

## Diel Vertical migration of *Daphnia longispina* (*Cladocera*) in an acid, fishless lake

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### Abstract

Five field surveys for the assessment of diel vertical migration (DVM) of *Daphnia longispina* in Prášílské Lake were carried out in 1997–1999. In all the cases *Daphnia* performed distinct vertical movements, staying in upper layers at night and in deep layers during the day. This is the most common migration pattern of zooplankton. According to the predation hypothesis, which is now generally accepted, this migration pattern minimises losses by visually hunting predators, like planktivorous fish. There is also extensive evidence that a necessary condition for performing these migrations is a chemical cue (kairomone) excreted by fish or by fish-associated bacteria. But Prášílské Lake is fishless, which excludes presence of any fish kairomone. On the other hand, it is inhabited by predatory water bugs *Glaenocoris propinqua* (Heteroptera), which may hunt for zooplankton in the open water. Two alternative hypotheses explaining the migratory behaviour of *Daphnia* in Prášílské Lake are proposed: (i) The migration pattern of the *Daphnia* population is fixed in the genotype and its manifestation does not need any kairomone released by fish. Although this genotype was selected by fish predation in the past, the migrations bring no benefit to the population at present. The competitive advantage of the present population does not lie in its high growth rate, but rather in its tolerance to the extreme chemical environment in an acidified lake. (ii) The observed pattern is in full accordance with the predation hypothesis, the predators are the water bugs *Glaenocoris*. Very little is known, however, on the abundance, behaviour, and the resulting predatory impact of *Glaenocoris* upon *Daphnia* in the lake under study.

*Key words:* zooplankton, *Daphnia*, *Glaenocoris*, *Corixidae*, vertical migration

### Introduction

Periodic changes in vertical distribution of zooplankton during day and night – the diel vertical migration (DVM) – is a phenomenon widely spread in both marine and freshwater habitats. Usually, zooplankton spend the day in deep layers and the night near the surface where temperature, oxygen concentration and food supply are more favourable for growth and reproduction. Hypotheses looking for ultimate causes of DVM are reviewed by LAMPERT (1989, 1993). The most convincing explanation supported by strong evidence is that staying in dark deep layers during the day and ascending to the surface at night reduces the risk of being grazed by visually hunting predators like fish (ZARET & SUFFERN 1976, STICH & LAMPERT 1981, GLIWICZ 1986). In this paper we want to present results of a field survey carried out in the years 1997–1999 in order to detect and describe DVM of the cladoceran *Daphnia longispina* in Prášílské Lake. The lake is fishless so that the presence of strong DVM of *Daphnia* attracted our attention.

## Description of the site and methods

Prášilské Lake (49°05'N, 13°24'E, 1079 m a.s.l.) is a small (4.2 ha) glacier lake with a steep forested catchment (65 ha). The maximum depth is 17.2 m, mean depth 7.4 m (ZBORIL 1994). It is a dimictic lake with sharp summer stratification. At the height of summer the epilimnion is confined to the upper 3–6 m and the metalimnion is about 3 m thick. While the summer surface temperature (July–August) varies from 14 to 20 °C, it does not exceed 5 °C in the lower hypolimnion. The summer oxygen curve is clinograde with values approaching zero at the deepest point. The oxygen depletion in the deep hypolimnion proceeds until the total mixing in the late autumn. The Secchi depth varies between 2.6–7.0 m. The lake has been acidified but recently some reversal in chemical variables has taken place. The recent (1997–1999) pH varied between 4.7 and 5.7, alkalinity (Gran titration) between –22 and 80  $\mu\text{mol.l}^{-1}$ . The highest values of both pH and alkalinity were found in the anoxic hypolimnion. The recent (1997–1999) total reactive aluminium was in the range 0.17–0.53  $\text{mg.l}^{-1}$ , dissolved organic carbon was 2.9–6.4  $\text{mg.l}^{-1}$  (SCHMIDT & al. 1993, VRBA & al. 2000).

