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Spatio-temporal distribution and feeding of age 0+ fish in different reservoir habitats

Ph.D. Thesis

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ANNOTATION

Early life history of age 0+ fish was studied in the pelagic and littoral zones of two deep-valley and a shallow, well-mixed reservoir. The sampling focused on diel vertical migrations and feeding behaviour of age 0+ percids in the pelagic zone early in the season and also on age 0+ fish distribution along the shoreline with respect to spatial heterogeneity over the growing season.

DECLARATION [IN CZECH]

Prohlašuji, že svoji disertační práci jsem vypracoval samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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České Budějovice, 8 April 2013 Michal Kratochvíl

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LIST OF PAPERS AND AUTHOR'S CONTRIBUTION

The thesis is based on the following papers (listed chronologically):

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Michal Kratochvíl participated in larvae and juvenile sampling in the field, processed the samples and provided diet and statistical analyses. He was responsible for writing the manuscript.

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Michal Kratochvíl was responsible for the sampling arrangement and surveys, the sample processing and writing the manuscript.

Kratochvíl, M., Vašek, M., Peterka, J., Draštík, V., Čech, M., Jůza, T., Muška, M., Matěna, J. & Kubečka, J., 2013. The effects of diel period and habitat on the littoral age 0+ fish distribution in a deep-valley reservoir. *Hydrobiologia*, submitted.
Michal Kratochvíl was responsible for the sampling arrangement and surveys, the sample processing and writing the manuscript.

CONTENTS

Spatio-temporal distribution and feeding of age 0+ fish in different reservoir habitats

INTRODUCTION

The natural standing waters in the landlocked Czech Republic are due to its geological and climatic history scarce and only of local importance. Therefore, many artificial reservoirs have been built for the flood protection, drinking water supply, recreational fisheries together with energetic, agricultural or industry purposes (Fernando & Holčík, 1991; Irz et al., 2002; Prchalová et al., 2008). In contrast to natural lakes, reservoirs are relatively young, have low retention time, different length/width ratio, frequent water level fluctuation and are supplied with high nutrient input loads (Irz et al., 2002; Vašek et al., 2006). From the morphological viewpoint, most of the typical Czech and also European reservoirs are characterized as narrow, deep-valley (or alternatively canyon-shaped), V- or U- shaped reservoirs of elongated morphology (Duncan & Kubečka, 1995; Jurajda & Regenda, 2004). The depth and elongated morphology predetermine heterogeneous spatial distribution of organisms in response to pronounced gradients within a reservoir – longitudinal gradient with the highest nutrient input and thus biological productivity in the upper part close to river inlet (Hejzlar & Vyhnálek, 1998; Seďa & Devetter, 2000; Vašek et al., 2004; Rychtecký & Znachor, 2011); horizontal gradient between shallow, heterogeneous littoral zone and deep, homogeneous open pelagic zone (Hülsmann et al., 1999; Kahl & Radke, 2006; Vašek et al., 2006); and vertical (depth) pelagic gradient within three thermally stratified layers, epilimnion, metalimnion and hypolimnion, changing in temperature, oxygen, illumination and food concentration (Fernando & Holčík, 1991; Vašek et al., 2004; Järvalt et al., 2005; Prchalová et al., 2008).

Age 0+ fish represent crucial component of fish population in freshwater ecosystems and serve as reliable and consistent indicator of ecological status (Jurajda et al., 2010). On contrary to adult fish assemblage, the absence of age 0+ fish may immediately reflect failure of natural reproduction, spawning/nursery habitats degradation, variability of the environment or human impacts on the ecosystem (Slavík & Jurajda, 2001; Jurajda et al., 2010). Age 0+ fish recruit older population classes and serve as important link in trophic cascade both as zooplankton/benthos foragers and predatory prey components (Treasurer, 1978). Considering these facts, to approach a true picture of the fish stock and to understand the ecological processes, the complex monitoring of age 0+ fish assemblage characteristics including abundance, species composition, growth plus mortality rates, length and feeding behaviour should be involved into standard sampling surveys of fish populations in standing waters (Kubečka et al., 2009). The knowledge of age 0+ fish distribution is also fundamental assumption to understand their effect in freshwater ecosystems.

Age 0+ fish assemblage of central European standing waters is largely consisted of two naturally breeding fish groups having substantial impact on ecosystem dynamics

