

## Migrations of haemoglobin-rich *Daphnia longispina* in a small, steeply stratified, humic lake with an anoxic hypolimnion

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### Abstract

Migrations of *Daphnia longispina* were studied in a small humic lake with an exceptionally shallow oxic epilimnion. Horizontal distributions showed clear avoidance of the shoreline, which might be explained by the lower density of predators (*Chaoborus* sp. and *Notonecta* sp.) in the central parts of the lake. In early summer all size classes of *D. longispina* exhibited upward nocturnal vertical migration, descending to the upper hypolimnion in daytime. Later in summer, when the nocturnally migrating *Chaoborus* sp. had grown large enough to graze on small *Daphnia*, the latter seemed to shift towards twilight migration. However, large *Daphnia* individuals showed no synchronized migration; rather their bimodal vertical distributions suggested asynchronous vertical migration. Large individuals showed a particular tendency to concentrate near to the oxycline, close to the dense phytoplankton and bacteria populations in the upper part of the anoxic hypolimnion. According to vertical trap experiments, large *D. longispina* visited the anoxic hypolimnion and might harvest its abundant food resources. The high haemoglobin content of large individuals seems a specific adaptation to allow access to low oxygen water and hence to maximize grazing potential, in both epi- and hypolimnion, and minimize predation pressure. By staying predominantly in cooler water near the oxycline, *Daphnia* might also minimize its energy consumption to adjust to low food availability while sustaining a sufficiently high population density to exploit those unpredictable short periods with abundant food which are common in small headwater lakes. It is suggested that migrations of zooplankton are a complex behavioural adaptation which may not be explained by any single factor. In humic lakes with shallow stratification, vertical migrations seem to offer particularly high potential advantages, because of the short distances between dramatically different environments in the water column. In further studies more emphasis should be placed on migrations of individuals rather than populations, and migrations should be considered as a dynamic part of the structure and function of the whole planktonic ecosystem.

### Introduction

Vertical migration is a widespread behaviour among planktonic invertebrates, and a variety of hypotheses has been proposed to explain selective advantage(s) of this behaviour. However,

with the exception of the predation hypothesis, postulating that feeding in the food rich surface waters during night but returning to dark, deep water in daytime minimizes the risk of being eaten by visual predators (Zaret & Suffern, 1976; Wright *et al.*, 1980; Gliwicz, 1986; Lampert,

1989), there is quite little agreement. Vertical migrations are found in all kinds of water bodies ranging from small ponds to the ocean. Although the basic behaviour of animals may be similar in different environments, local conditions are likely to modify patterns of vertical migration.

We have studied the migrations of a cladoceran, *Daphnia longispina*, in a small, humic, forest lake. In such lakes wind contributes little to the vertical mixing of water and the vertical distributions of light and temperature are largely determined by water colour (e.g. Jones & Arvola, 1984). High humic concentration typically leads to an anoxic hypolimnion and organisms with a variety of metabolic types may develop thin layers with high density within the oxygen gradient. In such cases zooplankton is often abundant around the oxycline (e.g. Sorokin, 1966; Hanazato *et al.*, 1989; Mazumder & Dickman, 1989). Thus, unlike in many large lakes, migration into deeper water does not mean reduced food availability. We paid particular attention to studying the adaptations of *Daphnia longispina* to cope with low or no oxygen which enable it to obtain food from the upper part of the anoxic hypolimnion or to escape predation by *Chaoborus* sp. and *Notonecta* sp. predators.

### Study site

Mekkojärvi is a small and shallow (area 0.35 ha, mean depth 3 m), highly humic lake in southern Finland, surrounded by coniferous forest. The shoreline is composed of floating *Sphagnum* and floating *Warnstortia* moss and hence there is no shallow littoral. The small size and very brown water (colour 300–600 mg Pt l<sup>-1</sup>) result in steep thermal and oxygen stratification. Annual primary production is below 10 g C m<sup>-2</sup>. Some physical, chemical and other biological properties of the lake are described elsewhere in this volume (Salonen *et al.*, 1992a; Salonen *et al.*, 1992b; Kuuppo-Leinikki & Salonen, 1992; Münster *et al.*, 1992).

*Daphnia longispina* is very abundant in Mekkojärvi throughout the summer and dominates the

zooplankton biomass almost exclusively. The few other species occur only occasionally and in summer their biomass is low compared with *D. longispina*. With the exception of very young pike, there are no planktivorous fish in the lake. Therefore the most important invertebrate predators are *Notonecta* sp. and larvae of *Chaoborus* sp.

### Material and methods

In the first stage of the study, vertical zooplankton samples were collected at 6 h intervals over a 24 h period on 5 sites along the lake (Fig. 1). Water was sampled from the surface to 2 m with a 0.5 m vertical tube sampler (volume 7.7 l) with lids opening so that water can freely pass through the sampler when it is lowered. The samples from each site were counted separately. Zooplankton was sieved through a 50 µm net, washed into bottles and preserved in sugar-formaldehyde solution (Haney & Hall, 1973). In the laboratory all species, except rotifers, were counted under a Wild M5 dissection microscope.

