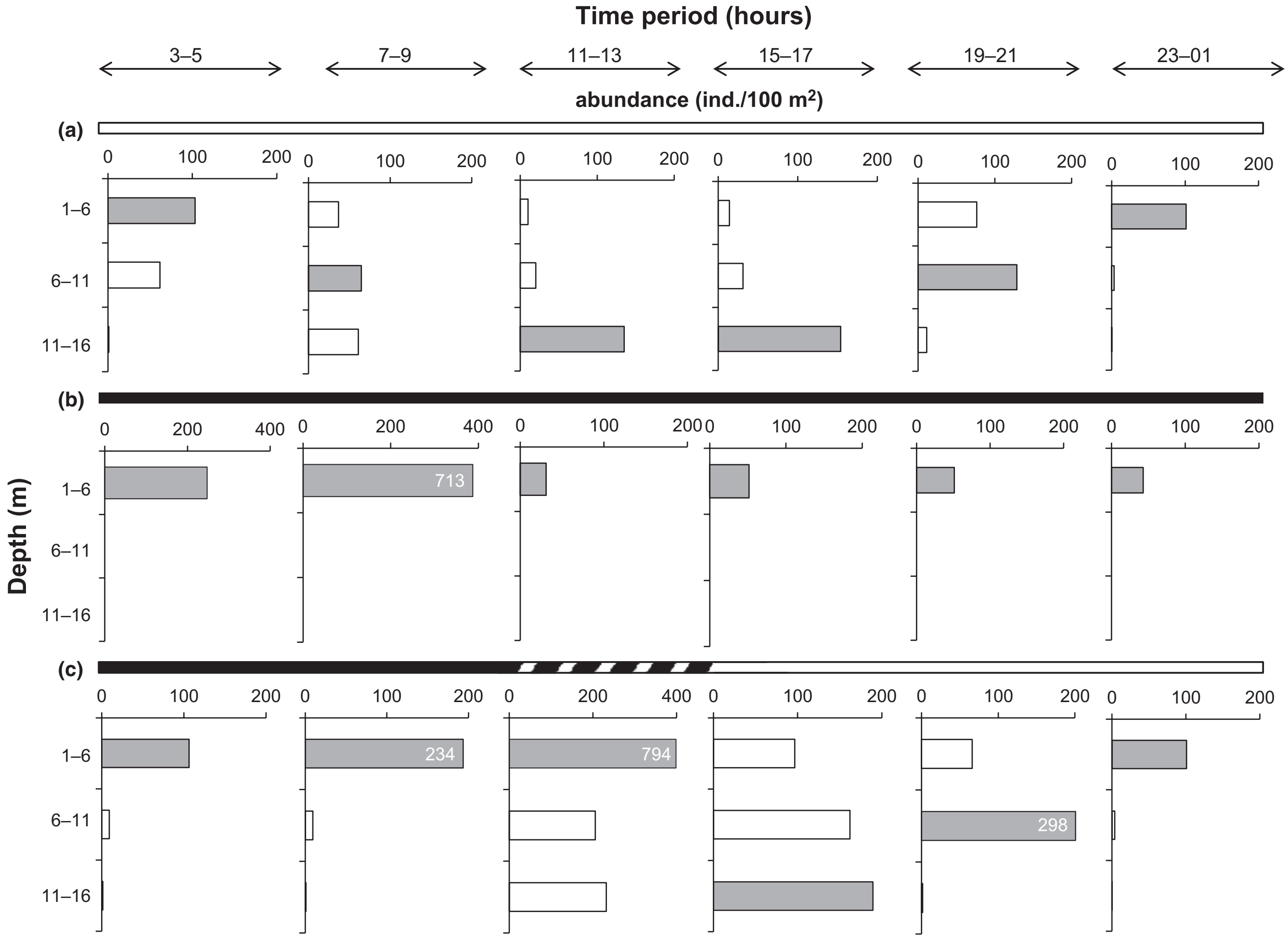

FIGURE 4 Acoustic area density of bathypelagic early juveniles in the Strahovská Bay (Římov Reservoir, Czech Republic) in June 2006 with respect to the depth and time periods during (a) the pre-foil sampling period, (b) the foil sampling period, (c) the foil and post-foil sampling periods. Open bars along the *x*-axis of the graphs represent the situation with an open water surface, while the black bars represent the surface covered with the foil. The dashed bar on the picture "c" indicates the period between 10:00–14:00 hr when the foil was progressively removed from the surface. The grey columns in each graph indicate depths with the highest early juveniles density (in four cases absolute values are provided in individual bars)

intensity declined from the average daylight level of 75 × 10^3 LUX (*SD* ± 39 × 10^3, max. 130 × 10^3 LUX) to 7 × 10^3 LUX (*SD* ± 3 × 10^3 LUX), the bathypelagic perch early juveniles started their regular ascent to above the thermocline where they co-occurred with the non-migrating, epipelagic community.