– percids and cyprinids. The spawning of fish species from these two groups predominantly occurs in the littoral zone of reservoirs and then different distribution patterns soon after hatching are recognized. General concept of larvae and juvenile life history in large standing waters including the feeding on zooplankton sources early after hatching has been well described for both abovementioned fish groups by many authors (e. g. Hartmann, 1983; Hammer, 1985; Whiteside et al., 1985; Rheinberger et al., 1987; Matěna, 1995a, b; Urho, 1996; Peterka & Matěna, 2009). The shifts from littoral to pelagic zone and obligate pelagic phase for a period of month or even longer were described for all three percid species – perch *Perca fluviatilis*, pikeperch *Sander lucioperca* and ruffe *Gymnocephalus cernua* (Coles, 1981; Matěna, 1995a, b; Urho, 1996; Specziár, 2005). After metamorphosis to juveniles, some individuals migrate back to the littoral zone (Coles, 1981; Wang & Eckmann, 1994; Urho, 1996). The described positive phototactic behaviour and preferences of upper epi- and/or metalimnetic layers during pelagic phase of two most important perch and pikeperch (Disler & Smirnov, 1977; Whitside et al., 1985; Craig, 1987; Wang & Eckmann, 1994) was impaired by a pilot study of Čech et al. (2005) who observed a portion of pelagic age 0+ percid population (almost exclusively perch) performing diel vertical migrations (DVMs) between epi- and hypolimnetic layers in a deep reservoir, whereas other portion stayed 24-h in epilimnion. Nonetheless, a real cause for diel vertical migrations of age 0+ perch in the deep reservoir was only hypothesized either by antipredator behaviour or optimal foraging strategy (Čech et al., 2005). Anyhow, in general, investigations on feeding and diet of hypolimnetic and/or vertically migrating age 0+ perch have been scarce so far (Slad, 1988). Thus, the first objective of my dissertation study follows and extends the observation of Čech et al. (2005) in order to explain or refuse DVMs of age 0+ perch as a tool for optimized foraging strategy. It is well documented that depth-dependent distribution, feeding behaviour and/or predatory avoidance are common strategies in a variety of large standing waters (Post & McQueen, 1988; Wang & Eckmann, 1994; Frankiewicz et al., 1997). To obtain better knowledge of these mechanisms in the pelagic zone of central European reservoirs, we further extended our research to a shallow, non-stratified part of the Lipno Reservoir where age 0+ pikeperch had dominated the pelagic age 0+ ichthyoplankton (Matěna et al., 1999) and where earlier hydroacoustic survey had also revealed vertical shifts of small, unidentified targets (M. Čech & J. Kubečka, pers. data). A combination of hydroacoustics and age 0+ fish trawling was carried out in this reservoir in order to analyze depth-dependent distribution and DVMs of age 0+ fish and to understand the relationship between these distribution patterns and foraging within 24-hour period. In contrast to deep and cold layers of a stratified reservoir (Čech et al., 2005), the near bottom zone with optimal physicochemical conditions (Brandl, 1973) was expected to provide sufficient daytime refuge.

Most cyprinids start their early life history in the shallow littoral of lakes and reservoirs or among submerged vegetation (Rheinberger et al., 1987; Matěna, 1995a, b). Some of them migrate to the pelagic zone later (Rheinberger et al., 1987; Matěna, 1995a, b), but not on a regular basis like percids and prefer to stay in epilimnion (Jachner, 1991; Kratochvíl et al., 2004; Matěna, 1995a; Vašek et al., 2006; Jůza et al.,

2009). Nonetheless, both percids and cyprinids occupy the littoral zone temporarily or permanently later in the season (Gliwicz & Jachner, 1992; Wang & Eckmann, 1994; Matěna, 1995b, Lewin et al., 2004) while pelagic age 0+ fish assemblage exists simultaneously (Duncan & Kubečka, 1995; Čech & Kubečka, 2006; Vašek et al., 2006). The heterogeneous littoral zone is characterized as the most productive area in the reservoir providing a sheltered niche for feeding, high temperatures for fast growth and/or as a refuge against predation (Rheinberger et al., 1987; Fernando & Holčík, 1991; Duncan & Kubečka, 1995; Winfield, 2004). The impoverished littoral zone of deep-valley reservoirs is characterized by sparse occurrence or even lack of water macrophytes and often constitutes only 5-12 % of the total reservoir area (Duncan & Kubečka, 1995; Čech et al., 2005). This deprivation is mainly caused by the presence of steep-sloped banks and frequent water level fluctuations (Vašek et al., 2006; Kahl et al., 2008). Despite the differences from the standard littoral zone perception characterized by gently sloped shoreline and aquatic macrophytes occurrence, the littoral zone in deep-valley reservoirs still constitutes unique environment serving as a feeding ground or as a sheltered refuge to avoid predation (Matěna, 1995b; Janssen & Luebke, 2004; Kahl et al., 2008). To comprehend the behaviour and processes within the littoral age 0+ fish assemblage, knowledge of distribution is the first necessary step to obtain this information. The routine littoral sampling of fish in reservoirs was usually a synonym for beach seining, performed only in attainable habitats and not taking other types of shoreline into consideration (Kubečka, 1990; Matěna, 1995b). The reasons for such routine, but restricted sampling were usually obstacles (roots, stumps, branches of dead trees, stones), steep-sloped banks and in years of high water level also inundated terrestrial vegetation (Kubečka & Švátora, 1993; Matěna, 1995; Vašek et al., 2006; Bonar et al., 2009; Říha et al., 2011). Nonetheless, it is generally known, that not only gently sloped beach habitats without obstacles are favoured by age 0+ fish (Duncan & Kubečka, 1995), but age 0+ fish also utilize deeper and steep-sloped shoreline with coarse-grained substrata where vegetation is usually not present (Irwin et al., 1997; Janssen & Luebke, 2004). Therefore, one may expect that sampling of just a single habitat could cause inaccuracy or underestimation of the littoral age 0+ fish assemblage when providing age 0+ fish assessment in the reservoir as a whole. Consequently, the second objective of this thesis focused on the assessment of the littoral age 0+ fish assemblage along the majority of shoreline and aimed to describe distribution patterns of age 0+ fish in relation to spatial heterogeneity within the reservoir on both diel and seasonal time-scales. In order to achieve and sample age 0+ fish in all important habitats of the littoral zone, point abundance sampling by electrofishing (PASE), similarly to that used in numerous riverine ecosystems (e.g. Copp & Garner, 1995; Copp, 2010; Janáč & Jurajda, 2013), was applied. Due to impossibility of achieving most of habitats by wading (steep slopes, depth, obstacles, heavy-duty electrofishing device), we modified the sampling scheme and the point abundance sampling of age 0+ fish was carried out from a boat rowing on oars, similarly to Lewin et al. (2004). This approach allowed us to sample all important habitats by the same method. To our best knowledge, this boat modified PASE technique was firstly applied for age 0+ fish sampling in the steep-sloped shoreline of a deep-valley reservoir.