Because of large variation in the total numbers of individuals between the sampling sites and times, and high numbers of *Daphnia* found in the night samples, we also studied the horizontal dis-

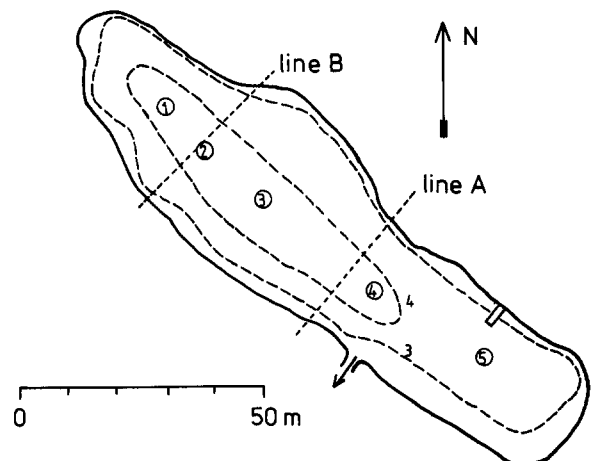


Fig. 1. Bathymetric map of Mekkojärvi (61° 17' N, 25° 7' E). The sampling sites (circled) of the first vertical study and the transects used in the horizontal study are shown.

tribution of *Daphnia* over one 24 h period in July 1985. Two lines (A: 26 m with 7 sampling points and B: 34 m with 8 sampling points; Fig. 1) were marked by string stretched across the lake ca. 1 m up from the surface. The first and last marks were 1–2 m from the shoreline. We sampled the depth zone 0–2 m (but at the shoreline 0–1 m) at 4 hour intervals, using a 1 m long (volume 6.2 l) tube sampler as described above.

In 1986 we built a new sampler (Fig. 2) which allowed more detailed vertical sampling of plankton. It has four 0.3 m long square section tubes with  $100 \times 100$  mm opening (volume 4.5 l) stacked on each other. The tube assemblage is fixed to a vertical metal rod which can be immersed to the desired depth. The vertical rod is connected to a horizontal one so that the sampler can be moved so far (ca. 2 m) in front of the boat that water movements caused by the boat do not disturb the vertical distribution. The boat was rowed slowly forward and water moved freely through the open lids. After some time the closing mechanism was released by pulling a thread. Then rubber bands closed all the lids simultaneously and the tube assemblage was taken into

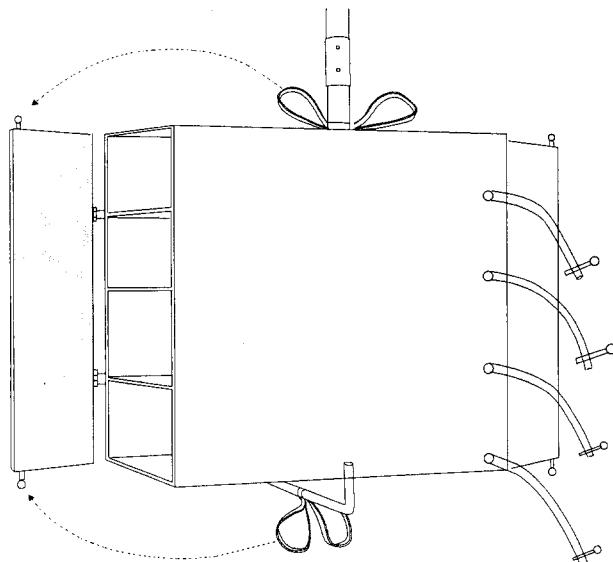


Fig. 2. Horizontal tube sampler. The trigger mechanism behind the box releases the threads which keep the sampler loaded and the rubber bands close to lids.

the boat. Water from each tube was drained through a  $100 \mu\text{m}$  plankton net and preserved. Care was taken always to sample water where the boat had not moved. Therefore water was sampled along longitudinal lines within the 4 m depth curve (Fig. 1). Three samples from each 10 cm depth zone taken at different localities were pooled. Altogether 20 pooled samples were taken between the surface and 2 m. Sampling of one set lasted 1–1.5 hours.

In the laboratory all animals in the zooplankton samples were counted. In addition, 100–150

