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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*;

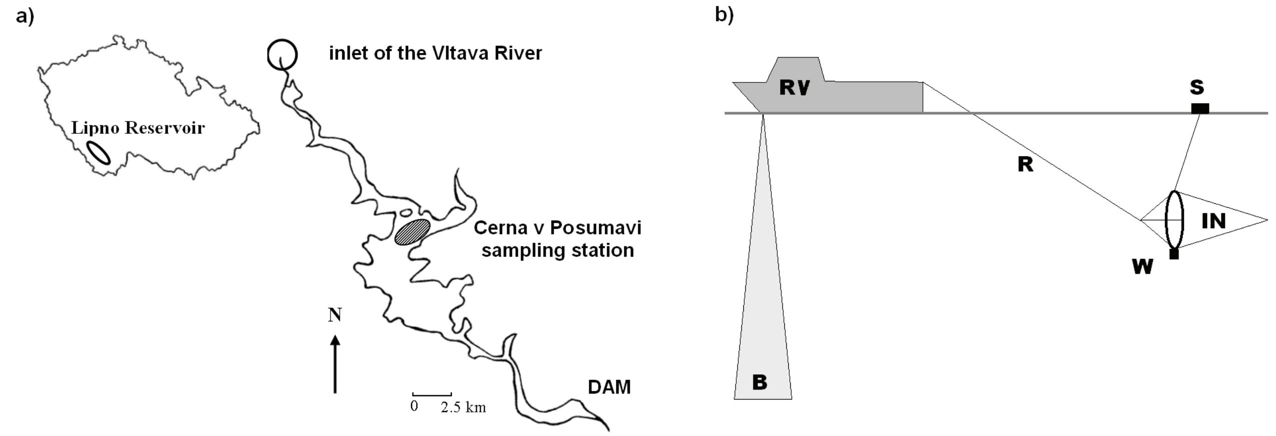

**Fig. 1**. (**a**) Location of the Lipno Reservoir within the Czech Republic and a map showing the position of the study site Cerna v Posumavi. (**b**) Schematic diagram of a sampling gear. RV, research vessel; B, beam of transducer; R, rope; S, styrofoam floater; W, weight; IN, ichthyoplankton net.

roach, *Rutilus rutilus*) and the most abundant predatory species are perch and pikeperch (M. Prchalová, unpublished data).

### *2.2. Data collection and analyses*

A 24-hour survey was carried out in the study area on 29-30 May, 2003. The vertical profiles of temperature and dissolved oxygen concentration were measured twice a day (11:00 and 01:00 hours) using a YSI 556 MPS probe. Light penetration was measured with the LICOR LI-250 underwater light meter. The Vltava River Authority provided data on chlorophyll, turbidity and DOC on 29 May, 2003.

Two methods, echosounding and net towing, were used simultaneously to examine the distribution patterns of age $0^+$ fish in the water column of the study area. A Simrad EY 500 split-beam scientific echosounder (at a frequency of 120 KHz), with the SIMRAD ES120-7G transducer transmitting a circular beam with a nominal angle of 7.1°, was used for acoustic investigations (for a detailed description of sampling details and post-processing procedure, see Čech *et al*. 2005). For direct sampling of age $0^+$ fish in the open water, a conical ichthyoplankton net (rectangular mesh-size 1 × 1.35 mm) on a circular frame (1 m in diameter) was used (Fig. 1b). A detailed description of the sampling device is given in Čech *et al.* (2005). The net was towed 100 m behind the research vessel at an average speed of approximately 4 km $h^{-1}$. Each haul took 5 minutes and filtered a water volume of 265 $m^3$. Day (10:00 – 12:30 hours) and night (00:00 – 02:00 hours) tows were performed in 5-6 water column layers (0-1, 1-2, 2-3, 3-4, 4-5, 5-6 m), except the near-bottom area, due to a danger of hitting obstacles and mud. Two parallel hauls were performed at the same time and towing depth.

Supplementary beach seining was done in the littoral zone to exclude diel horizontal migrations of age $0^+$ fish between pelagic and littoral areas. Two parallel hauls were performed at the same time during the day (13:00-13:30) and night (02:30-3:00). Sampling was performed on suitable shores with a bottom surface consisting of a fine substrate without mud or obstructions by using a beach seine of 10 m length and 2 m height with rectangular mesh-size of 1 × 1.35 mm. The net was laid out from a row boat propelled in parallel with the shore, where it was pulled with 15 m long ropes attached to each side. The catch was expressed as the number of age $0^+$ fish per 10 m of seine net. All fish were narcotized with MS-222 and preserved in 6-10% formaldehyde.