This thesis originates from the sampling surveys performed between years 2002 and 2007 in two deep-valley (Slapy and Římov) and a shallow (Lipno) reservoir of the Vltava river drainage basin. The timing of surveys was set over the entire growing season to recognize the most important periods in early life history, from late May to mid-October. The first sampling survey was synchronised with perch larvae massive appearance in the pelagic zone in May-June (Wang & Eckmann, 1994; Čech et al., 2005). The first littoral electrofishing survey was initiated immediately after 0+ perch returned back to the littoral zone in June (Wang & Eckmann, 1994; Matěna, 1995b; Urho, 1996). The sampling was also performed during summer (July-August) when age 0+ fish utilize the production potential of the reservoir at maximum (Vašek et al., 2006, Prchalová et al., 2008) and the last sampling occasion in mid-October preceded the migrations to deeper water for overwintering (Kubečka, 1990; Wang & Eckmann, 1994; Brosse et al., 2007).

RESULTS

This Ph.D. thesis contains four original papers – three of them published (**Paper I., II. and III.**) in international scientific journals. **Paper IV.** has been submitted to a scientific journal.

PAPER I – Diet of larvae and juveniles perch, *Perca fluviatilis* performing diel vertical migrations in a deep reservoir

Kratochvíl, M., Peterka, J., Kubečka, J., Matěna, J., Vašek, M., Vaníčková, I., Čech, M. & Seďa, J., 2008. Diet of larvae and juveniles perch, *Perca fluviatilis* performing diel vertical migrations in a deep reservoir. *Folia Zoologica* **57**, 313-323

Feeding behaviour of two functional groups of 0+ perch *Perca fluviatilis* (epilimnetic, staying all 24 hours in epilimnion; hypolimnetic, daily migrating between hypolimnion and epilimnion) were investigated in the deep canyon-shaped Slapy Reservoir (Czech Republic) during two 24-h periods in late May and mid June 2002. Densities of most favoured cladocerans and copepods were generally higher in epilimnetic than in hypolimnetic zones. The two 0+ perch groups fed predominantly on cyclopoid copepods during the daytime in May. In June, epilimnetic perch fed on cladocerans (*Daphnia* sp., *Diaphanosoma brachyurum*), whereas hypolimnetic perch preferred calanoid copepod *Eudiaptomus gracilis*. Throughout darkness, when nearly all perch occupied upper strata, their gut contents were clearly dominated by cladocerans *Daphnia* sp. and *Diaphanosoma brachyurum* in May and June, respectively. Digestive tract fullness (DTF) of hypolimnetic perch was 2.0 - 2.8-times lower than the DTF of epilimnetic perch, and a higher share of perch with empty digestive tracts was found in the hypolimnion. Maximum DTF occurred in the epilimnion during the day and/or dusk, whereas at night and dawn progressive evacuation of guts was recorded and migrants returned with low DTF back to the hypolimnion. Low zooplankton abundance, unfavourable light and temperature conditions in the hypolimnetic zone are suboptimal both for prey searching and for overall metabolic processes.

PAPER II – Diel vertical migrations of age 0+ percids in a shallow, well-mixed reservoir

Kratochvíl, M., Čech, M., Vašek, M., Kubečka, J., Hejzlar, J., Matěna, J., Peterka, J., Macháček, J. & Seďa, J., 2010. Diel vertical migrations of age 0+ percids in a shallow, well-mixed reservoir. *Journal of Limnology* **69**, 305-310.

The distribution of age 0+ percids (perch, *Perca fluviatilis* and pikeperch, *Sander lucioperca*) was investigated in a shallow, well-mixed reservoir during a 24-h period in late May, using acoustic and netting methods. Diel vertical migrations (DVMs) were acoustically recorded between the layers close to the bottom and the whole water column. The netting data showed a high abundance of larvae and juveniles at night (nearly 1 ind m^{-3}, or 6 ind m^{-2}), whereas negligible numbers of age 0+ percids were present in the water column during the day (3 % of night abundance). Age 0+ percids remained during the day in the layer very close to bottom. Smaller pikeperch larvae dominated the pelagic age 0+ fish assemblage during daylight, while larger perch prevailed at night. A strong difference between day and night abundances along with a clear pattern discerned by acoustic methods revealed the DVM of age 0+ percids. Analyses of the fish digestive tract contents indicate that DVM was not governed by feeding behaviour, but rather a defensive strategy against predation. This is in agreement with the size distribution of age 0+ percids, since they were smaller in water column during the day as opposed to the night.