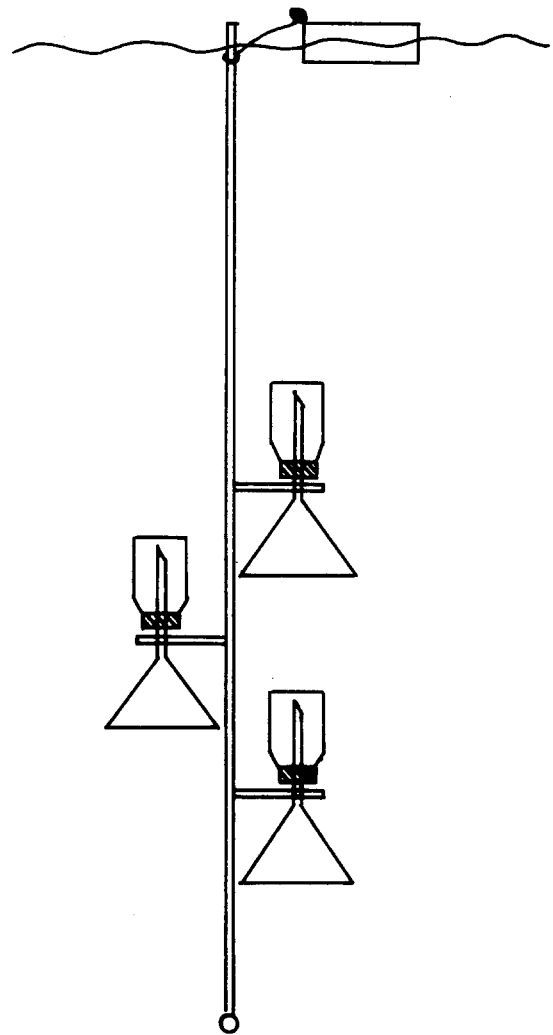


Fig. 3. Schematic view of the traps used to collect upswimming zooplankton.

animals selected at random from each sample were measured under a dissection microscope at  $25\times$  magnification and with a precision of 0.04 mm. The total length was measured from the top of the head to the base of the carapace spine.

To test if *Daphnia* visit the anoxic hypolimnion, we used vertical traps to collect upswimming individuals. These traps consisted of inverted glass funnels anchored to a suspending rod system (resembling the funnels used by Landon & Stasiak, 1983). Small (100 ml transparent plastic bottles were attached on the top of the funnel tube (Fig. 3). Three funnels were fixed to a rod at 0.1 or 0.2 m intervals alternately on different sides of the rod. Two rods were suspended in the lake so that traps covered a 0.5 or 1 m depth zone. The bottom of the bottles was of 300  $\mu\text{m}$  plankton net, which was dense enough to retain young individuals. The funnels were filled with filtered water from the lake surface and closed with a plastic film kept in place with rubber bands. The rods with funnels full of water were lowered to the desired depth and the plastic films were drawn away after releasing the rubber bands. Thus we excluded the possibility that zooplankton could enter the traps during their installation. The funnels were fixed to a buoy at the desired depth and kept in the lake 1–2 days. At the end of the experiment the traps were removed and zooplankton in the bottles were washed out and preserved in sugar-formaldehyde. Whenever traps were suspended in the lake we also collected (as described above for the sampling of along the horizontal lines across the lake) at 5 sites altogether 621 pooled zooplankton samples covering the depth 0–2 m.

Haemoglobin in *Daphnia* was determined according to Landon & Stasiak (1983). The animals were frozen in small plastic tubes in lake water. Haemoglobin of 30–100 individuals of about the same size was measured with a Shimadzu UV 240 spectrophotometer. Crystallized rabbit haemoglobin (H-7255, Sigma Chemical Company) was used as a standard. The haemoglobin content of *Daphnia* was calculated per individual dry mass, which was obtained as a mean of 15–40 individuals, dried for 24 hours at 60 °C and

weighed on an electronic microbalance at a precision of 0.001 mg.

Temperature and oxygen concentrations were measured at every sampling with a combined probe (Yellow Spring Instruments). Light penetration into water was measured with a quantum sensor and integrator (Lambda Instruments, Li 2190). Samples for chemical determinations and bacterio- and phytoplankton were collected from water filtrate obtained in sampling zooplankton (Arvola *et al.*, 1991).

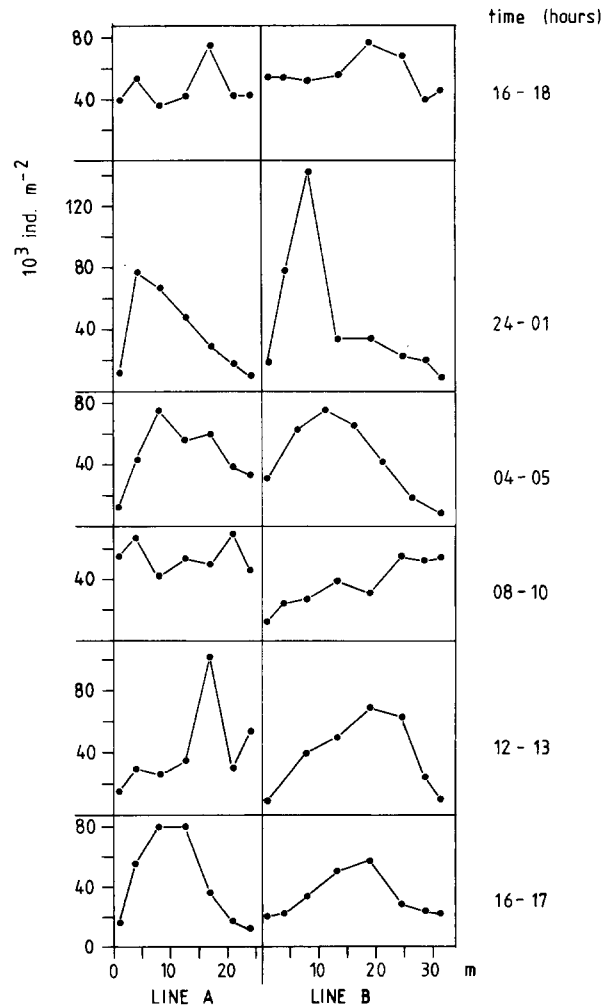


Fig. 4. Diel horizontal distribution of *Daphnia longispina* in July 1985 along two transects over Mekkøjärvi. The distances are measured from the northeastern side of the lake.