In contrast to the open water surface conditions, a completely different behaviour of the migrating community was observed during the foil sampling period when the foil covered the surface and light intensity <1 LUX was recorded throughout the 24 hr (Figure 7, Appendix S3). At this time, daytime acoustic densities of bathypelagic early juveniles in the hypolimnion were significantly lower compared to the pre-foil sampling period (ANOVA, $F_{1,142} = 15.37$, $p < .001$; Figure 4a,b and cf. Figure 7). The highest acoustic density of early juveniles found during the 24 hr was in the epilimnion (Figure 4b). However, immediately after the removal of the foil at midday, in the post-foil sampling period, the early juveniles exposed to sharply and rapidly increasing light intensity (from <1 to >100 × 10^3 LUX) formed in the bathypelagic layer and, reaching a vertical velocity of 10.5 m/hr, they escaped into the hypolimnion (Figure 4c, Appendix S4). There, a significantly higher acoustic density of bathypelagic early juveniles was found compared to that in the morning hours, before the foil was removed (ANOVA, $F_{1,14} = 15.27$, $p < .001$; Figure 4c).

In the hypolimnion, bathypelagic perch early juveniles were safe from visual predation by adult fish that attacked early juveniles in a bright epilimnion, as was evidenced by both the hydroacoustic records (Appendix S4), gillnet catches and subsequent stomach analyses. In stomachs of 14 dissected adult perch (average 210 mm L_T, *SD* ± 4.6), caught into the epipelagic gillnets in the area of the experiment, 231 individuals of pelagic early juveniles were found (max. 50 individuals per predator; Appendix S5). At this time, adult perch represented the only catch of epipelagic gillnets. In contrast, empty bathypelagic gillnets (five individual days of exposure) indicated complete absence of any potential adult fish predators in the hypolimnion. This finding was well in accordance with all the hydroacoustic results (no fish of TS ≥ −45 dB, i.e. fish ≥ 100 mm L_T observed under the depth of 8 m by both mobile and stationary recordings).

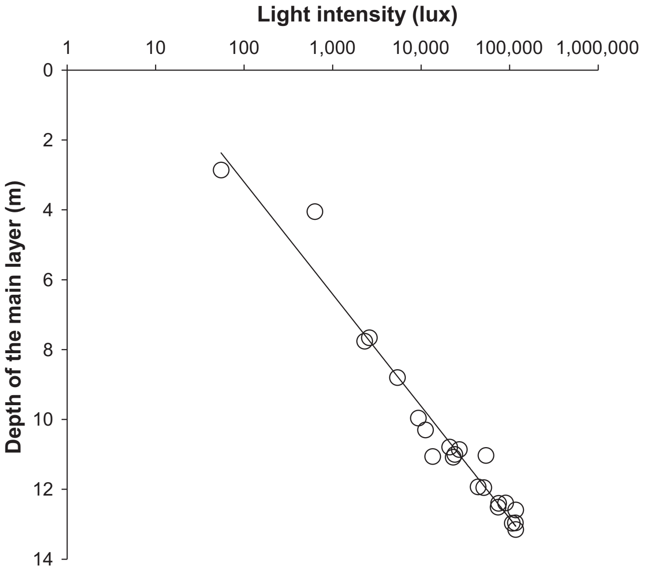

FIGURE 5 The relationship between the light intensity and the depth of the main layer of the bathypelagic early juveniles community (mean for five minutes interval; only records from the conditions of constant light intensity are included). Light intensity is expressed in a logarithmic scale. Regression line: $y = 1.39 \ln(x) - 3.21$; $r^2 = 0.96$