PAPER III – Littoral age 0+ fish distribution in relation to multi-scale spatial heterogeneity of a deep-valley reservoir

Kratochvíl, M., Mrkvička, T., Vašek, M., Peterka, J., Čech, M., Draštík, V., Jůza, T., Matěna, J., Muška, M., Seďa, J., Znachor, P. & Kubečka, J., 2012. Littoral age 0+ fish distribution in relation to multi-scale spatial heterogeneity of a deep-valley reservoir. *Hydrobiologia* **696**, 185-198.

Littoral age 0+ fish were studied with respect to spatio-temporal heterogeneity in the deep-valley Římov Reservoir (Czech Republic) from June to October 2007 using point abundance sampling by electrofishing. The abundance and diversity of age 0+ fish in different types of littoral habitats were examined along the longitudinal gradient of the reservoir during daytime. The impact of some physical attributes of the studied littoral habitats, e.g. slope steepness and substrate size, along with the season was the main factors affecting the distribution of age 0+ fish. The level of structural complexity was not a strong determinant, because the overall diversity and structural complexity of the available littoral habitats were relatively too low to have greater impact on the age 0+ fish distribution. The physical factors markedly influenced the spatial segregation between the two most important taxa in the reservoir – percids and cyprinids. Perch was the only representative of age 0+ percids in the littoral zone, which occupied steep-sloped habitats early in the season. In contrast, gently sloped habitats were mainly occupied by cyprinids later in the season. Species diversity was reflected in the occurrence of age 0+ cyprinids, achieving a maximum in gently sloped habitats in October. The effect of the longitudinal gradients on age 0+ fish distribution and diversity was generally far less significant, but was rather decisive during the period of a pronounced longitudinal trophic gradient during the summer season.

PAPER IV – The effects of diel period and habitat on littoral age 0+ fish distribution in a deep-valley reservoir

Kratochvíl, M., Vašek, M., Peterka, J., Draštík, V., Čech, M., Jůza, T., Muška, M., Matěna, J. & Kubečka, J., 2013. The effects of diel period and habitat on the littoral age 0+ fish distribution in a deep-valley reservoir. *Hydrobiologia*, submitted.

The effects of temporal and spatial small-scale factors, i.e. diel period and habitat, on littoral age 0+ fish distribution were studied using point abundance sampling by electrofishing (PASE). The complex sampling was performed twice per a 24-hour period (during daytime and at night) along the longitudinal axis of the reservoir from late spring to mid-autumn 2007. Littoral habitats were categorized by slope steepness (gently or steep-sloped) and structure (unstructured or structured). Diel period significantly affected the total abundance of age 0+ fish with an increase in all habitats found at night. The majority of fish species were more abundant in the littoral zone at night, with the exception of bleak (*Alburnus alburnus*) and gudgeon (*Gobio gobio*). Bleak occupied the littoral zone almost exclusively during daytime, whereas ruffe (*Gymnocephalus cernua*) almost exclusively at night. The structure of age 0+ fish assemblage was foremost determined by littoral habitats. Moreover, different species-specific patterns were distinguished with response to main habitat characteristics on a diel scale; species principally detected in structured littoral habitats and indifferent to slope steepness (perch, *Perca fluviatilis*), species with the affinity to gently sloped, unstructured habitats (ruffe, bleak, gudgeon and dace, *Leuciscus leuciscus*) and species commonly found in gently sloped shoreline, somewhat preferring structured habitats (roach, *Rutilus rutilus*). Diel changes in body size were also detected, but only at beaches had regular basis. These differences were caused by diel changes in species composition rather than by diel shifts of larger conspecifics. Diel habitat use by age 0+ fish in the studied reservoir was not size-dependent, but more likely was species-specific. Species diversity was primarily linked to habitats with low diel effect detected.

GENERAL DISCUSSION, CONCLUSIONS AND PERSPECTIVES

The presented dissertation substantially contributes to knowledge of distribution mechanisms of age 0+ fish assemblage in central European reservoirs. Only holistic studies on different spatial and temporal scales performed in both pelagic and littoral zones over the entire growing season could give answers to questions related to better understanding of age 0+ fish assemblage and its function within the ecosystem dynamics.

The occupation of hypolimnetic layers and DVMs appeared to be a regular phenomenon for at least a part of the population of percids in the pelagic zone of deep-valley reservoirs (Čech et al., 2005; Čech & Kubečka, 2006; Čech et al., 2007a, b; Jůza et al., 2012). The foraging hypothesis as one of commonly accepted explanations for DVMs (Wurtsbaugh & Neverman, 1988; Mous et al., 2004) failed and the results revealed that these shifts are most probably a defensive response to predatory rather than a feeding strategy profit (Paper I, Paper II). Recently, Petrtýl et al. (2013) compared RNA/DNA ratio as an index of short-term growth and nutritional conditions between epilimnetic (non-migrating) vs. hypolimnetic (migrating) age 0+ perch finding lower RNA/DNA