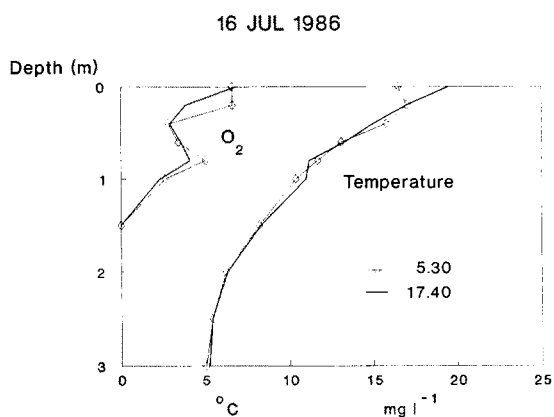
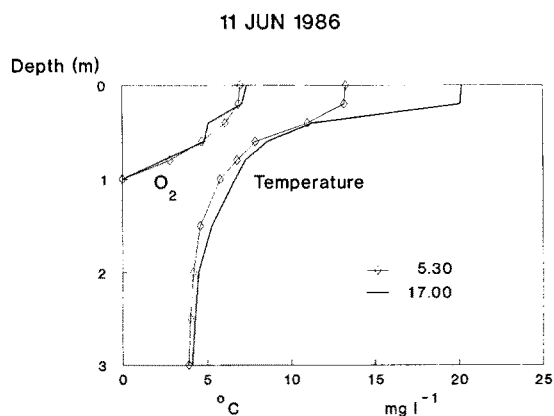
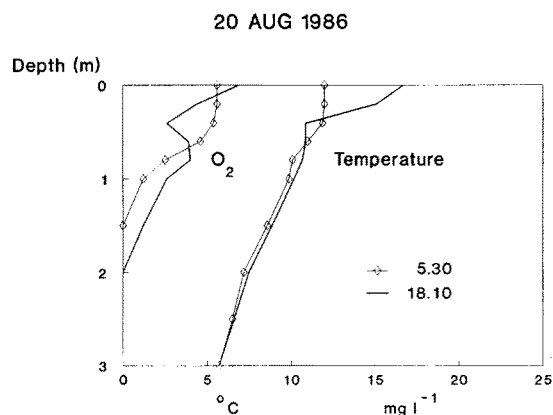
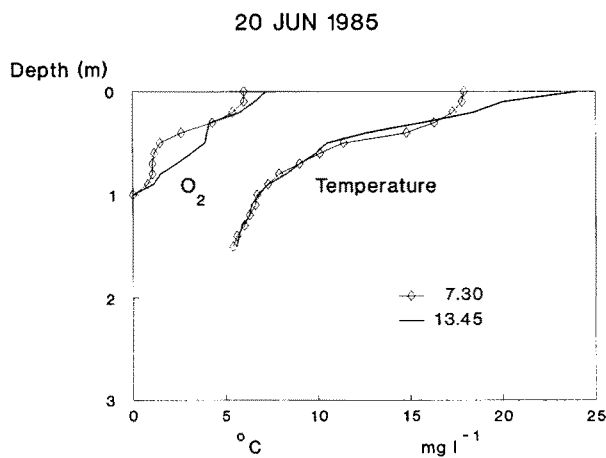


Fig. 5. Vertical distributions of temperature and oxygen in the water column during the vertical migration studies. Only distributions during the minimum (diamonds) and maximum surface temperature are shown with the time of their occurrence.

terms of biomass. Among other cladocerans *Polyphemus pediculus* was present at low density. *Chaoborus* larvae and *Notonecta* sp. were probably the main invertebrate predators. Most *D. longispina* were in the 0–1 m water layer (mean 92% and minimum 87% of that in the 0–2 m water layer). Therefore although the sampling points nearest to the shoreline extended only to the depth of 1 m rather than the depth 2 m at other sampling points, this does not significantly bias the observed horizontal distributions. The mean densities of *D. longispina* along both transects over the lake were similar (line A:  $43.3 \pm 5.6 \times 10^3$  ind. m<sup>-2</sup>, line B:  $42.3 \pm 8.6 \times 10^3$  ind. m<sup>-2</sup>; both with SD). With the exception of samplings at 16–18 and 8–10, the horizontal distributions (Fig. 4) demonstrated a tendency for *D. longispina* to avoid water near to the shoreline. The two sample sets taken in the evening on successive days (Fig. 4) showed quite a marked difference, which might have been caused by weather conditions. The results along the transects were different at each sampling time ( $P < 0.01$ ; Kolmogorov-Smirnov test, equalising the number of observation points arbitrarily by omitting the fifth observation from line B), but the distributions do suggest some agreement and possibly diel horizontal migration which might be explained by the development of illumination and

## Results

### Horizontal distribution

During the time of the horizontal migration study in July 1985, *Daphnia longispina* was by far the most abundant zooplankton species in

the direction of sunlight. The verification of diel horizontal migration in Mekkojärvi would, however, have required several successive sampling days. During the experiment wind was low and at night and in the morning conditions were completely calm and cloudless, but in spite of this the movements of water masses in the shallow epilimnion might still have been significant and led to differences in the observed horizontal distributions.