Phytoplankton of the lake were studied in the open water period (May–October) 1997–98 by NEDBALOVÁ & VRTISKA (2000). The species mostly contributing to phytoplankton biomass (measured as biovolume) were dinoflagellates *Gymnodinium uberrimum* and *Peridinium umbonatum* (syn.: *P. inconspicuum*). Their share to the total phytoplankton biovolume often exceeded 80%. Other common groups were chrysomonads (*Dinobryon* sp. div., *Chromulina* sp. div., *Ochromonas* sp. div.) and cryptomonads (*Cryptomonas erosa* and other species). They were less important than dinoflagellates in terms of biomass but possibly more important as food for *Daphnia*.

Prášilské Lake is the only one of the acid lakes on the Czech side of the Bohemian Forest inhabited by typical planktonic *Crustacea* (FOTT & al. 1994). Two species occur: *Daphnia longispina* and *Cyclops abyssorum*. These species were common also in other lakes of the Bohemian Forest but they died out due to acidification. Their survival in Prášilské Lake has been explained by lower aluminium concentration when compared with other acid lakes in the area (FOTT & al. 1994). This difference has persisted until now: in July 1997 concentration of total reactive aluminium was 0.22  $\text{mg.l}^{-1}$  in the surface water of Prášilské Lake while 0.45 and 0.64  $\text{mg.l}^{-1}$  were found in the lakes Černé and Plešné. The pH values (4.66–4.69) were similar in all the three lakes (KOPÁČEK & HEJZLAR 1998).

Samples of zooplankton were taken close to the point of maximum depth. We used a van Dorn sampler of 6.36 litre volume and 1 m height. As a rule, 6 samples were taken between the surface and the bottom. Sampling the vertical profile took about half an hour. Samples were preserved with 4% formaldehyde and counted in the laboratory using an inverted microscope.

While *Cyclops abyssorum* did not perform any distinct diel vertical movements (most of adults, copepodites and nauplii were staying in the hypolimnion and only few were found in surface layers), we confined our attention to *Daphnia*. In July and October 1997 we sampled just one vertical profile in the daytime and one at night. In August and October 1998 we sampled over 24 hours in 6-hour intervals. The last sampling was carried out in August 1999 but it did not lead to our full satisfaction due to accidentally low abundance of *Daphnia*.

## Results

July 23–24, 1997 (Fig. 1)

Environmental conditions: Sunny – partly cloudy, calm – mild wind. Secchi depth 5.8 m. In the depths 0.5 m/14.5 m: temperature 14.1/4.0 °C, oxygen 8.5/0.2 mg.l<sup>-1</sup>, pH 4.7/5.3, TR-Al 0.22/0.26 mg.l<sup>-1</sup>. Surface chlorophyll-a: 0.35 µg.l<sup>-1</sup>, surface POC 0.24 mg.l<sup>-1</sup>.

Net zooplankton (> 200 µm): *Cyclops abyssorum* and *Daphnia longispina*, mean column (0–14.5 m) biomass: 126 µg .l<sup>-1</sup> DW, share of *Daphnia* 81%. Most of *Daphnia* were staying between 4 and 9 m in the morning, while at night they occupied the upper 5 m. Their maximum abundance was between 30–40 ind.l<sup>-1</sup> (morning: 6–7 m, night: 0–3 m).

Phytoplankton consisted of chrysomonads (mostly *Chromulina* sp.), cryptomonads (mostly *Cryptomonas erosa*) and dinoflagellates (mostly *Gymnodinium uberrimum*). Their morning vertical distribution revealed prevalence (in terms of biomass) of chrysomonads in the upper 2 m, dinoflagellates in the 2–5 m layer and cryptomonads below 6 m. The total phytoplankton biovolume (except of the lowermost layer) did not exceed 0.15 mm<sup>3</sup>.l<sup>-1</sup> (~ 30 µg .l<sup>-1</sup> org. C). Bacterial biomass at the surface was 20 µg .l<sup>-1</sup> org.C (conversions from algal and bacterial biovolume to org. C according to STRÁŠKRABOVÁ & al. 1999).