ratio in hypolimnetic perch and thus supported our results of lower feeding rate and assumptions of slower metabolism rate in perch when staying in cold hypolimnion. Nonetheless, two distinct DVMs patterns were established between stratified and non-stratified reservoirs: whereas only a portion of percid population (28.1 % and 4.7 % in May and June, respectively) migrated to deep, cold and dark hypolimnion in a deep-valley reservoir (Čech et al., 2005), a vast majority of pelagic age 0+ percid population performed DVMs between the pelagic zone and near bottom zone in a shallow, non-stratified reservoir (Paper II). In a deep-valley reservoir, two strategies were further distinguished: 1) epilimnetic strategy with sufficient feeding and higher growth rate, but certainly suffering higher predation, and 2) hypolimnetic strategy with insufficient feeding and lower growth rate, but most probably with low mortality rate caused by predation during the critical daytime phase. This assumption was supported by larger fish recorded in epilimnion than in hypolimnion (Čech et al., 2005) and by decreased or even stopped feeding activity in hypolimnion as a consequence of low zooplankton densities together with suboptimal light and temperature conditions (Paper I). In a shallow reservoir, age 0+ pelagic fish distribution showed two strategies like in a deep reservoir, but reversely, vast majority of age 0+ percids performed DVMs and only negligible numbers of age 0+ percids stayed in the water column during the daytime (Paper II). It also supports our assumption that unproven depth-dependent effect on quantitative feeding and safe bottom refuge with stable optimal physical conditions provide better chance to survive in a shallow reservoir during the critical period of early ontogenetic stage when starving and predation are the most significant factors affecting mortality rate (Miller et al., 1988; Mooij, 1996). To conclude, it is clearly evident that age 0+ percids profit more when perform DVMs in a shallow reservoir than when adopt any of the two strategies in a deep-valley reservoir. That could be the main reason why DVMs are performed massively in a non-stratified, shallow reservoir type compared to a deep, stratified reservoir.

The complex littoral surveys revealed that age 0+ fish occupied all types of littoral habitats during both diel periods for most of the growing season (Paper III, Paper IV). Small-scale spatial heterogeneity of littoral habitats influenced age 0+ fish distribution more than the longitudinal profile of the reservoir. These findings corroborate the short termed studies of Prchalová et al. (2008) and Jůza et al. (2009) who suggested that 1) the longitudinal distribution of juvenile fish affected by benthic habitats was more important than the longitudinal trophic gradient and 2) longitudinal age 0+ fish gradient in the pelagic zone was a result of reservoir morphology (changing littoral/pelagic ratio) rather than response to abiotic or biotic factors. The study of Čech et al. (2005) and also results of this dissertation demonstrated that portion of age 0+ perch population inhabited less favourable habitats of deep-valley reservoirs. Some age 0+ perch were initially recorded in cold and dark hypolimnetic layers as larvae and later in more opened steep-sloped habitats as juveniles. Although it seems to be likely disadvantageous strategy, such high ecological plasticity could bring an advantage of higher surviving probability at least for one separate ecological group of population under unpredictable and fluky conditions, typical for man-made reservoirs. Further, it is believed that age 0+ perch dispersion to those habitats not favoured by age 0+ cyprinids helped to establish spatial

segregation between age 0+ perch and 0+ cyprinids. Such separation is also known on vertical and horizontal axes in the pelagic zone of lakes and reservoirs (Jachner, 1991; Gliwicz & Jachner, 1992; Vašek et al., 2006; Jůza et al., 2009). The ecological differentiation and spatial segregation of a portion of age 0+ perch population both in the pelagic and littoral zones could probably help to provide a partial release from competition for habitat and food with conspecifics and chiefly with cyprinid species. Mainly roach is known to have competitive advantage whereas feeding on zooplankton in less structured habitats and under more turbid conditions (Winfield, 1986; Diehl & Eklöv, 1995; Vašek et al., 2006) as typical for eutrophicated deep-valley reservoirs.

Besides substantial contribution to knowledge of ecological processes in the reservoir, the main results of this dissertation might also facilitate to arrange future standard monitoring surveys and could provide important information about where and when the sampling should be performed in order to obtain the most comprehensive assessment of age 0+ fish assemblage. Foremost, sampling in broad spectrum of habitats appeared to be crucial to identify all ecological groups occupying both pelagic and littoral zones and to get more precise evaluation of the year class strength throughout the season. As a good example, the Papers III and IV documented that littoral age 0+ fish assemblage of routinely sampled shallow, unstructured gently sloped habitats is mainly occupied by cyprinid species. On the other hand, steep-sloped and/or structured habitats appeared to be an essential refuge for age 0+ perch population as mentioned above and described also in other age 0+ percids (Irwin et al., 1997; Janssen & Luebke, 2004). Therefore, previous studies on age 0+ fish assemblage utilizing beach seining or gillnetting only at unstructured, gently sloped habitats of deep-valley reservoirs most probably underestimated littoral age 0+ perch assemblage in the reservoir (Kubečka & Švátora, 1993; Matěna, 1995b; Vašek et al., 2006; Prchalová et al., 2008; Jůza et al., 2013). Further, temporal distribution changes on both diel and seasonal time-scales evidenced that accurate age 0+ fish estimates are highly dependent on selection of the sampling period. Diel sampling recognized mostly all species commonly found in the littoral zone with higher age 0+ fish abundance recorded at night (Paper IV). Nonetheless, only night littoral sampling could underestimate some daytime cyprinid species. Seasonal sampling recognized different distribution patterns within individual littoral habitats with some notable changes of species presence/absence between June and October. In order to obtain cost-effective data about littoral age 0+ fish assemblage structure, gently sloped habitats with highest species richness during late summer or early fall seemed to be most appropriate spatio-temporal combination for the littoral age 0+ fish assessment (Paper III; Bryan & Scarnechia, 1992; Pierce et al., 2001).