#### Vertical distribution

In June 1985 Mekkojärvi was so steeply stratified (Fig. 5) that at the warmest time of the day there

was no homothermic epilimnion at all. Although the concentration of oxygen was low below the uppermost 0.3 m (Fig. 5), *Daphnia longispina* inhabited the whole oxygenated zone down to the upper anoxic hypolimnion and probably migrated towards the surface at night (Fig. 6). However, the high variability of the results and rather crude resolution of 0.5 m layer samples makes the interpretation difficult. Further difficulties arose from the considerably higher total number of animals in the vertical column at night ( $99 \times 10^3 \text{ ind. m}^{-2}$ ) than at other sampling times ( $36\text{--}67 \times 10^3 \text{ ind. m}^{-2}$ ), indicating either horizontal migration or differences in the efficiency of the sampling under different illuminations.

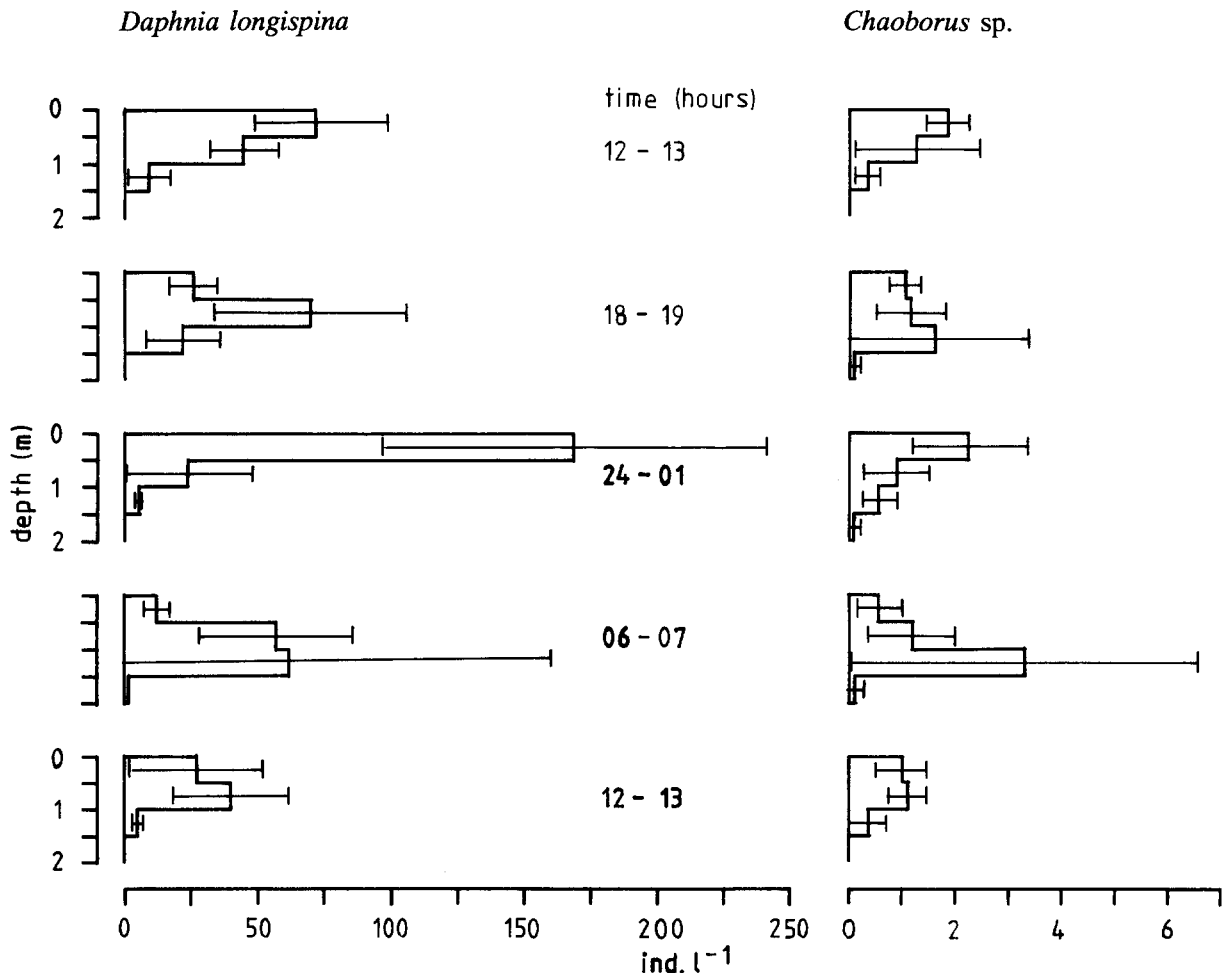


Fig. 6. Diel vertical distributions (with SD) of *Daphnia longispina* and *Chaoborus* sp. in June 1985.