October 15–16, 1997 (Fig.2)

Environmental conditions: Overcast, calm – fresh wind. Secchi depth 6.0 m. In the depths 0.5 m/14.5 m: temperature 9.0/4.1 °C, oxygen 8.9/0.1 mg.l<sup>-1</sup>, pH 4.8/5.4, TR-Al 0.22/0.34 mg.l<sup>-1</sup>. Surface chlorophyll-a: 3.6 µg.l<sup>-1</sup>, surface POC 0.46 mg.l<sup>-1</sup>.

Net zooplankton (> 200 µm): *Cyclops abyssorum* and *Daphnia longispina* (ephippial and non-ephippial females, males), mean column (0–14.5 m) biomass: 113 µg .l<sup>-1</sup> DW, share of *Daphnia* 70%. Morning distribution of *Daphnia*: below 6 m, maximum in 12–13 m. Nocturnal distribution: upper 7 m. Abundance (except of the lowermost layer in the morning): less than 10 ind.l<sup>-1</sup>.

Phytoplankton main taxa were the same as in July, but their proportions and vertical distribution were different. Total biovolume of chrysomonads + cryptomonads was less than 0.05 mm<sup>3</sup>.l<sup>-1</sup> (< 10 µg .l<sup>-1</sup> org. C). In the upper 6 m dinoflagellates (*Gymnodinium uberrimum*) contributed to the biovolume by 0.5 mm<sup>3</sup>.l<sup>-1</sup> (100 µg .l<sup>-1</sup> org. C). Bacterial biomass was the same as in July: ~ 20 µg .l<sup>-1</sup> org.C both at the surface and at the 14.5 m depth.

August 5–6, 1998 (Fig. 3)

Environmental conditions: Sunny – partly cloudy, calm – mild wind. Secchi depth 7.2 m. The following parameters were measured nine days before our sampling date, but they seem to characterise well the summer conditions, being not too far from those measured previous summer: in the depths 0.5 m/14.5 m: temperature 18.9/4.3 °C, oxygen 8.1/0.2 mg.l<sup>-1</sup>, pH 4.9/5.2, TR-Al 0.18/0.35 mg.l<sup>-1</sup>, chlorophyll-a 1.0/8.2 µg.l<sup>-1</sup>. Surface POC: 0.31 mg.l<sup>-1</sup>.

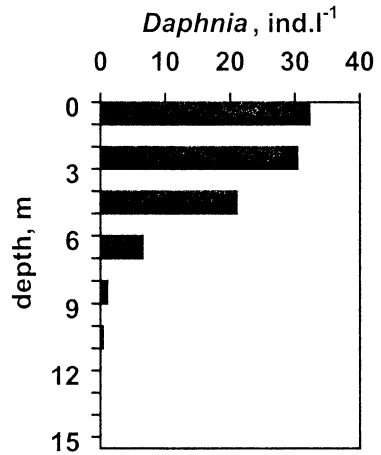
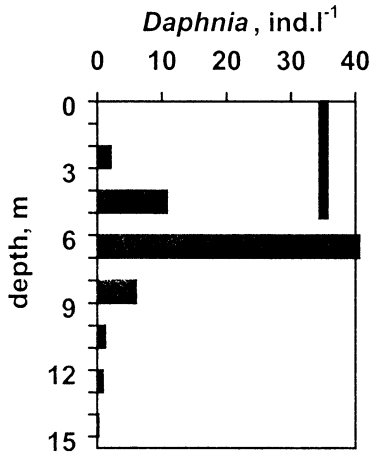
Net zooplankton (> 200 µm): *Cyclops abyssorum* (large copepodites) and *Daphnia longispina*, mean column (0–14.5 m) biomass: 200 µg .l<sup>-1</sup> DW, share of *Daphnia* 67%. *Daphnia* stayed below 6 m in the daytime, towards midnight they migrated above 4 m, maximum abundance (35 ind.l<sup>-1</sup>) in the 0–1 m layer.