4 | DISCUSSION

Fish often have to balance between a risk of predation and competition for food sources, which leads them to shifting between habitats (Gaudreau & Boisclair, 1998, 2000; Hardiman et al., 2004; Olsson, Greenberg, Bergman, & Wysujack, 2006; Werner, Gilliam, Hall, & Mittelbach, 1983). In agreement with preceding studies regarding light as the main environmental factor affecting diel activity and distribution of fish (Appenzeller & Leggett, 1995; Busch & Mehner, 2009; Probst & Eckmann, 2009; Rechencq et al., 2011), our findings suggest that the diel activity of a bathypelagic community of perch early juveniles was strongly affected by light illumination on the water surface (Figure 5). In the daytime, when average light intensity reached 75 × 10^3 LUX, perch early juveniles predominated in the hypolimnion and created an acoustically distinct scattering layer, as previously observed in various waterbodies by Čech and Kubečka (2006), Čech, Kubečka, Frouzová, Draštík, Kratochvíl, Matěna, et al., 2007; Čech, Kubečka, Frouzová, Draštík, Kratochvíl, Matěna et al. (2007), Čech et al. (2005) or Sajdlová, Jůza, Frouzová, Seďa, and Čech (2017).

In contrast, after dusk, when the light intensity dropped to less than 1 LUX, the bathypelagic perch early juveniles migrated into the epilimnion where they occurred simultaneously with the non-migrating, and usually more abundant, epipelagic community which occupied the epilimnion 24 hr a day (Čech et al., 2005; this study). Such a pattern of diel migrations can be observed at various life stages of fishes but is often more evident during the first year of life when early juveniles, vulnerable to predation in a bright epilimnion, seek safe, temporary refuge in the deep, dark water layers (Hardiman et al., 2004; Scheuerell & Schindler, 2003).

In the present study, it was hypothesised that if DVMs were under direct light control and not genetically fixed, then their daily pattern would be interrupted under constant light intensity and reinstated under changing light intensity. In the high latitudes of polar regions, conditions of constant light intensity occur naturally during summer (polar day/midnight sun) and winter (Gjelland et al., 2009; Jurvelius & Marjomäki, 2008), but in temperate regions, where day and night periods alter daily, constant light intensity had to be achieved experimentally, by prolonging the night period. From the acoustic recordings obtained during the foil period, the bathypelagic perch early juveniles started with their natural downward shift at dawn but, because of no obvious change in light intensity, they continued occupying the epilimnion (Figure 7b). In this respect, our observations match those of other studies that have revealed no DVMs under constant light intensity (polar day/night; Gjelland et al.,

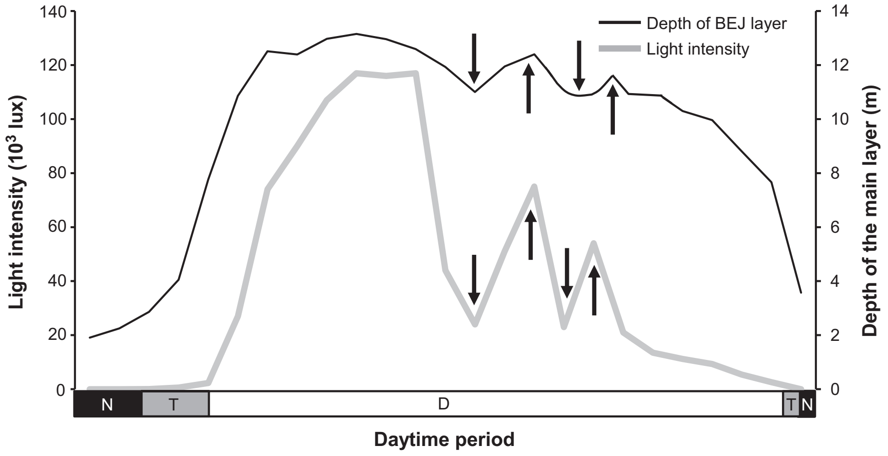

FIGURE 6 Light intensity in the experimental area in the course of the diel cycle and the vertical distribution of bathypelagic early juveniles (BEJ) during the open water surface conditions (8 June 2006). The black bars indicate night, the white bar indicates day and the grey bars indicate twilight periods (dawn, dusk). Note that the light intensity was markedly fluctuating during the daytime, which was caused by clouds shadowing the sun, to which early juveniles responded by changing their vertical distribution (black arrows highlight both atmospheric and behavioural effects)