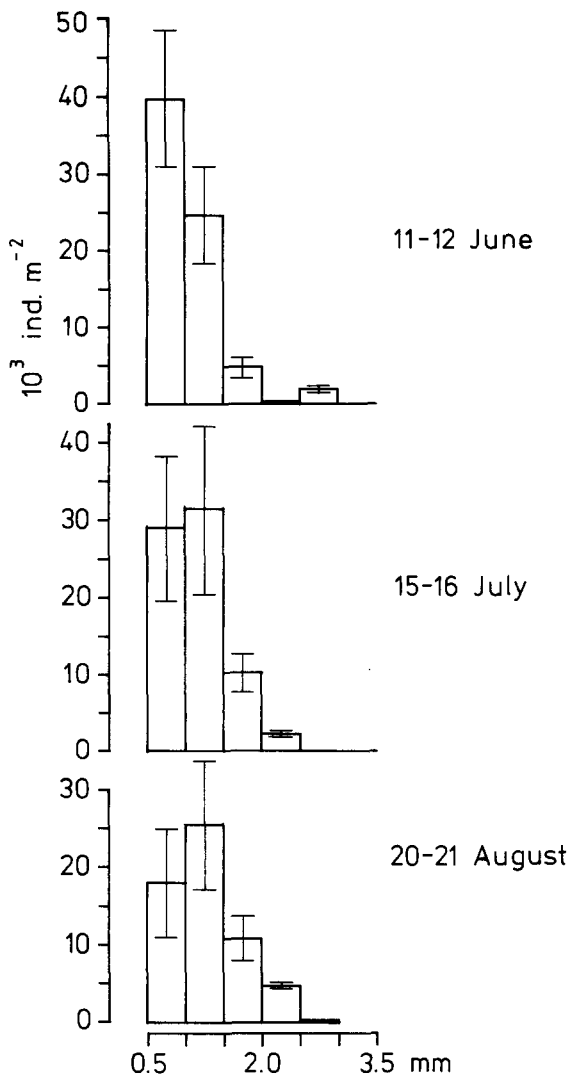


Fig. 7. Mean size distributions (with SD) of *Daphnia longispina* populations in diel samples in 1986.

In June 1986 *Daphnia longispina* again dominated the biomass, but nonmigrating *Cyclops* sp. was also abundant, consisting of naupliar and C III–IV copepodite stages with a maximum at ca. 1 m (110–220 ind.  $l^{-1}$  for both). The *D. longispina* population was mainly young females, but there were also large females hatched from ephippia (Fig. 7).

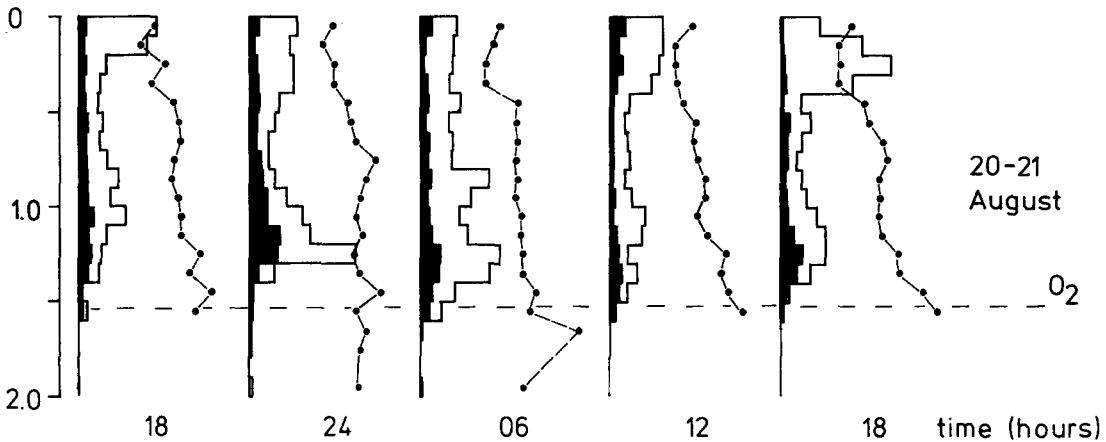
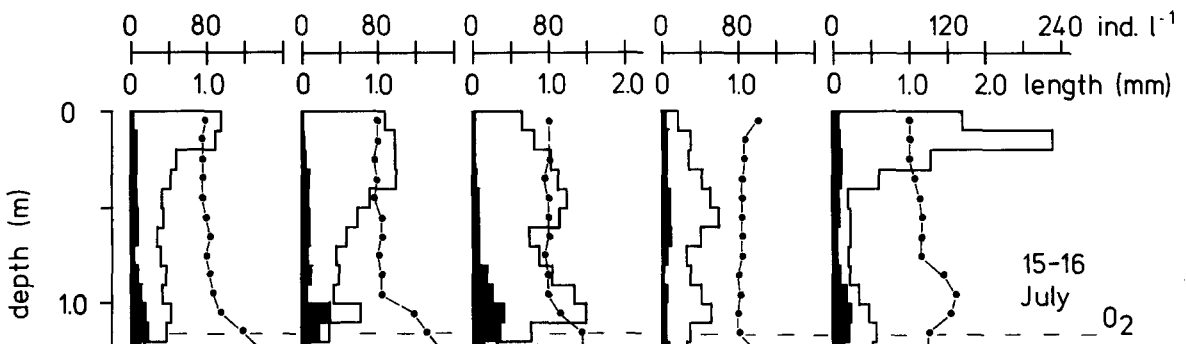
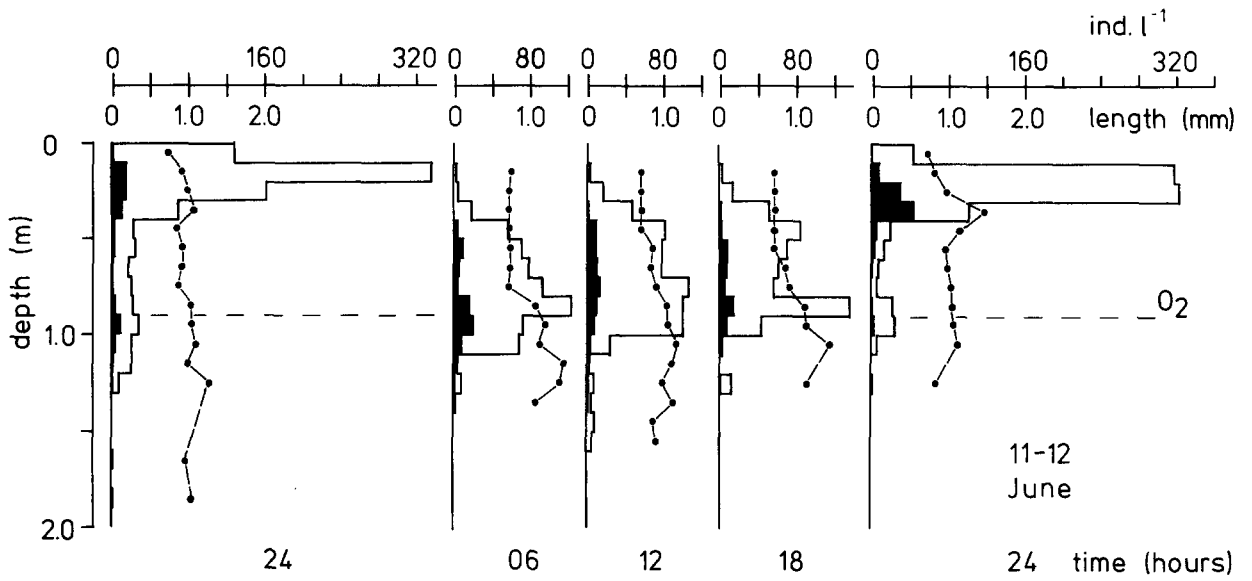
The smoothness of vertical distributions obtained with our high resolution horizontal tube sampler in 1986 (Fig. 8) indicates a high reliability for the results. This may be explained by the