October 14–15, 1998 (Fig. 4)

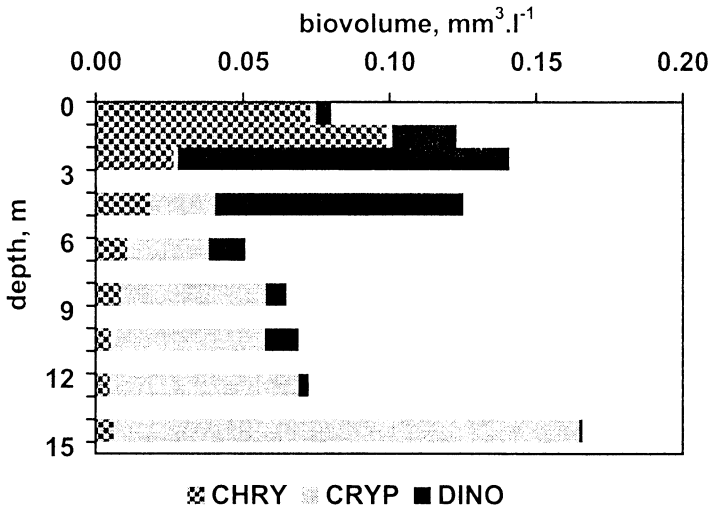
Environmental conditions: Overcast and foggy, mild – fresh wind. Secchi depth 4.8 m. Measurement two days before, depths 0.5 m/14.5 m: temperature 8.4/4.5 °C, oxygen 9.6/0.1 mg.l<sup>-1</sup>, pH 4.7/5.5, TR-Al 0.25/0.36 mg.l<sup>-1</sup>, chlorophyll-a 5.6/5.0 µg.l<sup>-1</sup>. Surface POC: 0.44 mg.l<sup>-1</sup>.

23.7.1997 - 9:45

24.7.1997 - 2:15



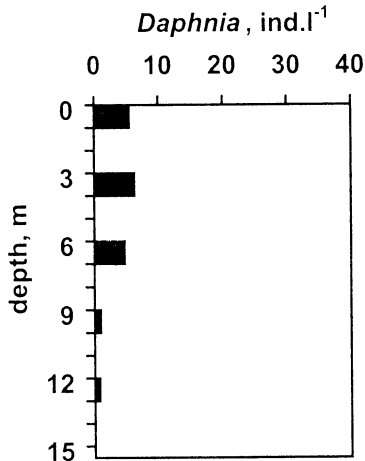
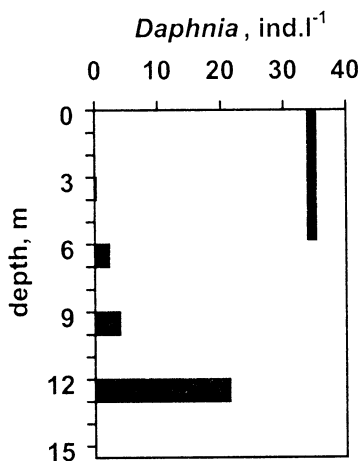
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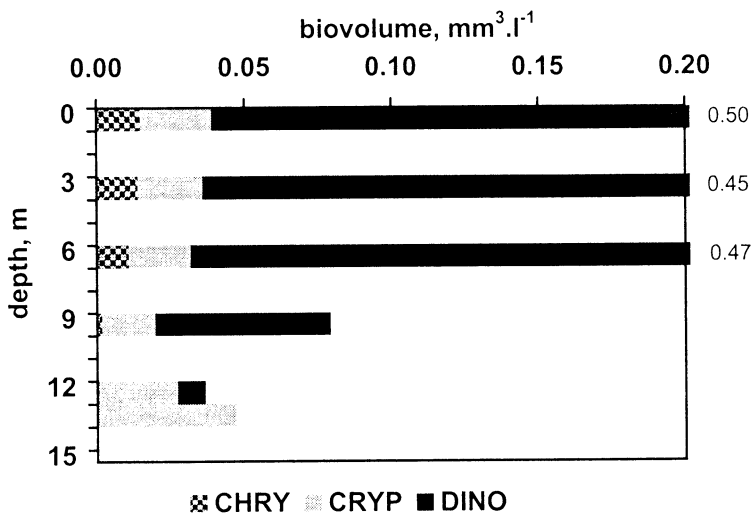
**Fig. 1** – Vertical distribution of *Daphnia longispina* (above) and phytoplankton (below), July 23–24, 1997. Secchi depth indicated by the vertical bar in the upper graph. CHRY- chrysoomonads, CRY- cryptomonads, DINO- dinoflagellates.