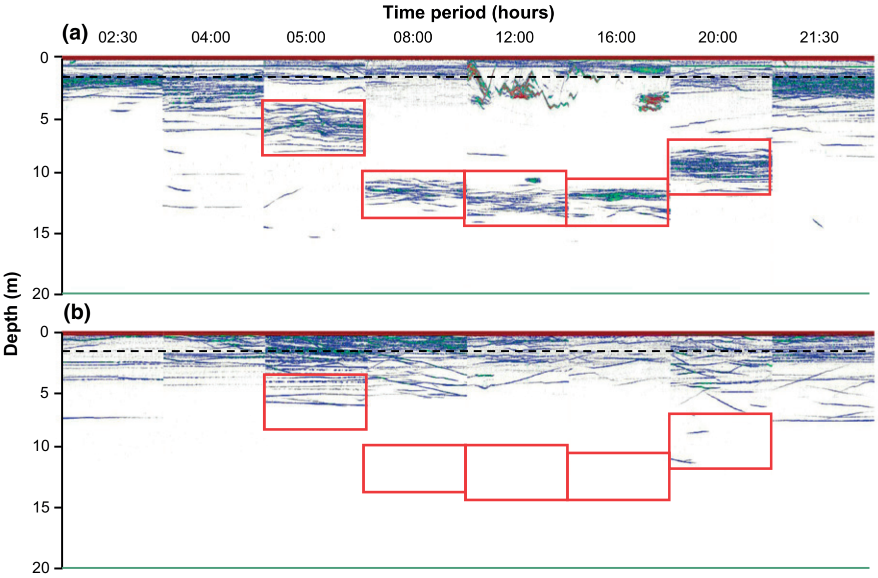

FIGURE 7 A sequence of the up-looking echograms made by the echosounder SIMRAD EK 60 (120 kHz) showing (a) a common pattern of diel vertical migration of the bathypelagic early juveniles community and (b) early juveniles behaviour, when the water surface was covered with the black foil (identical periods of the day). Red rectangles define the position of the migrating bathypelagic early juveniles community during the open water surface conditions (cf. (a) and (b)). The dashed line indicates the upper border of the thermocline

2009; Kahilainen et al., 2009). During their 24-hr stay in the epilimnion, the bathypelagic perch early juveniles showed no obvious sign of disturbance by the foil cover. The only phenomenon observed was a slightly deeper distribution of early juveniles at the edges of the foil (down-looking observation) which was probably due to sunlight penetrating the water surface at a low angle, particularly in the morning hours when the eastward-oriented bay was exposed to the rising sun (M. Čech, unpubl. data).

In addition to the light intensity, the depth distribution of fish often depends on water transparency and temperature (Mous, Van Densen, & Machiels, 2004; Vašek et al., 2006). Relatively high water transparency (4.5 m) was measured in the Římov Reservoir, and the maximum amplitude of early juveniles vertical migrations reached 13 m. A similar pattern of vertical distribution was observed by Čech et al. (2005) in the Slapy Reservoir, Czech Republic, where movement of bathypelagic perch early juveniles between the epilimnion and hypolimnion reached an amplitude of 12.5 m. There definitely seems to be no doubt that low light intensity in the hypolimnion may provide spatial refuge for early juveniles from visual predators (low light refuge). In temperate waterbodies, a similar effect may cause a steep vertical gradient of temperature (low temperature refuge; Jůza et al., 2012) or oxygen depletion in the metalimnion and upper hypolimnion (hypoxic refuge; Vejřík, Matějíčková, Jůza, et al., 2016). Also in the present study, pronounced thermal stratification was recorded with >7°C difference between the epilimnion and hypolimnion. Perch early juveniles could therefore profit from hypolimnion as a day refuge that is usually avoided by fish (both large/adult and predatory) preferring a warm epilimnion (Čech & Kubečka, 2002; Jarolím et al., 2010; Vejřík, Matějíčková, Seďa, et al., 2016). Young-of-the-year perch have their optimum temperature between 16 and 25°C (Wang & Eckmann, 1994) and can temporarily tolerate even 11°C in their daytime refuge, in the hypolimnion. It has been shown, however, that preventing these fish from regular crepuscular ascent into a warm epilimnion resulted in the death of all individuals (Čech et al., 2017).