Extended sampling of the littoral habitats to the majority of shoreline as suggested in present thesis together with recent advances in pelagic age 0+ sampling (Jůza et al., 2009, 2013) show the way towards holistic understanding of the age 0+ fish assemblage in the standing freshwater systems as a whole. These recent studies have proved that some species are almost exclusively faithful to their littoral or pelagic habitats. Strong affinity to shallow littoral habitats was detected in some of typically rheophilous species (gudgeon, dace and chub), fitting into the riverine-reservoir concept of Fernando & Holčík (1991). Age 0+ pikeperch and bream, species practically missing along the

shallow shoreline on diel and seasonal time-scales during our extensive survey in 2007 and also in late summer of the following years (M. Kratochvíl, unpubl. data), were found to highly prefer the pelagic zone at night (Jůza et al., 2013). Some other species, i.e. perch, roach, bleak and ruffe, seem to perform extensive diel shifts between the habitats since they were found in sufficient numbers both in shallow littoral (Paper III, Paper IV) and pelagic (Jůza et al., 2013) zones. Some of these movements can be traced by the combination of the information on abundances and size distributions of the age 0+ fish in different habitats or proved by diet analyses (Vašek et al., 2006; Jůza et al., 2013). Deeper benthic habitats, not accessible by active sampling methods as trawling or electrofishing, probably host at least a portion of some migrating species providing them a daytime refuge and hence definitely represent the challenge for future research. Nonetheless, when age 0+ fish tend to dare closer to the surface at night, the depth dimension of distribution becomes most likely less important and the combination of complex littoral and pelagic sampling should be able to provide rather quantitative information on most reservoir age 0+ fish.

Although the present dissertation thesis fulfilled some substantial objectives related to understanding distribution patterns of age 0+ fish and managing the standard monitoring methodology, some other tasks for future research emerged during our surveys. Whereas the pelagic age 0+ fish assemblage with regularly observed DVMs and year-to-year variation has been in detail examined in deep-valley reservoirs recently (Čech et al., 2005; Čech & Kubečka, 2006; Vašek et al., 2006; Jůza et al., 2009; Jůza et al., 2013), more attention is still needed to focus onto the complex studies performed in the heterogeneous littoral zone. The main question points out to year--to-year variations in littoral habitats utilization, particularly in relation to years differing by unequal water level, typical for man-made reservoirs (Irz et al., 2002; Vašek et al., 2006; Kahl et al., 2008). Our littoral survey was carried out in the year of low water level with the absence of flooded vegetation, which is generally characterized by less successful spawning of dominant cyprinid species and lack of adequate shelter for age 0+ fish primarily resulting in lower cyprinid year-class strength (Martin et al., 1981; Kahl et al., 2008; Jůza et al., 2013). It is assumed that in other years when the water level in spring and summer is high enough and the terrestrial vegetation (mostly reed Canary grass, *Phalaris arundinacea* in the studied Římov Reservoir) is constantly flooded, it might result in 1) significant increase of some cyprinid species abundance (Slavík, 1992; Matěna, 1995a; Kahl et al., 2008; Jůza et al., 2013) and 2) providing almost complete place of refuge with high structural complexity ensuring high level of protection and rich feeding grounds (Bryan & Scarnecchia, 1992; Lewin et al., 2004; Kahl et al., 2008). These radical changes might completely alter the mechanisms of distribution of age 0+ fish in the littoral habitats. To fill these gaps of our knowledge, some other tasks concerning the year-to-year variations in age 0+ fish abundance, distribution, feeding and/or antipredatory behaviour whereas utilizing different littoral habitats should be also examined further.

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Paper I

Diet of larvae and juveniles perch, *Perca fluviatilis* performing diel vertical migrations in a deep reservoir

Kratochvíl, M., Peterka, J., Kubečka, J., Matěna, J., Vašek, M., Vaníčková, I., Čech, M. & Seďa, J.