Zooplankton samples were collected using a plankton net (diameter 24 cm, mesh size 150 μm) both during the day and night (two vertical hauls per each diel period). The hauls were performed throughout the whole water column (0-6 m) since previous observations have shown that the vertical distribution of zooplankton in the water column is homogenous (J. Seďa, unpubl. data).

In the laboratory, all fish were identified to the species (percids) or family (cyprinids) level (according to Koblickaya 1981) and counted. The length of the larvae was measured to the nearest 0.5 mm from the snout tip of the head to the end of the *chorda dorsalis*. In the case of juveniles, standard length ($L_s$) was measured to the nearest 0.5 mm. The contents of the entire digestive tract were analysed in 76 perch and 132 pikeperch larvae and early juveniles. Prey items obtained from individual digestive tracts were identified to the relevant taxonomic groups and counted (heads and mandibles of cladocerans and furcas of copepods were enumerated in cases where prey items were digested beyond recognition). The amount of consumed prey was expressed using the numerical method (number of prey individuals digestive $tract^{-1}$) described by Hyslop (1980).

### *2.3. Statistical analyses*

Data on zooplankton densities were analysed using the chi-square ($\chi^2$) test. The nonparametric Mann-Whit-

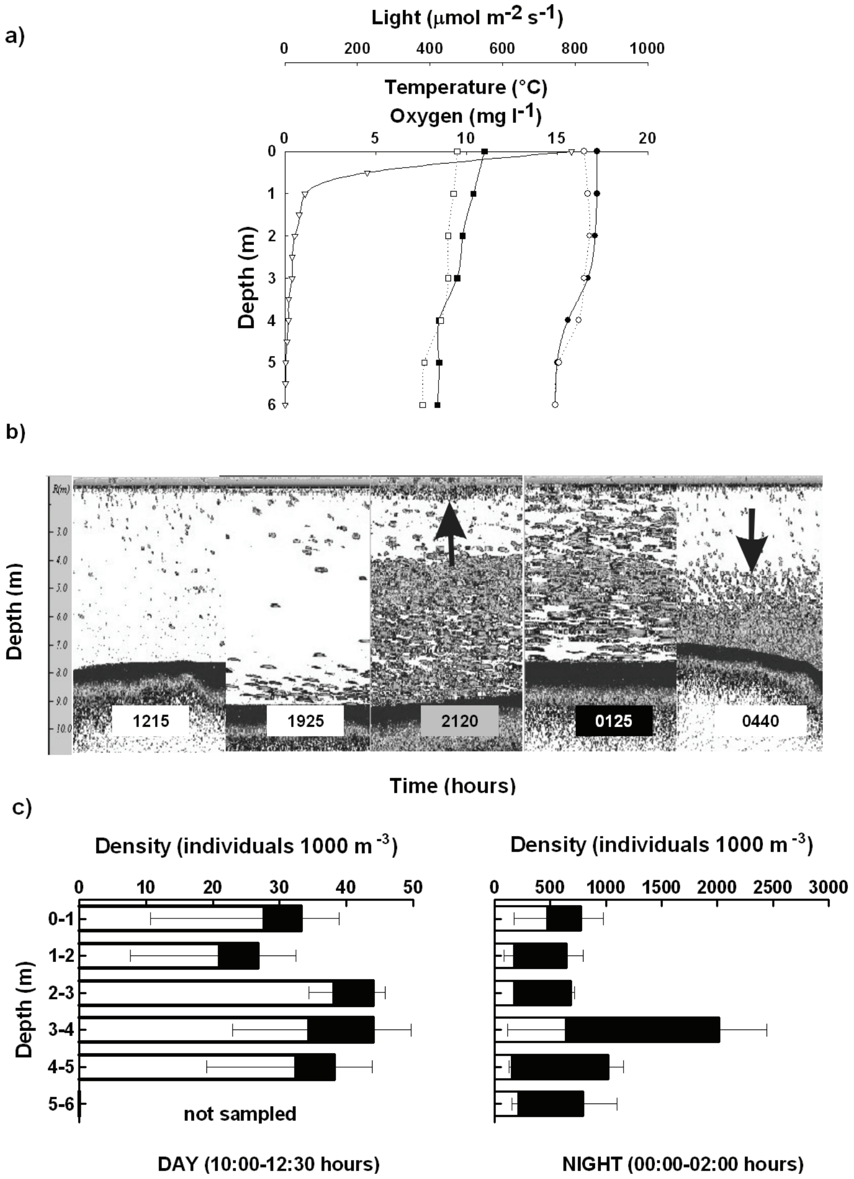

**Fig. 2**. (**a**) Vertical stratification of temperature (○, ●) and oxygen (□, ■) measured every 1 m of the water column from the surface to the bottom during daytime (○, □) and at night (●, ■). Photosynthetically active radiation (PAR) was measured every 0.5 m of the water column from the surface to the bottom during daytime (□). (**b**) Echograms of vertical day/night distribution and dusk/dawn migrations. Arrows show the direction of vertical movements from and to the bottom. (**c**) Perch (■) and pikeperch (□) densities (mean, 1 SD; based on two samples in each depth layer) estimated from the ichthyoplankton net. Note different scales on the x-axis.