Up to now, proximate triggers of DVMs have been discussed. The often-mentioned, ultimate cause is predation risk (Kahilainen et al., 2009; Mehner, 2012). Sometimes negative experience from ghost of predation in the past may be stronger than present external signals/proximate triggers received from the external environment and cause diel migrations to become a genetically fixed behaviour (Gaudreau & Boisclair, 1998; Gliwicz & Jachner, 1992). Also in the present study, predation seemed to be the main ultimate cause of DVMs. The direct evidence of predation on pelagic early juveniles was provided by 14 dissected specimens of adult perch, captured by epipelagic gillnets in the experimental area, that had their stomachs full of pelagic early juveniles. Young-of-the-year perch are a common prey of adult perch (Thorpe, 1977) but occasionally also of cyprinids. This was well described by Vejřík, Matějíčková, Seďa et al. (2016) who found that young-of-the-year perch, even in mid-summer conditions, comprised the majority of the gut contents of large common bream (*Abramis brama*: Cyprinidae, L.) and common carp (*Cyprinus carpio*: Cyprinidae, L.).

Unlike genetically fixed behaviour, diel shifting between refuges in the present study had an exogenous origin. The evidence was obtained when the foil cover was removed at midday, at the end of the foil sampling period, and the surface started to be fully illuminated. The sudden increase in the light intensity (from <1 LUX to more than 100×10^3 LUX) caused the area below the foil to become accessible to visual fish predators, whose attacks on pelagic early juveniles were acoustically recorded (Appendix S4). In contrast to non-migrating, epipelagic early juveniles, the bathypelagic community responded to visual predation by escaping immediately into the hypolimnion (Appendix S4), that is within the post-foil period of the experiment, bathypelagic early juveniles re-established their regular pattern of DVMs.

It has been demonstrated that environmental factors, particularly light intensity and temperature, can importantly affect the diel distribution, density and even survival of fish early juveniles. The evidence that diel migrations were under direct light control was obtained, which supported the exogenous origin of this behaviour.

Moreover, the current study significantly contributed to an explanation of the spatial segregation in pelagic perch early juveniles communities that undergo completely different ecological trade-offs (Čech et al., 2017). Bathypelagic early juveniles, compared to the non-migrating epipelagic community, have chosen a potentially less favourable strategy of temporarily occupying a hostile environment in the hypolimnion. Nevertheless, particularly in waterbodies where predatory fish are abundant and where both emergent and submerged littoral vegetation is absent, the advantage of moving into a deep, dark pelagic refuge remains indisputable.