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Diet of larvae and juvenile perch, *Perca fluviatilis* performing diel vertical migrations in a deep reservoir

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A b s t r a c t . Feeding behaviour of two functional groups of 0+ perch *Perca fluviatilis* (epilimnetic, staying all 24 hours in epilimnion; hypolimnetic, daily migrating between hypolimnion and epilimnion) were investigated in the deep canyon-shaped Slapy Reservoir (Czech Republic) during two 24-h periods in late May and mid June 2002. Densities of most favoured cladocerans and copepods were generally higher in epilimnetic than in hypolimnetic zones. The two 0+ perch groups fed predominantly on cyclopoid copepods during the daytime in May. In June, epilimnetic perch fed on cladocerans (*Daphnia* sp., *Diaphanosoma brachyurum*), whereas hypolimnetic perch preferred calanoid copepod *Eudiaptomus gracilis*. Throughout darkness, when nearly all perch occupied upper strata, their gut contents were clearly dominated by cladocerans *Daphnia* sp. and *Diaphanosoma brachyurum* in May and June, respectively. Digestive tract fullness (DTF) of hypolimnetic perch was 2.0–2.8-times lower than the DTF of epilimnetic perch, and a higher share of perch with empty digestive tracts was found in the hypolimnion. Maximum DTF occurred in the epilimnion during the day and/or dusk, whereas at night and dawn progressive evacuation of guts was recorded and migrants returned with low DTF back to the hypolimnion. Low zooplankton abundance, unfavourable light and temperature conditions in the hypolimnetic zone are suboptimal both for prey searching and for overall metabolic processes.

Key words: 0+ fish, Slapy Reservoir, digestive tracts fullness, zooplankton

Introduction

A shift from littoral to pelagic habitat occurs (P o s t & M c Q u e e n 1988, M a t ě n a 1995a, U r h o 1996) during the early life history of both species of perch, the European perch (*Perca fluviatilis* L.) and its close relative, the North-American yellow perch (*Perca flavescens* (Mitchill)) (P o s t & M c Q u e e n 1988, U r h o 1996). Larvae of both species migrate from the littoral zone into the pelagic habitat soon after hatching, and stay there for a month or even longer while they feed predominantly on zooplankton (T h o r p e 1977, K o k e š & S u k o p 1984, M a t ě n a 1995b). Some juveniles then switch to demersal mode of life and return back to the littoral zone (C o l e s 1981, P o s t & M c Q u e e n 1988, T r e a s u r e r 1988, W a n g & E c k m a n n 1994, U r h o 1996), or to the benthic zone (L i n 1975). It has been hypothesized that these shifts are connected with depletion of zooplankton resources in the pelagic area (T r e a s u r e r 1988, W a n g & E c k m a n n 1994) or with higher predation vulnerability of pigmented, non-transparent juveniles (fully metamorphosed), that can be detected by cruising pelagic predators more easily than transparent ichthyoplankton (K e l s o & W a r d 1977, W h i t e s i d e et al. 1985).

Paper II

Diel vertical migrations of age 0+ percids in a shallow, well-mixed reservoir

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Diel vertical migrations of age 0^+ percids in a shallow, well-mixed reservoir

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ABSTRACT

The distribution of age 0^+ percids (perch, Perca fluviatilis *and pikeperch,* Sander lucioperca*) was investigated in a shallow, well-mixed reservoir during a 24-h period in late May, using acoustic and netting methods. Diel vertical migrations (DVMs) were acoustically recorded between the layers close to the bottom and the whole water column. The netting data showed a high abundance of larvae and juveniles at night (nearly 1 ind m^{-3}, or 6 ind m^{-2}), whereas negligible numbers of age 0^+ percids were present in the water column during the day (3% of night abundance). Age 0^+ percids remained during the day in the layer very close to bottom. Smaller pikeperch larvae dominated the pelagic age 0^+ fish assemblage during daylight, while larger perch prevailed at night. A strong difference between day and night abundances along with a clear pattern discerned by acoustic methods revealed the DVM of age 0^+ percids. Analyses of the fish digestive tract contents indicate that DVM was not governed by feeding behaviour, but rather a defensive strategy against predation. This is in agreement with the size distribution of age 0^+ percids, since they were smaller in water column during the day as opposed to the night.*

Key words: Perca fluviatilis*,* Sander lucioperca*, Lipno Reservoir, DVM, juvenile*

1. INTRODUCTION

Two percids, perch (*P. fluviatilis*) and pikeperch (*S. lucioperca*) are important members of fish communities in many European lakes and reservoirs. Their larvae and early juveniles undergo a pelagic phase for a month or longer (Urho 1996a; Specziar 2005). In deep stratified lakes and reservoirs, the diel vertical migrations (DVMs) of age 0^+ percids over a few meters (Kelso & Ward 1977), within an amplitude of 11-13 m (Čech *et al*. 2005) or even more (Eckmann & Imbrock 1996) have been described. In some cases, DVMs exhibit a trade off between predator avoidance and starvation (Kratochvíl *et al*. 2008), with potential exposure to suboptimal physicochemical conditions within a deepwater refuge (Čech *et al*. 2005). These refuges are absent in shallow waters, where the only sheltered niche may be the bottom or littoral zone. In fact, Gliwicz (1990) reported that in the shallow Sulejow Reservoir, age 0^+ fish avoided open water strata during the day. Another study by Frankiewicz *et al*. (1997) in the same reservoir showed that even during the night under intensive moonlight, the population of age 0^+ pikeperch preferred the deep strata, independently of the availability of zooplankton food, temperature and oxygen concentrations. Diel migrations of fish seem to be clearly triggered by light intensity (Cole & MacMillan 1984; Frankiewicz *et al*. 1999), and yet age 0^+ fish migrate to refuges in littoral or in deep water layers (Gliwicz & Jachner 1992; Čech *et al*. 2005).