15.10.1997 - 11:30

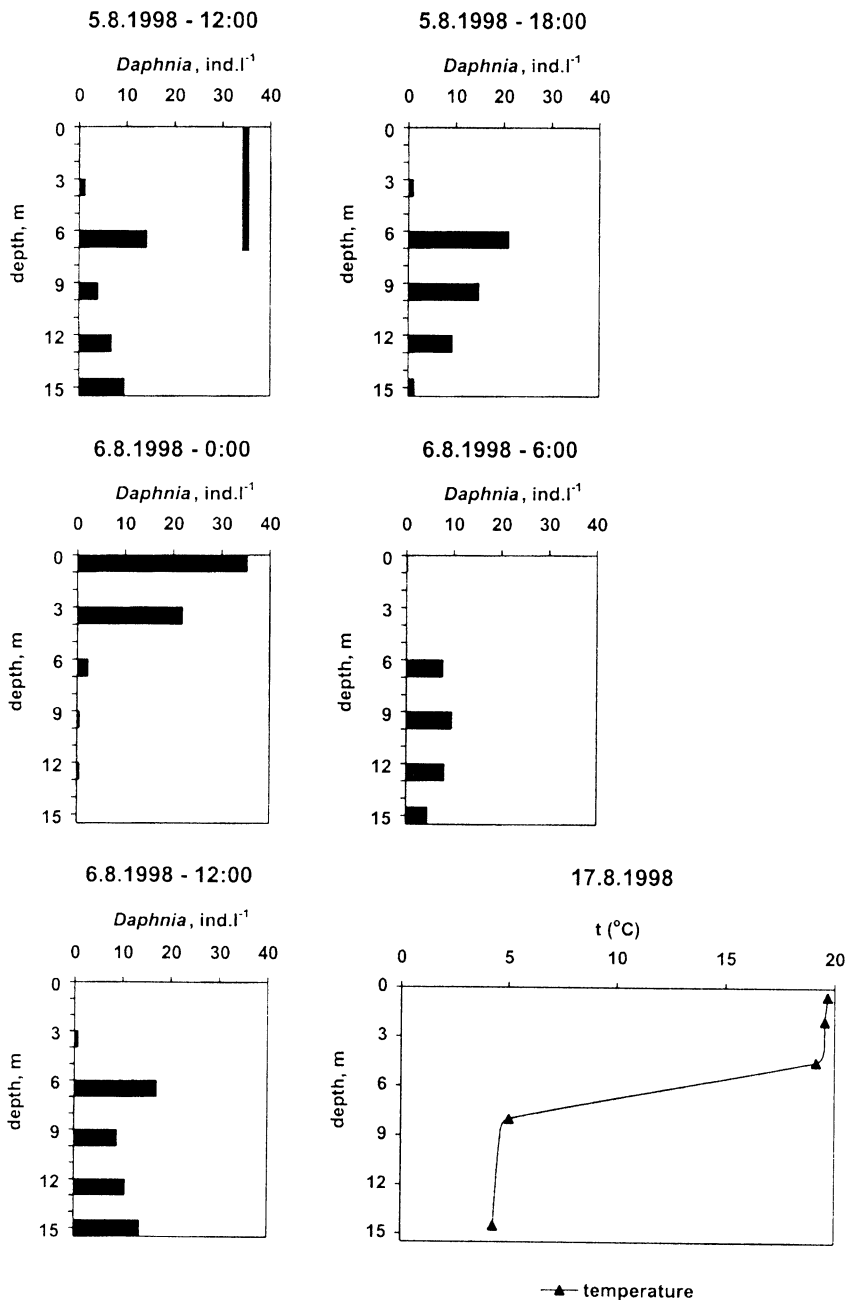
16.10.1997 - 4:00



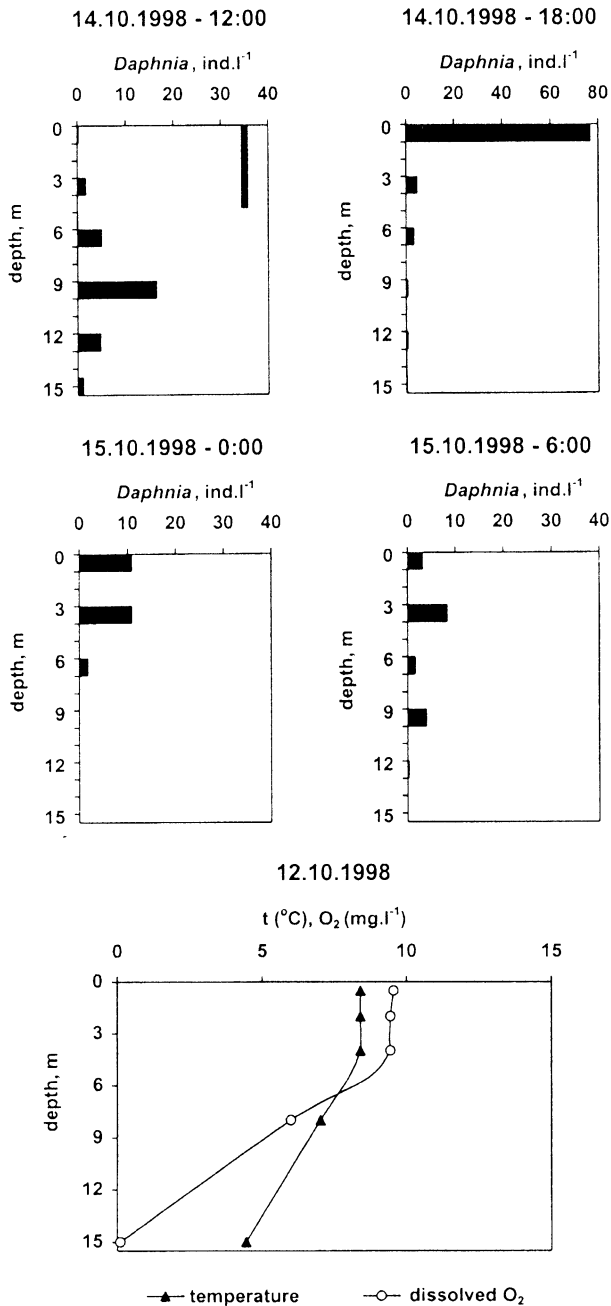
15.10.1997 - 11:30



**Fig. 2** – Vertical distribution of *Daphnia longispina* (above) and phytoplankton (below), October 15–16, 1997. Secchi depth indicated by the vertical bar in the upper graph. CHRY- chrysomonads, CRY- cryptomonads, DINO- dinoflagellates.



**Fig. 3** – Vertical distribution of *Daphnia longispina*, August 5–6, 1998. Secchi depth indicated by the vertical bar in the upper graph. Temperature profile as measured on August 17.



**Fig. 4** – Vertical distribution of *Daphnia longispina*, October 14–15, 1998. Secchi depth indicated by the vertical bar in the upper graph. Temperature and oxygen as measured 2 days earlier.