Large-scaled field experiments involving entire wild fish communities are extremely rare and demanding. These current findings therefore not only broaden knowledge about the biology of perch, but they also provide novel, general insight into the real causes of DVMs, one of the most pronounced and remarkable phenomena in waterbodies.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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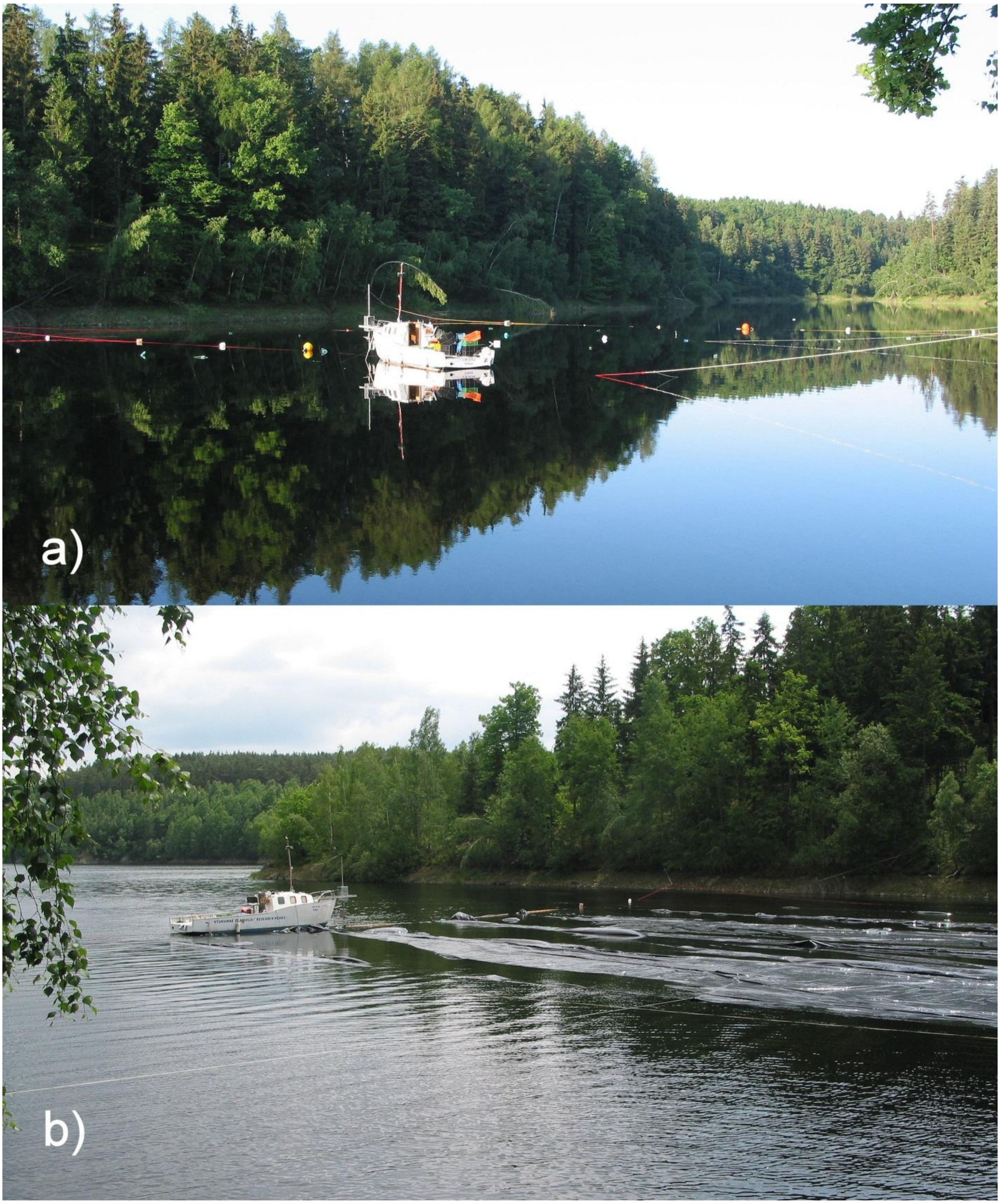
Appendix S1. Time schedule of the pre-experimental, experimental and post-experimental sampling methods used in the Římov Reservoir, Czech Republic, in June 2006 during the black foil experiment.

