

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

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Abstract. 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 (Post & McQueen 1988, Matěna 1995a, Urho 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)) (Post & McQueen 1988, Urho 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 (Thorpe 1977, Kokeš & Sukop 1984, Matěna 1995b). Some juveniles then switch to demersal mode of life and return back to the littoral zone (Coles 1981, Post & McQueen 1988, Treasurer 1988, Wang & Eckmann 1994, Urho 1996), or to the benthic zone (Lin 1975). It has been hypothesized that these shifts are connected with depletion of zooplankton resources in the pelagic area (Treasurer 1988, Wang & Eckmann 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 (Kelso & Ward 1977, Whiteside et al. 1985).

In lakes, maximum abundances of pelagic 0+ perch have been reported from surface layers of the water column (Coles 1981, Whiteside et al. 1985, Post & McQueen 1988, Treasurer 1988, Wang & Eckmann 1994). Consequently, a lot of studies have focused on the diet of pelagic 0+ perch living in epi- or metalimnion of reservoirs or lakes (e.g. Whiteside et al. 1985, Jachner 1991, Flík et al. 1997, Matěna 1998). Some studies have reported 0+ perch communities from greater depths (Cooper et al. 1981, Perrone et al. 1983, Kubečka & Slad 1990), but papers on diet of hypolimnetic and/or vertically migrating populations of 0+ perch are scarce (Slad 1988).

Recently, Čech et al. (2005) described the distribution of two sympatrically living 0+ perch groups in the pelagic area of a canyon shaped reservoir. The majority of perch larvae and juveniles utilized the epilimnion (non-migrating fry), but a portion of the pelagic 0+ perch population moved from warm epilimnetic layers during the night to the cold and dark hypolimnion during the day.

Thus, the main objective of this study was to extend the findings of Čech et al. (2005) and describe the diet of migrating and non-migrating 0+ perch. This study focused on 1) the assessment of available planktonic prey in epi- and hypolimnetic habitats; 2) qualitative and quantitative aspects of food intake of migrating and non-migrating perch; and 3) diel patterns of zooplankton consumption.

Study Area, Materials and Methods

Slapy Reservoir, located in the Czech Republic (49°49'28" N, 14°25'58" E) is a steep-sided meso- to eutrophic, dimictic reservoir covering an area of 1392 ha (length 42 km, mean width 313 m), with a volume of 269×10^6 m³ and maximum depth of 58 m. The average theoretical retention time reflects a relatively high annual inflow of only 38.5 days (Hrbáček & Straškraba 1966). The reservoir was constructed as a part of the Vltava River Cascade during the period 1949–1954. From a fish fauna and fishery perspective it differs from other canyon-shaped reservoirs in the Czech Republic due to high percid contributions to the stock (Kubečka 1993). In the lacustrine study site characterized by steep shores with poorly-developed vegetation zones, depth of the thermocline was well below 4 m during the sampling (Čech et al. 2005).

Age 0+ perch were collected in open water zone of the reservoir during two 24-h surveys on 29–30 May and 17–18 June 2002. Both May and June investigations were divided into four time periods – day (8:00–19:00), dusk (20:00–22:30), night (0:00–3:00) and dawn (4:00–6:00). To locate 0+ fish in the water column acoustic observations were performed using a scientific echosounder (Simrad EY 500) located on the net-towing research vessel (for more details see Čech et al. 2005). On the basis of fish signals, a conical ichthyoplankton net (2 m diameter frame; mesh size 1*1.35 mm) with a 10 kg weight and a styrofoam floater was used for sampling fish larvae and juveniles within upper 16 m of the water column. The length of the connecting line between the floater and the net frame was adjusted according to required sampling depth. The net was towed 50 m behind the research vessel for 5 minutes with an average speed of 3–4 km/h as estimated by Garmin eTrex Summit GPS. A supporting boat with a commercial echosounder (Eagle Ultra Classic) was used to ensure the exact towing depth of the net. Several separate vertical tows from the deep layers were done additionally to ensure that fish from the upper strata did not contaminate

the net while it was lifted from lower towing depths to the surface. All fish collected were immediately preserved in ~10% formaldehyde for later analyses.