ney U test was used to test differences in fish body sizes. To compare food quantity in the digestive tracts of fish, the two-way ANCOVA was applied with species (perch, pikeperch) and time period (day, night) as treatments, whereas fish size was included in the analysis of covariance as a covariate in order to eliminate possible side effects. Redundancy analysis (RDA), a multivariate linear method (Lepš & Šmilauer 2003), was used for the description of the relationship between diet (quantity and quality aspects) and explanatory or environmental variables (length of fish, depth position, time period). Data were log-transformed $y' = \log(y + 1)$ and centred by species to subtract the mean so that the resulting variable had an average of zero. To test single effects of explanatory variables on feeding patterns, additional regression analyses were performed.

## 3. RESULTS

### *3.1. Physicochemical conditions*

During the survey, clear thermal and oxygen stratifications were not observed at the sampling area (Fig. 2a). The photosynthetically active radiation (PAR) was recorded to be ~ 50 lx (=0.98 μmol $m^{-2} s^{-1}$) at 6 m depth (close to the bottom) and the euphotic zone (1% of PAR at the surface) nearly reached a depth of 4 m. The con-

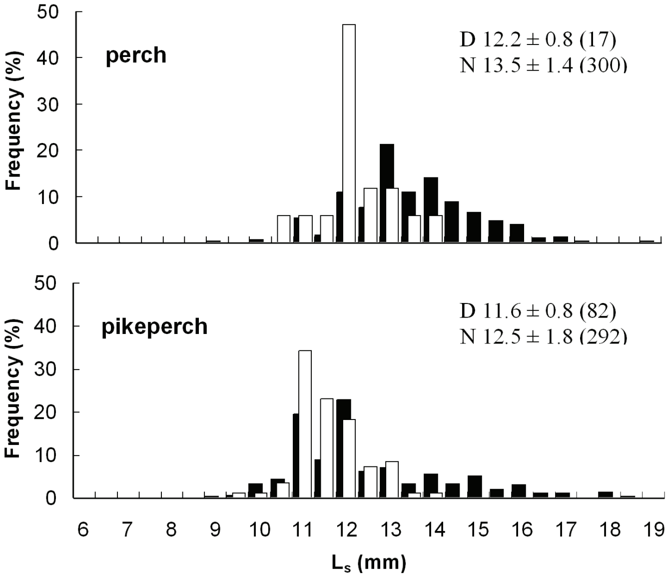

**Fig. 3**. Length-frequency distributions of age 0+ perch and pikeperch throughout the water column during the day (□) and at night (■) at the Cerna v Posumavi sampling point. The mean standard length (Ls) ± 1 SD (mm) is given above each histogram, numbers of fish measured are given in parentheses.

centration of chlorophyll-*a* was 2.3 µg $L^{-1}$ and turbidity did not exceed 2 NTU (nephelometric turbidity units). These low values are not very typical for this eutrophic reservoir and were influenced by the clear water phase. The observed water transparency was also influenced by a higher concentration of humic acids (DOC = 7 mg $L^{-1}$), which were leached from peat bogs located above the reservoir during several flooding events in 2002.

### *3.2. Distribution and size of age 0+ percids*

The pattern of vertical distribution of acoustical single targets (age $0^+$ fish and macroinvertebrates; target strength –67 to –57 dB at 120 kHz) showed clear differences with respect to the time of day (Fig. 2b). The abundance of acoustical targets in all layers of the water column was 3.3 ind $m^{-2}$ during daytime and 41.7 ind $m^{-2}$ at night. During twilight, remarkable vertical shifts occurred. At dusk, the vast majority of targets swam upwards from the bottom and dispersed throughout the water column. At dawn, a reverse shift towards the bottom was observed.