The present study aimed to describe in detail the vertical distributions and DVM of two species of age 0^+ percids in a shallow reservoir using acoustics and net sampling. It was hypothesized that the only refuge for small percids larvae during the daytime would be the water layer close to the bottom, because such small fish cannot swim long distances. Due to the different spawning time of perch and pikeperch, their larval size was different during the time of the study. Thus, the different depth selection behaviour of these two species can be presumed. An inspection of the gut contents of the sampled fish was performed to determine a potential interaction of foraging strategy and defensive behaviour.

2. METHODS

2.1. Study area

The study was carried out in the shallow eutrophic Lipno Reservoir (48°37'57"N; 14°14'13"E; 726 m a.s.l; surface area 4820 ha; mean depth 6.6 m) (Fig. 1a). Samples were collected in the middle of the reservoir (between the 52nd and 65th km of the river at a station close to Cerna v Posumavi). The maximum depth of the studied area was 8-10 m, but most of this area had a flat bottom with depths of 6 m. The lacustrine area of the Lipno Reservoir is large and shallow enough to be well-mixed even by moderate winds, and consequently no long-term thermal stratification occurs through the growing season (Brandl 1973). The adult fish fauna is dominated by cyprinids (bleak, *Alburnus alburnus*;

Paper III

Littoral age 0+ fish distribution in relation to multi-scale spatial heterogeneity of a deep-valley reservoir

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PRIMARY RESEARCH PAPER

Littoral age 0+ fish distribution in relation to multi-scale spatial heterogeneity of a deep-valley reservoir

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Abstract Littoral age 0+ fish were studied with respect to spatio-temporal heterogeneity in the deep-valley Římov Reservoir (Czech Republic) from June to October 2007 using point abundance sampling by electrofishing. The abundance and diversity of age 0+ fish in different types of littoral habitats were examined along the longitudinal gradient of the reservoir during daytime. The impact of some physical attributes of the studied littoral habitats, e.g. slope steepness and substrate size, along with the season was the main factors affecting the distribution of age 0+ fish. The level of structural complexity was not a strong determinant, because the overall diversity and structural complexity of the available littoral habitats were relatively too low to have greater impact on the age 0+ fish distribution. The physical factors markedly influenced the spatial segregation between the two most important taxa in the reservoir—percids and cyprinids. Perch was the only representative of age 0+ percids in the littoral zone, which occupied steep-sloped habitats early in the season. In contrast, gently sloped habitats were mainly occupied by cyprinids later in the season. Species diversity was reflected in the occurrence of age 0+ cyprinids, achieving a maximum in gently sloped habitats in October. The effect of the longitudinal gradients on age 0+ fish distribution and diversity was generally far less significant, but was rather decisive during the period of a pronounced longitudinal trophic gradient during the summer season.

Keywords Habitat preference · Electrofishing · Growing season · Slope steepness · Percids · Cyprinids

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Introduction

The distribution of age 0+ fish as well as their interactions with prey and/or predators in highly structured littoral habitats has been documented in numerous studies from natural lakes and shallow reservoirs (Bryan & Scarnecchia, 1992; Jacobsen & Berg, 1998; Hülsmann et al., 1999; Lewin et al., 2004; Okun & Mehner, 2005; Dembski et al., 2008). Less attention has been focused onto the littoral zone of

Paper IV

The effects of diel period and habitat on the littoral age 0+ fish distribution in a deep-valley reservoir

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THE EFFECTS OF DIEL PERIOD AND HABITAT ON THE LITTORAL AGE 0+ FISH DISTRIBUTION IN A DEEP-VALLEY RESERVOIR

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ABSTRACT

The effects of temporal and spatial small-scale factors, i.e. diel period and habitat, on littoral age 0+ fish distribution were studied using point abundance sampling by electrofishing (PASE). The complex sampling was performed twice per a 24-hour period (during daytime and at night) along the longitudinal axis of the reservoir from late spring to mid-autumn 2007. Littoral habitats were categorized by slope steepness (gently or steep-sloped) and structure (unstructured or structured). Diel period significantly affected the total abundance of age 0+ fish with an increase in all habitats found at night. The majority of fish species were more abundant in the littoral zone at night, with the exception of bleak (*Alburnus alburnus*) and gudgeon (*Gobio gobio*). Bleak occupied the littoral zone almost exclusively during daytime, whereas ruffe (*Gymnocephalus cernua*) almost exclusively at night. The structure of age 0+ fish assemblage was foremost determined by littoral habitats. Moreover, different species-specific patterns were distinguished with response to main habitat characteristics on a diel scale; species principally detected in structured littoral habitats and indifferent to slope steepness (perch, *Perca fluviatilis*), species with the affinity to gently sloped, unstructured habitats (ruffe, bleak, gudgeon and dace, *Leuciscus leuciscus*) and species commonly found in gently sloped shoreline, somewhat preferring structured habitats (roach, *Rutilus rutilus*). Diel changes in body size were also detected, but only at beaches had regular basis. These differences were caused by diel changes in species composition rather than by diel shifts of larger conspecifics. Diel habitat use by age 0+ fish in the studied reservoir was not size-dependent, but more likely was species-specific. Species diversity was primarily linked to habitats with low diel effect detected.

KEYWORDS: slope steepness, structured habitat, juveniles, night, electrofishing