Zooplankton was collected only during day (16:00) and night (0:30) periods, simultaneously with 0+ fish. In both sampling periods 5–7 different depth strata were sampled. In May, a Van Dorn sampler (volume 5.6 l, height 0.5 m with a 40 μm mesh) was used to collect zooplankton. Nauplii and rotifers were not included in the counts of June zooplankton because they were consumed in negligible amounts by 0+ perch at that time, so zooplankton samples were collected using a closing 140- μm plankton net (diameter 24 cm). During both sampling periods, samples were immediately preserved in 4% formaldehyde solution.

Temperature and oxygen vertical profiles were measured using a calibrated YSI 556 MPS probe. In June, light penetration through the water column was measured using LICOR LI-250 underwater light meter. The data on temperature, oxygen and light distribution have already been published in Č e c h et al. (2005).

Zooplankton and fish diet analyses

In the laboratory at least 2/3 of each zooplankton sample or 250–300 individuals were counted and identified to genus or species level. Only zooplankton samples from epilimnetic (0–4 m) and hypolimnetic (9–15 and 10–16 m in May and June, respectively) zones were subjected to statistical analyses.

Fish were identified (according to K o b l i c k a y a 1981) and enumerated. Their standard lengths (SL) and wet weights were measured to the nearest 0.5 mm and 0.1 mg, respectively. The length from the snout tip to the end of the chorda dorsalis for larvae and standard length (SL) for juveniles were taken. Prey items from the gut of fish up to 15 mm SL (no stomach differentiated) and from both stomach and gut (fish above 15 mm SL), were identified to the relevant taxonomic level, counted, and whenever possible, measured from the top of the head to the base of the tailspine (cladocerans), or to the base of the caudal rami (copepods). In *Leptodora kindtii* (Focke), length of the tailspines was used and the total body size was estimated from the regression between tailspine length and body length after H o r n i g & B e n n d o r f (1985). Wet body mass of zooplankton was estimated from the length-volume regression given by H o e h n et al. (1998). Prey volume calculated from median body length of prey type was converted to wet weight assuming a specific gravity 1.0 g/ml. Digestive tract fullness, DTF (mg wet weight of food per 100 mg wet body weight of perch) was determined after H y s l o p (1980):

$$\text{DTF} = 100 \sum_{i=1}^n G_i * (W)^{-1}$$

where G_i is the wet weight (mg) of relevant prey type i in the digestive tract and W the wet body mass (mg) of fish before dissection. In total 575 digestive tracts of perch (size 9–24 mm SL) were analysed.

For graphical presentation of the stomach content data, A m u n d s e n et al. (1996) modification of Costello's method was used. This method relates the frequency of occurrence (F_i – the share of digestive tracts in which prey i occurs from all filled digestive tracts) to prey-specific abundance (P_i – percentage a prey i comprises of all prey items in only those predators in which prey i occurs), and enabled us to determine prey importance and also

feeding strategy of predators. Prey taxa close to 1% occurrence and 1% abundance are negligible in the diet; and conversely prey species approaching the upper right corner of the diagram (100% occurrence and 100% abundance) are considered as the most important prey. Points close to 1% occurrence and 100% abundance are considered as a specialization on certain prey taxa by a few predators; points close to 100% occurrence and 1% abundance indicate generalized diet of most predators.

Statistical analyses were performed using a t-test to compare the DTF of perch between the epilimnetic (0–4 m) and hypolimnetic (9–16 m) zones during the daytime. To compare DTF at different times, one-way ANOVA was applied with day, dusk, night and dawn as treatment factors. Data on zooplankton densities were analysed using two-way ANOVA with habitat (epilimnetic, hypolimnetic), time (day, night), or month (May, June) as treatments. Prior to analysis, the transformation $\log(x+1)$ on data was applied, when necessary.