In total, 1083 individuals of pelagic age $0^+$ fish were caught during 10 day and 12 night hauls. The most abundant age $0^+$ fish were species of the family Percidae, including perch (67.1%) followed by pikeperch (32.4%) and ruffe (*Gymnocephalus cernuus*) (0.3%). Cyprinids comprised only 0.2% of the total catch. At night, the mean density of perch and pikeperch reached nearly 1000 ind 1000 $m^{-3}$ (abundance 6.0 ind $m^{-2}$) and perch (68.7%) dominated over pikeperch (30.8%) (Fig. 2c). During the daytime, a negligible number of age $0^+$ fish were recorded in the water column (on average 32 ind 1000 $m^{-3}$) and their abundance reached only 0.2 ind $m^{-2}$. Pikeperch dominated daytime catches with 82.8%, while perch represented 17.2%. No other fish species was present in the pelagic age $0^+$ fish community during the day. Beside age $0^+$ fish, larvae of *Chaoborus* sp. (Diptera, Chaoboridae) exhibited similar distribution patterns and also performed DVM. The abundance of chaoborid larvae (estimated from ichthyoplankton net catches) reached 0.25 ind $m^{-2}$ at night, whereas they were not recorded in the open water during the daytime.

Significant differences in body sizes were found, with the size of age $0^+$ perch caught in negligible numbers during the day was significantly smaller than those occupying the water column during the night (Mann-Whitney U test, d.f. = 316, $P$ <0.001) (Fig. 3). The size of age $0^+$ pikeperch caught during the day was again significantly smaller than those caught at night (Mann-Whitney U test, d.f. = 373, $P$ <0.001).

The littoral zone was almost exclusively occupied by age $0^+$ perch and pikeperch. In total, 230 individuals of perch and pikeperch were caught by two day and night seine hauls. The abundance of age $0^+$ percids was recorded to be 45.5 ± 24.7 and 64.5 ± 19.1 (mean ± 1 SD) per 10 m of beach seine during day and night, respectively. Perch dominated daytime catches with 87.9%, while the ratio of both species was similar at night (52.5% and 47.5% for perch and pikeperch, respectively). The mean standard length ($L_s$) of age $0^+$ percids was 15.8 ± 1.9 (mean ± 1 SD) for perch and 15.1 ± 2.4 mm (mean ± 1 SD) for pikeperch sampled in the littoral zone.

### *3.3. Zooplankton and diet of age $0^+$ percids*

The total zooplankton density did not vary between day and night ($\chi^2$-test, $P$ >0.05) and their relative taxon composition remained the same ($\chi^2$-test, $P$ >0.05). The

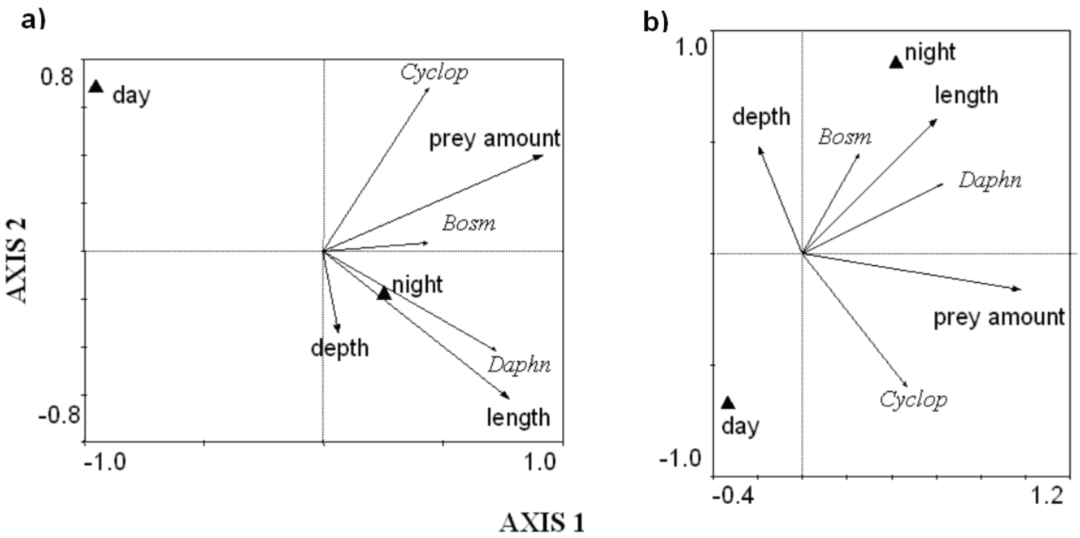

**Fig. 4**. Biplot of (**a**) perch and (**b**) pikeperch digestive tract contents (amount of prey by numbers) from the redundancy analysis (RDA). Prey (arrows), environmental (arrows) and nominal environmental (triangles) variables are demonstrated. Only prey categories significantly represented in the diet of percids are shown. The length of an arrow of a particular prey indicates its importance in the diet. Length – $L_s$ of fish (mm), prey amount – quantity of consumed prey (ind digestive tract$^{-1}$), *Bosm* – Bosminidae, *Daphn* – *Daphnia* sp., *Cyclop* – Cyclopidae (copepodite stages + adults).