Net zooplankton ( $> 200 \mu\text{m}$ ): *Cyclops abyssorum* (copepodites) and *Daphnia longispina* (ephippial and non-ephippial females, males), mean column (0–14.8 m) biomass:  $136 \mu\text{g.l}^{-1}$  DW. Vertical movements of *Daphnia* were pronounced and similar to those observed previous summer. At 18:00 (one hour after the local sunset) most of *Daphnia* were already at the top of the column (0–1 m), reaching the abundance of almost  $80 \text{ ind.l}^{-1}$ . At 24:00 they were more evenly distributed in the 0–4 m layer. At 6:00 (half an hour before the local sunrise) some animals descended already to 12 m, while other were staying still at the surface.

Phytoplankton consisted almost entirely of large dinoflagellates *Gymnodinium uberrimum*, the total phytoplankton biomass was between  $0.5\text{--}1.0 \text{ mm}^3.\text{l}^{-1}$  in the upper 8 m (NEDBALOVÁ & VRTIŠKA 2000).

August 23–24, 1999

Zooplankton were very scarce, reasons of which are not understood. Mean column biomass (0–14.8 m) of *Daphnia* + *Cyclops* was only  $11.5 \mu\text{g.l}^{-1}$  DW, share of *Daphnia* 12%. The maximum abundance of *Daphnia* did not exceed  $2 \text{ ind.l}^{-1}$ . Despite of inevitable random errors affecting the counts the overall pattern of *Daphnia* vertical movements (not shown here) was quite evident and similar to what was observed before.

## Discussion

As it is evident from the Figs. 1–4, the observed daily movements of *Daphnia* were pronounced and they followed the most common pattern: evening ups and morning downs. Finding diel vertical migrations of *Daphnia* in a presumably fishless lake was a surprise as it contradicted the common experience on the role of fish kairomones as cues for these periodic movements (cf. DODSON 1988, DAWIDOWICZ & LOOSE 1992, DE MEESTER 1993, LARSSON & DODSON 1993, LOOSE 1993, LOOSE & al. 1993, DE MEESTER & al. 1995, RINGELBERG & VAN GOOL 1998, SEELY & LUNETSKY 1998). It was therefore desirable to find out as much as possible on the past and present fish status of Prášilské Lake. Brown trout (*Salmo trutta*) should have inhabited the lake in the middle of the 19<sup>th</sup> century but later it was not observed any more (VESELÝ 1994). ŠVAMBERA (1914) mentioned attempts of stocking brown trout between 1908 and 1914. Later on in the 20<sup>th</sup> century further uncontrolled stocking brown trout and also brook trout (*Salvelinus fontinalis*) were likely but no information on the fate of the introduced fish is available. FOTT & al. (1994) and VESELÝ (1994) concluded the lake was fishless, just like the other acidified lakes in the area. In August 1999 KUBEČKA & al. (in press) surveyed the lake for presence of fish using both nets and echo-sounding. They did not catch any fish neither they found any signals which could have been interpreted as fish.

The echo-sounding revealed, however, small targets in the open water, which were identified as nymphs and adults of a predaceous water bug *Glaenocoris propinqua* (Heteroptera, Corixidae). Their abundance, estimated by both echo-sounding and by horizontal hauls of a large ichthyoplankton net, reached up to  $1 \text{ ind.m}^{-3}$ . The maximum abundance was achieved near the surface at night. During the day *Glaenocoris* were scarce in the open water and so they were supposed to concentrate close to the shore of the lake. The authors found the same species in a large and deep water reservoir Josefův Důl (Czech Republic). In this reservoir, which is also acidified and fishless, *Glaenocoris* migrated between the 6–7 m depth (day) and the surface layer (night). The species inhabits also the open water of acidified lakes in Scandinavia where Corixidae became the top aquatic predators after the extinction of fish (HENRIKSON & OSCARSON 1981, SAVAGE 1989).