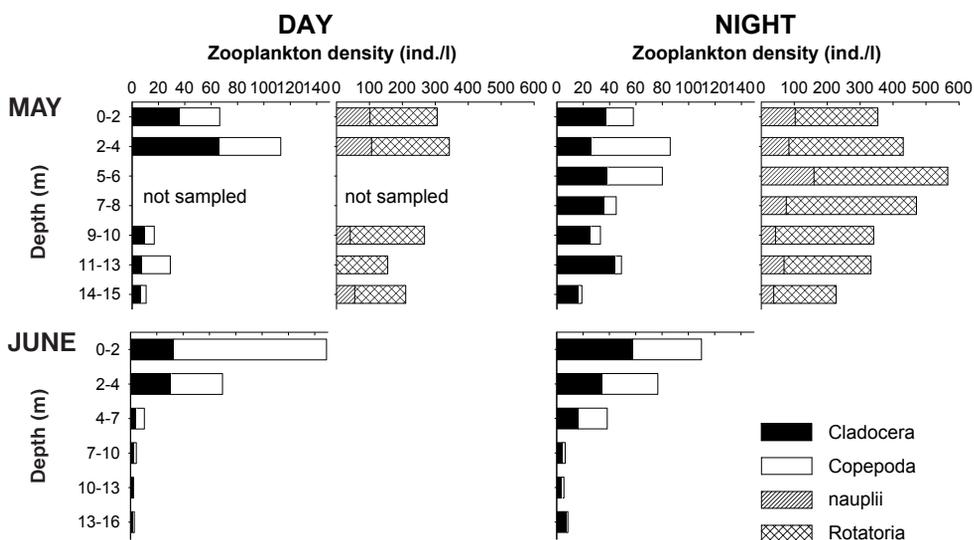


Fig. 1. Day and night densities (ind./l) of main zooplankton taxa on the vertical profile of Slapy Reservoir in May and June.

Results

Zooplankton distribution

Densities of cladocerans and copepods were higher in epilimnion than in hypolimnion zones during daylight periods at both sampling dates (two-way ANOVA; habitat: $F_{1,14}$, $P < 10^{-6}$) (Fig. 1). The same densities of cladocerans and copepods in epilimnion zone occurred during day and night periods ($F_{1,12}$, $P = 0.56$) as well as between months ($F_{1,12}$, $P = 0.39$).

In May, the cladoceran assemblage was dominated by *Daphnia* sp. (nearly exclusively *Daphnia galeata* Sars) in the epilimnetic zone during both day and night (Table 1). Bosminidae (particularly *Bosmina longirostris* (O. F. Müller)) dominated the hypolimnion zone at night, but *Daphnia* sp. was the most abundant cladoceran in the hypolimnion zone during daylight. In June, the epilimnetic zone was dominated by the typical summer species *Diaphanosoma brachyurum* (Lievin), and Bosminidae prevailed the hypolimnetic

Table 1. Day and night densities (ind./l) of different zooplankton taxa in 0–4 and 9–16 m depth layers in May and June. Category other cladocera represents *Ceriodaphnia* sp. and Chydoridae.