age $0^+$ percids preyed predominantly on cyclopoid copepods during the day (Fig. 4). Large cladocerans (*Daphnia* sp.) were found more frequently in the digestive tracts at night. The quantity of food in the digestive tracts was higher in perch than pikeperch, but was not time period dependent (two-way ANOVA; species: $F_{1,204}$, $P < 0.001$, time: $F_{1,204}$, $P > 0.05$). The number of cyclopoid copepods in pikeperch digestive tracts declined in those caught at increasing depths (regression analysis; $F_{1,118}$, $P < 0.001$). In perch, the amount of cyclopoid copepods consumed declined with increasing water depth as well (Fig. 4a), but this trend was not statistically significant (post hoc regression analysis; $F_{1,69}$, $P > 0.05$). The total number of prey in the digestive tracts of both age $0^+$ percids was not dependent on depth at which the fish were sampled (regression analysis; perch, $F_{1,74}$, $P > 0.05$; pikeperch, $F_{1,130}$, $P > 0.05$).

## 4. DISCUSSION AND CONCLUSIONS

The diel migrations described in the present study were most likely triggered by light intensity, as has been previously suggested by Eckmann & Imbrock (1996) and Čech *et al.* (2005). The same migratory behaviour has been detected in *Chaoborus* sp. larvae. These migrations are induced by the presence of fish predators (Dawidowicz *et al.* 1990). Low turbidity combined with sufficient illumination does not interfere with the visual detection of predators, and thus prey fish could reduce predator pressure by increasing the level of their avoidance in clear water (Abrahams & Kattenfeld 1997). Thus, it seems to be likely that objects of similar size (i.e., age $0^+$ percids and larvae of *Chaoborus* sp.) were similarly threatened by abundant visually foraging large perch and pikeperch.

Besides DVM, horizontal migrations from daytime refuges into the littoral zone may be theoretically responsible for the increased nocturnal abundance of age $0^+$ fish in the pelagic zone (Gliwicz & Jachner 1992). However, horizontal migration was unlikely to cause the increase of age $0^+$ percid density in the pelagic zone at night because similar day and night abundances of age $0^+$ fish were found in the littoral zone. Furthermore, acoustic observations in the pelagic zone revealed vertically oriented diel migration of age $0^+$ percids. An obligatory pelagic phase is documented for percid larvae as well as their return to the littoral after metamorphosis from the larval to juvenile stage (Coles 1981; Matěna 1995). This trait was also observed in our study since percid larvae were found in the pelagic zone and almost all of age $0^+$ percids found in the littoral zone were at the juvenile stage with fully developed fins. Vertical migration within a distance of ~6 m to a relatively safe bottom habitat at dawn, as observed with the echosounder, was also certainly energetically less demanding for fish larvae than extensively long horizontal migrations.

Variation in the sizes of age $0^+$ percids between day and night could be caused by several factors. Small and transparent percids present in the pelagial during daytime are less conspicuous to predators than larger fry (Kovalev 1976; Coles 1981), which are more easily detectable due to their increasing opaqueness, pigmentation and size (Kelso & Ward 1977; Whiteside *et al.* 1985). A higher proportion of age $0^+$ pikeperch present in the pelagial during daytime hours could be explained by their weak pigmentation and smaller size in comparison to perch, and hence their reduced conspicuousness to predators (Urho 1996b). The second possibility to be considered is the greater swimming capacity of larger fish (Godø *et al.* 1990) and their better avoidance in front of sampling gear between dawn and dusk (Cole & MacMillan 1984; North & Murray 1992; Guest *et al.* 2003).

The actual depth of fish swimming in the water column during either daylight or at night had no significant impact on the total amount of prey consumed. However, age $0^+$ percids and, particularly, pikeperch consumed more cyclopoid copepods close to the surface during daylight hours, probably because this evasive and small prey was easier to capture in well-illuminated waters.

In conclusion, the obtained results have shown DVM to be an important phenomenon for a majority of age $0^+$ percids in a shallow reservoir during their pelagic phase. In contrast, only a minority of this population (28.1%) performing DVM migrated to the hypolimnion of a stratified reservoir (Čech *et al.* 2005). The cost of DVM and staying close to the bottom during the day seems to be lower for age $0^+$ percids as compared to migrations to the hypolimnion in a deep, stratified reservoir.

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