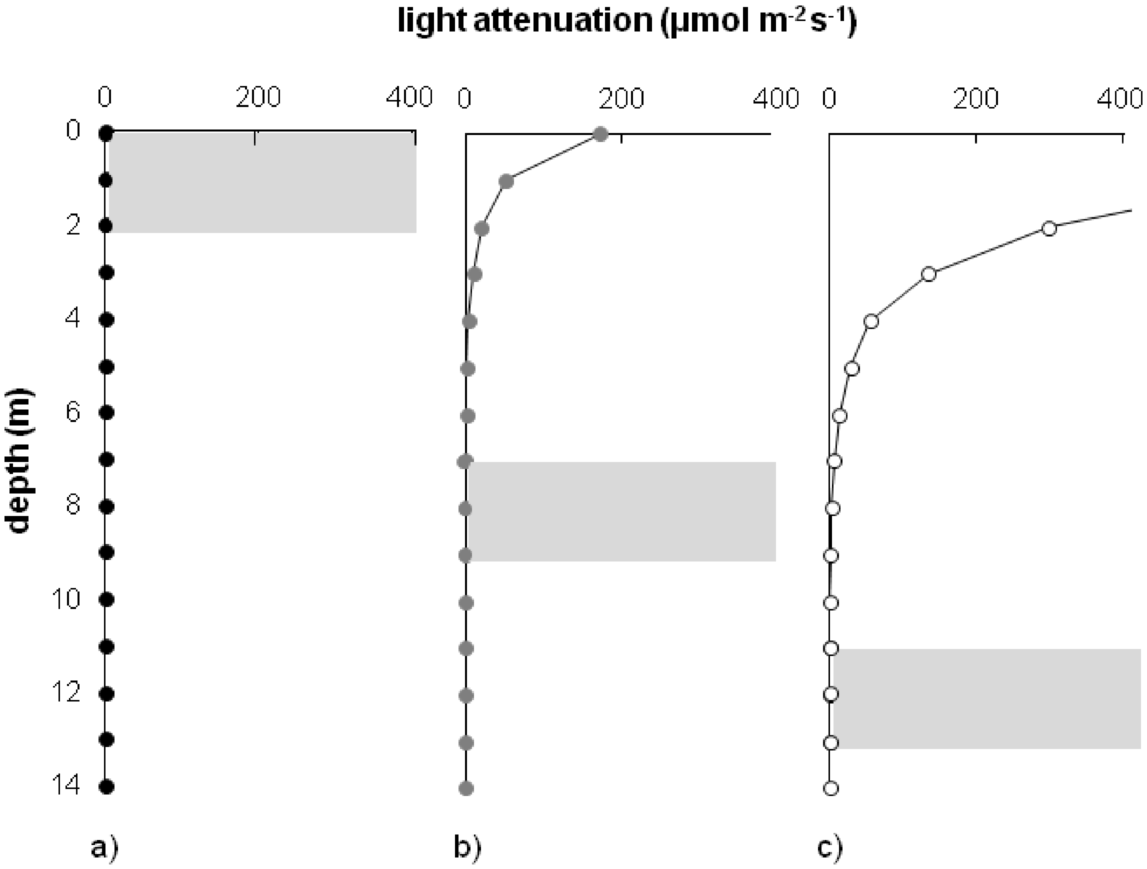
SAMPLING PERIOD	DATE	METHOD/ACTIVITY	FIGURE ref.:	PURPOSE
Initiation	6 – 7 June	> Acoustic scanning of early juveniles along the longitudinal profile of the RR* (SIMRAD EK 60, f= 120 kHz; sampling effort 8 hr). > Trawling of early juveniles along the longitudinal profile of the RR including the SB**.		> Confirming the presence of the BEJ*** scattering layer prior the experiment. > Early juveniles caught by a trawl and used for endoparasite (Kuchta et al., 2009) and genetic analyses (Kalous et al., 2017).
Pre-foil	7 – 8 June	> Installation of a frame of ropes for later foil attachment, assembling acoustic equipment. > Stationary up-looking and semi-mobile down-looking acoustic recording (SIMRAD EK 60, f=120, 400 kHz) lasted from 17:11 hr (7 June) until 22:18 hr (8 June).	Appendix S2 Fig. 1b	> Acoustic recording of the pelagic early juveniles distribution and behaviour before the coverage of the surface by a sheet of black foil. > Monitoring of DVMs**** of BEJ with open surface conditions.
Foil	8/9 June midnight to 11 June midday	> Foil installation begun at midnight, when all early juveniles passively dwelled in the epilimnion (cf. Čech et al., 2005). > Stationary up-looking and semi-mobile down-looking acoustic recording (SIMRAD EK 60, f=120, 400 kHz; sampling effort 32 hr).	Appendix S2	> Acoustic recording with the surface covered, under conditions of constant, complete darkness during both day and night. > Midnight installation ensured that the migrating community was present below the foil and did not escape the area sampled by sonars.
Post-foil	11 June midday to 12 June midday	> Foil removal under high light intensity (>100×10^3 LUX) at midday. > Stationary up-looking and semi-mobile down-looking acoustic recording with the surface open until 14:14 hr (12 June; sampling effort >24 hr). > Epipelagic gillnets exposed 18:00–20:45 hr (11 June) and 7:30–10:00 hr (12 June), followed by consequent stomach analysis of predatory fish. Bathypelagic gillnets exposed daily 8:00–20:00 hr through the whole sampling period (since 8 June).	Fig. 1b	> Monitoring of early juveniles hidden below the foil and the escape of BEJ from the epilimnion to the hypolimnion during foil removal. > Confirming reinstated pattern of DVMs. > Evidencing that DVMs of BEJ were under direct light control. > Evidencing strong predation pressure in the epilimnion, and absence of adult (predatory) fish in the hypolimnion.
Termination	13 June	> Day time trawling of early juveniles at the localities Dam, SB, Plaňák along the longitudinal profile of the RR and mobile acoustic survey (SIMRAD EK 60, f= 120 kHz; sampling effort 5 hr).	Fig. 1a	> Confirming the presence of the BEJ scattering layer after the experiment. > Captured early juveniles analyzed for species composition.