	May				June			
	day		night		day		night	
	0–4 m	9–15 m	0–4 m	9–15 m	0–4 m	10–16 m	0–4 m	10–16 m
Cladocera:								
Bosminidae	2.6	10.0	4.2	56.9	1.7	2.4	1.8	10.7
<i>Diaphanosoma brachyurum</i>	0.5	0.0	1.5	2.3	37.6	0.7	51.8	0.3
<i>Daphnia</i> sp.	97.2	13.5	58.8	28.4	24.6	1.2	37.6	1.3
<i>Leptodora kindtii</i>	2.2	0.5	0.5	0.0	0.2	0.0	1.8	0.0
other	0.0	0.8	0.6	0.0	0.0	0.0	0.0	0.2
Copepoda:								
<i>Acanthocyclops trajani</i>	2.1	3.3	0.0	1.8	14.6	0.1	10.0	0.2
<i>Cyclops vicinus</i>	20.7	7.7	48.5	7.8	8.3	0.1	4.4	0.1
<i>Eudiaptomus gracilis</i>	30.3	2.2	21.2	1.8	38.9	0.6	32.9	0.6
<i>Mesocyclops leuckarti</i>	13.8	0.0	4.7	0.6	78.6	0.1	31.4	0.4
<i>Thermocyclops crassus</i>	9.9	18.4	5.0	1.2	14.2	0.1	15.1	0.1

cladoceran assemblage. Copepodite stages and adult copepods contributed significantly to the total zooplankton abundances only in the epilimnetic zone (Fig. 1). The detailed species composition of copepods is also given (Table 1). No evidence for apparent diel vertical migrations of zooplankton was found during May and June.

Diet of 0+ perch – spatial and diel variability

Analyses of digestive tract fullness (DTF) revealed different diel patterns in feeding activity on both investigated dates (Fig. 2). In May, the most intensive feeding was reported throughout the day (in the epilimnion zone) and during dusk, when the shift of hypolimnetic

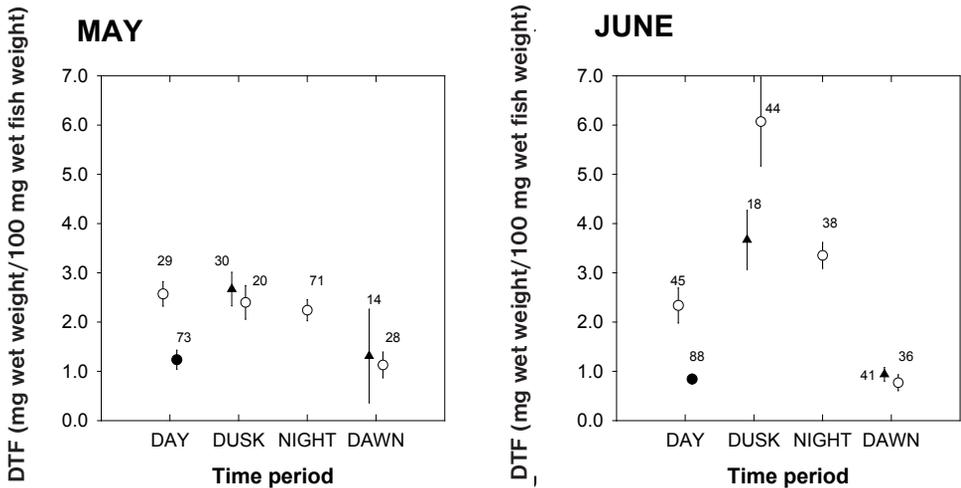


Fig. 2. Mean digestive tract fullness (DTF; ± 1 S.E.) of perch larvae and juveniles during a diel cycle in May and June. Open circles represent perch in epilimnion, solid dots represent perch in hypolimnion and solid triangles represent hypolimnetic perch during migrations (5–9 m) at dusk and dawn. Numbers of analysed fish are shown close to symbols or error bars.