Table 1. The observed relative abundances (%) of *Daphnia longispina* at different times of day in 1986. Densities at noon were taken as a reference.

Date	Evening	Night	Morning	Noon	Evening	Night
11–12 June	–	131	89	100	81	132
15–16 July	116	157	216	100	156	–
20–21 August	110	131	131	100	135	–

smoothing effect of pooled samples and minimal disturbance of plankton by boat during sampling, unlike during sampling by the 0.5 m vertical tube sampler. The variation (CV 14–29%) between the diel sampling times was moderate, but again samples taken at solar noon generally yielded the lowest densities (Table 1). The sampling in June was an exception; then the minimum was found in the evening, but the maximum was still at midnight. The differences were probably caused by different horizontal distributions at different times of the day. For example, the diel changes in the horizontal distributions observed in late July 1985 would have resulted in similar variation in observed numbers as was found in June 1986.

In June, when daylight hours were nearly at their longest and solar radiation most intensive (Fig. 9), *Daphnia longispina* exhibited a typical pattern of diel vertical migration. At night > 70% of the individuals were concentrated at the depth of 0–0.3 m and their maximum density was very high, more than 300 ind.  $l^{-1}$ . At other times only 1–3% of the individuals appeared at this zone while the maximum density was observed at 0.7–1.0 m, immediately above anoxic water (Fig. 5), and corresponding to ca. 1% of the surface light intensity at noon (Fig. 9). Large females (> 1.5 mm) migrated similarly, but occurred in deeper water layers (Fig. 8). Although the observed vertical migration was pronounced, the results might still have suffered from possible diel horizontal migration (Fig. 4) or efficiency of sampling. All size classes clearly avoided the uppermost water layers, but it was most striking among ovigerous females (Figs. 10–11). The difference in temperature between the surface and 1 m was high (ca. 14 °C) but because of the ca. 7 °C diurnal variation of temperature, the daily temper-