* Římov Reservoir, ** Strahovská Bay, *** bathypelagic early juveniles, ****diel vertical migrations

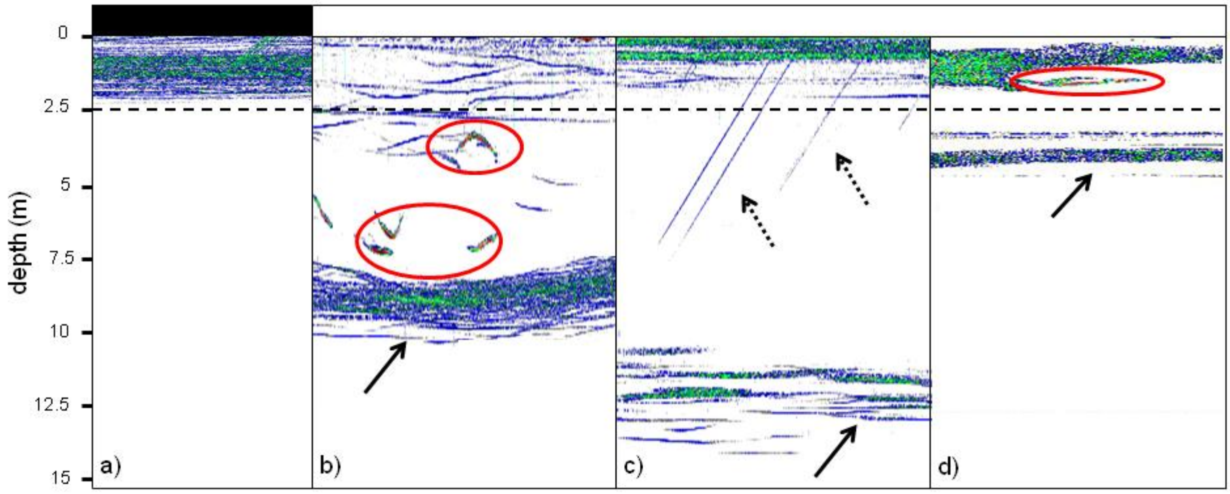
Appendix S2. The experimental area in the Strahovská Bay (Římov Reservoir, Czech Republic) with a) the open water surface (only the rope construction for the foil attachment can be seen), and b) the water surface covered with the black foil. Photo: Jan Kubečka.



Appendix S3. Examples of the depth distribution of bahtypelagic early juveniles (grey bars) under different underwater light conditions: a) with the foil cover (equivalent to <1 LUX in 0 m depth), b) with cloud shadowing (equivalent to 10 × 10^3 LUX in 0 m depth), c) with the water surface fully illuminated (equivalent to 100 × 10^3 LUX in 0 m depth).



Appendix S4. Avoidance behaviour of bathypelagic early juveniles (indicated by black arrows) immediately after the foil packing and starting of the foraging activity of predatory fish (most probably adult perch; in red circles; target strength from -39 to -37 dB, i.e. from 191 to 238 mm L_T according to the calculation provided by Frouzová & Kubečka, 2004). a) Situation closely before the foil packing when the whole pelagic community of early juveniles was found above the thermocline (9:30 hr). b) Fish affected by a strong increase of light intensity; bathypelagic early juveniles quickly shifted into the hypolimnion creating a scattering layer (10:45 hr). c) Bathypelagic early juveniles at their daytime refuge and gas bubbles ascending towards the surface (dashed arrows; 14:15 hr). d) Observation of epipelagic early juveniles attacked by adult fish in the epilimnion and bathypelagic early juveniles ascending from their day time refuge (20:30 hr). Note classical disruption of otherwise homogeneous shoal when predator is present. The upper border of the thermocline is shown as a dashed line. a-c) The up-looking observation (SIMRAD EK 60; 120 kHz; transducer ES 120-7G). d) The down-looking observation (SIMRAD EK 60; 400 kHz; transducer ES 400-7C).



Appendix S5. A typical catch of epipelagic gillnets in the area of the experiment – adult perch (*Perca fluviatilis*). An example of the stomach content (partly digested cyprinid and percid early juveniles) of one fish is provided in the rectangle. Photo: Martin Čech.

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