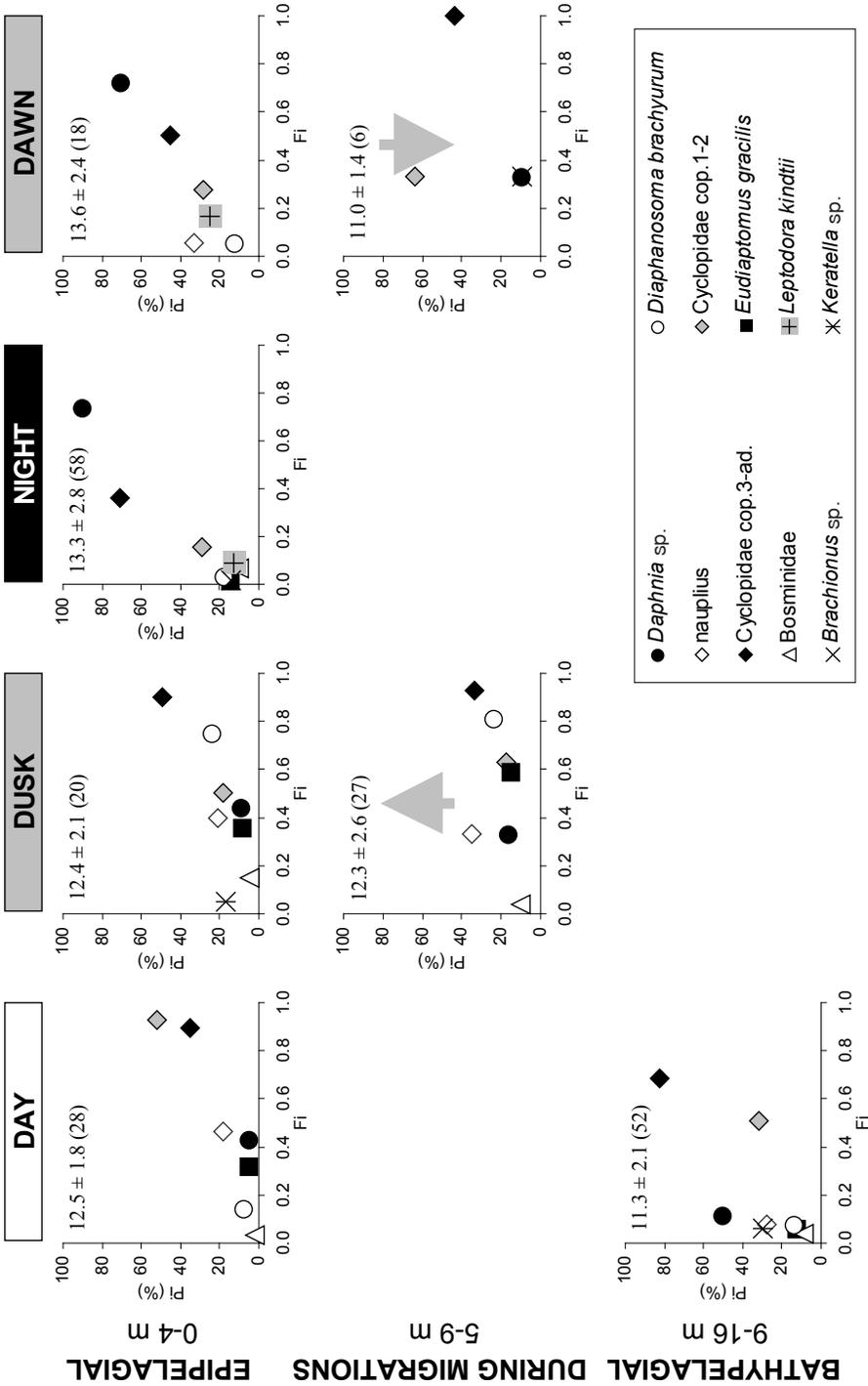


Fig. 3. Spatial and temporal prey occurrence (P) and prey-specific abundance (Fi) in the digestive tracts of perch larvae and juveniles in May, based on prey numbers. Arrows indicate the dusk and dawn transfers towards and from the surface, respectively. Mean standard lengths (SL) ± 1 S.D. (mm) of analysed fish are given. Numbers of digestive tracts with any prey content are shown in parentheses.