Like any other observation our field study cannot lead to any definite conclusion but it may help in formulating hypotheses which are open to further testing. At least three hypotheses explaining the observed DVM pattern can be suggested:



(A) The observed pattern of DVM in *Daphnia* population under study resulted from selection by planktivorous fish in the past and it is firmly fixed in the genotype. The proximate factor timing the ascents and descents might be changes in light intensity (RINGELBERG 1961) and no chemical signals are needed. An obvious objection against this hypothesis would point to the consequences of „unnecessary“ staying in the cold hypolimnion resulting in a considerable retardation of growth and reproduction (DAWIDOWICZ & LOOSE 1992, DAWIDOWICZ 1994). Such a maladaptation would lead to competitive exclusion by another filter-feeder, which would make profit of staying in the metabolically more profitable layers. It should be noted, however, that Prášílské Lake represents, by its low pH and high concentrations of aluminium, a very extreme environment. It is well possible that the potential competitors of the present population of *Daphnia longispina* would not survive in the lake; there is extensive evidence on sensitivity of many *Daphnia* species to low pH and high aluminium (BRETT 1989).

Other field studies, however, have shown that when fish populations were strongly reduced either naturally (STIRLING & al. 1990) or by biomanipulation (DINI & CARPENTER 1991) *Daphnia* did not perform migrations.

(B) The observed migrations of *Daphnia* are controlled by a kairomone released by invertebrate predators – the water bugs *Glaenocoris propinqua*. Minimising the predatory impact by performing DVM is more important for survival of *Daphnia* population than the metabolic disadvantage of staying in the cold hypolimnion. This hypothesis includes an assumption that *Glaenocoris* are visual predators like fish – otherwise, the encounter of both populations in the upper layers at night could hardly be of any adaptive value to *Daphnia*. Unfortunately, very little is known on *Glaenocoris* in Prášílské Lake. This makes the assessment of their predatory impact difficult. Sampling by traditional limnological gear did not bring any evidence on their presence in the open water and the result of the survey carried out by ichthyological methods is the first of its kind.

In a laboratory bioassay DODSON (1988) was able to induce a negative phototactic response in 4 species of *Daphnia* by a chemical cue released by predatory water bug *Notonecta*; in other *Daphnia* species the response was positive.

(C) *Daphnia* descend down in order to avoid the harmful UV radiation, be the mechanism of this adaptation whatever.

No measurements of light attenuation were done but some estimates are possible. In a study on optical properties of Adirondack lakes BUKAVECKAS & ROBINS-FORBES (2000) related absorption coefficients of UV-A and UV-B radiation to dissolved organic carbon; the univariate models accounted for 90% of variation. Using the range of DOC in Prášílské Lake 2.9–6.4 mg.l<sup>-1</sup> and substituting to the equations derived from Adirondack lakes we can estimate the attenuation depths ( $z_{1\%}$ ) as 0.4–1.4 m for UV-A and 0.2–0.7 m for UV-B. In the daylight *Daphnia* descend deeper, which makes the UV-hypothesis less likely.

Finally, some remarks on food conditions of the migrating *Daphnia*. In July 1997 the estimated (conversions from biovolume of phytoplankton and bacteria) concentration of food was 0.03–0.04 mg.l<sup>-1</sup> C in both the 0–3 m layer (*Daphnia* at night) and the 6–7 m layer (*Daphnia* during the day). Comparable figures in October 1997 were 0.12 mg.l<sup>-1</sup> in the 0–4 m layer and 0.03 mg.l<sup>-1</sup> in the 12–13 m layer. The higher value at the surface was due to presence of *Gymnodinium uberrimum*; whether this large dinoflagellate can serve for *Daphnia* as a food source or not is uncertain (NEDBALOVÁ & VRTIŠKA 2000). Another uncertainty emerges from the fact that the flagellates, and especially the large ones, can migrate themselves (FOGG & THAKE 1987).

Surface POC (all seston, chemical determination) in July and October 1997 was 0.24 and 0.46 mg.l<sup>-1</sup>, respectively. If we accept the incipient limiting food concentration of *Daphnia*

*longispina* as 0.3–0.4 mg.l<sup>-1</sup> C of suitable food (LAMPERT 1987), we can conclude that in the time of our 1997 observations *Daphnia* lived well below the incipient limiting level regardless their position in the water column.

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