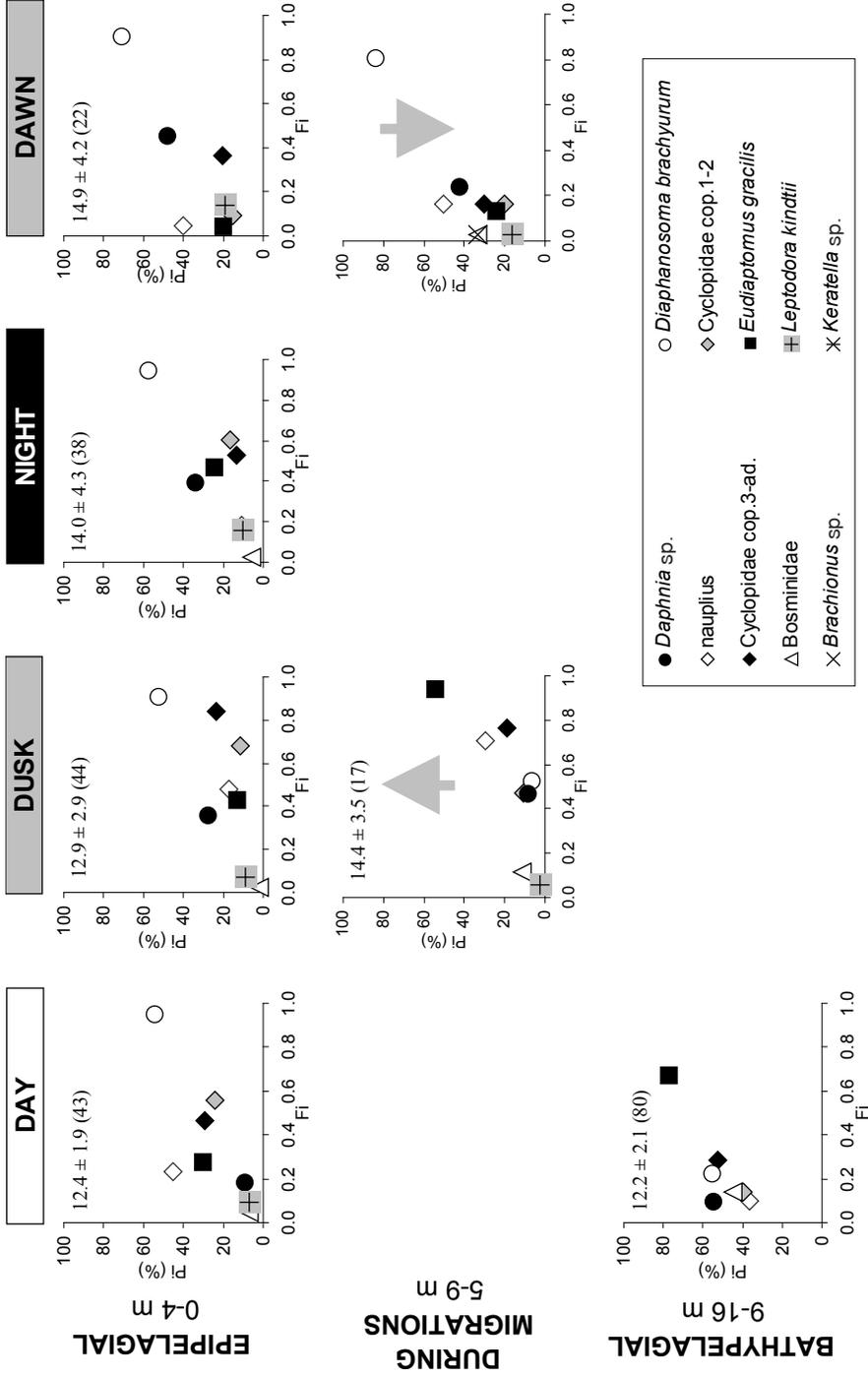


Fig. 4. Spatial and temporal prey occurrence (P) and prey-specific abundance (Fi) in the digestive tracts of perch larvae and juveniles in June, based on prey numbers. Arrows indicate the dusk and dawn transfers towards and from the surface, respectively. Mean standard lengths (SL) \pm 1 S.D. (mm) of analysed fish are given. Numbers of digestive tracts with any prey content are shown in parentheses.

perch towards surface occurred. During night, DTF decreased and was the lowest at dawn (ANOVA, $F_{3,144}$, $P = 0.004$). In June, DTF of perch clearly peaked during dusk and the lowest DTF was found at dawn again (ANOVA, $F_{3,181}$, $P < 10^{-6}$). As in May, migrating individuals returned back to the hypolimnion zone with relatively empty digestive tracts. During daylight, DTF was significantly lower in hypolimnetic perch during both May and June (t-test, d.f. = 100, $P < 0.001$ for May and t-test, d.f. = 143, $P < 0.001$ for June, respectively) (Fig. 2). Moreover, a higher ratio of individuals with empty digestive tracts was reported in hypolimnetic perch (28.8% and 9.1% in May and June, respectively) than in non-migrants (3.4% and 4.4% in May and June, respectively).

Pelagic 0+ perch fed almost exclusively on planktonic microcrustaceans. In May, younger (C 1-2), and older (C 3-5) copepodite stages and adult cyclopoid copepods were favoured by nearly all epilimnetic perch during daylight, whereas hypolimnetic perch were more focused on older copepodite stages and adult cyclopoid copepods (Fig. 3). During dusk nearly all of the prey taxa contributed equally on average by about 20% to the diet of the epilimnetic and migrating hypolimnetic perch, but their occurrence in digestive tracts was of different importance. *Daphnia* sp. was the most important prey category found in the digestive tracts of epilimnetic perch during the night and at dawn. In perch migrating to the hypolimnion zone, the most important prey taxa were again older copepodite stages and adult cyclopoid copepods, and the importance of *Daphnia* sp. in the digestive tracts decreased rapidly. In June, the highest occurrence was reported for *Diaphanosoma brachyurum* in the digestive tracts of most (> 90%) perch individuals in the epilimnetic zone throughout the diel cycle (Fig. 4). This species' contribution ranged between 50–70% with the highest values recorded at dawn. The diet of most migrants returning back to hypolimnion was constituted mainly by *D. brachyurum*. During daylight, *Eudiaptomus gracilis* (Sars) was the most common prey in the majority of hypolimnetic perch. This prey still remained the most important in the digestive tracts of hypolimnetic perch migrating upwards. Other prey taxa did not exceed 30% of the relative abundance at dusk.

Discussion

This study has revealed some notable differences in food intake of two functional groups of 0+ perch. The main differences were found in the digestive tract fullness (DTF) between epilimnetic and hypolimnetic perch in both months. The lower amount of prey and higher percentage of fish with empty digestive tract suggest lower feeding activity of hypolimnetic perch during both sampling occasions. This lower feeding activity of perch in the hypolimnetic habitat could be caused by three factors.

First, the densities of the most favoured prey (cladocerans and copepods) were much lower in the hypolimnetic zones and reached only 21% and even 2.4% of the epilimnetic densities in May and June, respectively. Similar densities of cladocerans and copepods were recorded in the epilimnetic zone through day and night periods and no DVMs of zooplankton occurred (pers. obs.). Thus migrations of 0+ perch do not seem to follow any potential prey.

Second, perch are considered as visually oriented particulate feeders adapted to high light conditions (Ali et al. 1977); therefore it is unlikely that hypolimnetic light conditions would allow them to feed efficiently. However even in the hypolimnetic dark layers, with the light intensity changing from 0 to 60 lx (less than 0.05% of the surface light intensity; Čech et al. 2005), perch are able to detect prey, but their reaction distance is considerably

restricted (R i c h m o n d et al. 2004). Similarly, diel-feeding activity of the epilimnetic perch coincided with light intensity. Highest DTF was reported throughout the day and/or dusk, DTF decreased throughout the night and DTF was lowest at dawn, when migrating individuals returned to hypolimnetic zone. Such a diel cycle of feeding activity corresponds with results of P o s t & M c Q u e e n (1988) and M a c h á ě k & M a t ě n a (1997). Besides prey density and light conditions, temperature should have a significant effect on feeding and survival of hypolimnetic perch. Optimal temperatures for perch larvae were found at 16–26°C (W a n g & E c k m a n n 1994). Results of K u d r i n s k a y a (1970) showed that 80–90% of perch larvae stopped feeding and decreased their growth rate up to five times at temperatures <16°C. In Slapy Reservoir, temperatures in the hypolimnion were well below 12°C (Č e c h et al. 2005), and so the hypolimnetic perch larvae and juveniles stayed in unfavourable conditions, which could significantly reduce their metabolic activity (B r e t t 1971) and growth (M o o i j et al. 1994). Upward migrations to warmer layers, on the other hand, would stimulate digestion (W u r t s b a u g h & N e v e r m a n 1988), and return of perch to epilimnion zones (16–23°C) during dusk seems to be connected with increased feeding rate. However, staying in cold hypolimnion during the daytime and feeding in warm epilimnion overnight appears unlikely to be an energetic advantage as mentioned by G l i w i c z & J a c h n e r (1992) on juvenile smelt.

Comparison of diet composition in larval and juvenile perch revealed slight differences between perch in epi- and hypolimnion. Epilimnetic perch preferred cyclopoid copepods in May and focused on cladocerans in June. Hypolimnetic perch consumed predominantly copepodites (cyclopoids in May and the most abundant copepod *E. gracilis* in June) and did not prefer cladocerans, although cladocerans generally dominated in the hypolimnion (except the situation from the daytime in May). Feeding on small, evasive copepods (J a c h n e r 1991, F l i k et al. 1997, E a s t o n & G o p h e n 2003) seems to be less profitable, and can even diminish growth (R o m a r e 2000). The preference for copepods was unexpected especially under low light conditions in hypolimnion when larger and more easily detectable daphnids would seem to be the more appropriate prey (M i l l s et al. 1986, F l i k et al. 1997). In our case, 0+ perch switched to large and more visible *Daphnia* sp. during low light conditions in May, and this prey became dominant in digestive tracts at night. An increase of preference for *D. galeata* at dusk and night was also mentioned in M a c h á ě k & M a t ě n a (1997). In June, however, the majority of perch focused on the epilimnetic dominant cladoceran species – *D. brachyurum* throughout the whole 24-h period.

The main question, why a part of 0+ perch perform migrations to hypolimnion, remains still unanswered. Hypolimnetic individuals were found to decrease or even stop their feeding activity in the hypolimnetic zones, most probably due to low zooplankton densities, insufficient light intensity and cold water. Although no foraging benefit of the hypolimnetic strategy was found, it is supposed that more important stimulus to trigger these shifts could be a predator fear, most probably caused by in Slapy reservoir dominant large perch (D r a š t í k et al. 2004). A part of 0+ perch is assumed to migrate downward to avoid potential predators (fish > 100 mm), which are very scarce in hypolimnion of deep, stratified reservoir (Č e c h & K u b e ě k a 2006). The epilimnetic 0+ perch group choose a strategy of higher predatory risk, but sufficient feeding all the time. Therefore it is most likely, that the group living in food-rich epilimnion grows faster, but suffers a higher mortality. The opposite trend is expected for hypolimnetic migrants. However, further and more detailed

investigations should be performed to evaluate the nutritional conditions of both segregated 0+ perch groups using the RNA: DNA ratio (Clapp & Dettmers 2004), estimate predator pressure in habitats above and below the thermocline, and to reveal ultimate consequences of the two early life strategies.

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