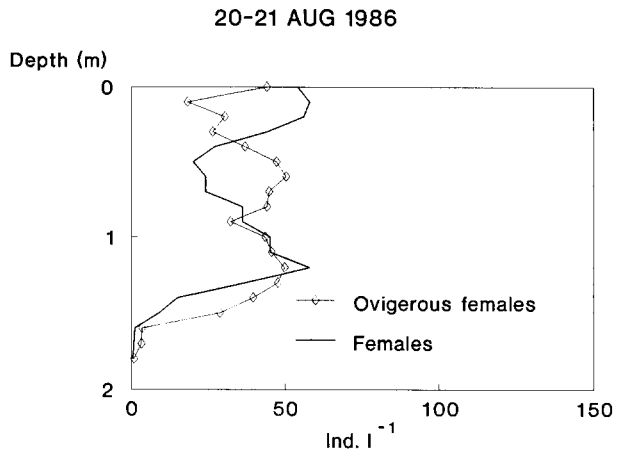
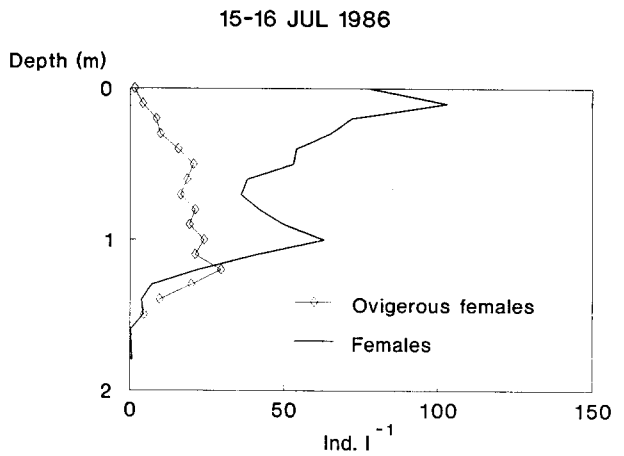
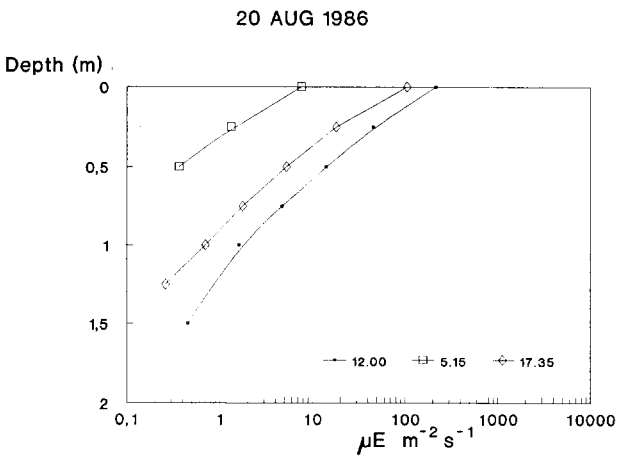
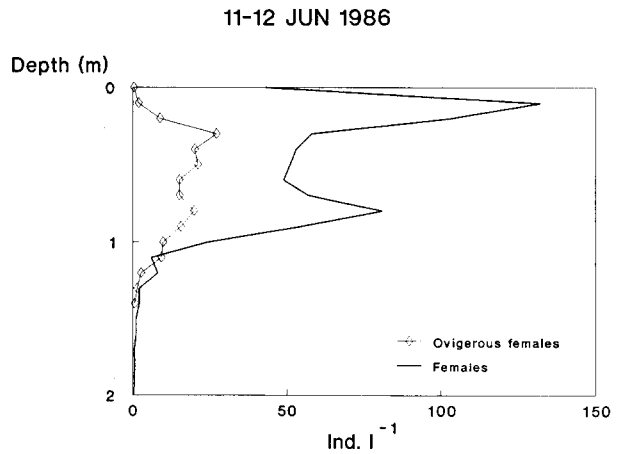
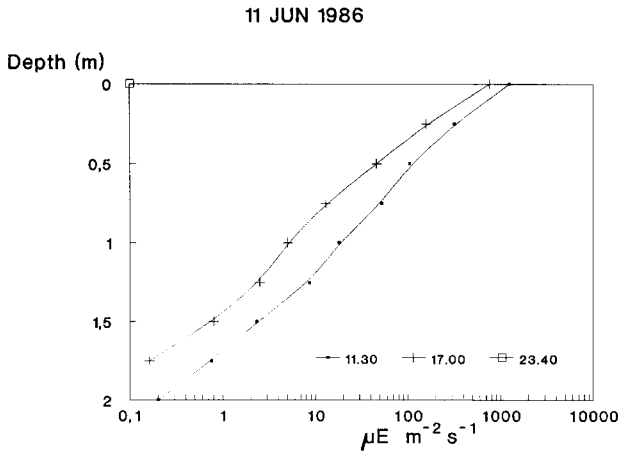


Fig. 9. Some vertical distributions of light intensity at different times of day in the water column during the vertical migration studies.

ature gradient calculated from the modal depths in the distributions of animals was in practise only ca. 10 °C.

In August *Daphnia longispina* exclusively dominated the community. Later in summer the nights got longer and light intensity decreased. During the sampling periods in July and August the weather was colder leading to an increase in the depth of the epilimnion and decrease in its temperature (Fig. 5). Thus the temperature gradient between the surface and 1 m was only 8 °C in

Fig. 10. Mean daily vertical distributions of *Daphnia longispina* and its ovigerous females. The arrows at the time scale denote sunrise and sunset.

Fig. 8. Diel vertical distributions of *Daphnia longispina* in the summer 1986. The broken horizontal lines indicate the oxygen limit. Open bars - Whole population; Black bars - > 1.5 mm long animals; Dots - Mean length of animals.

Table 2. Some mean population parameters for *Daphnia longispina* (with SD for examples taken at different times of the day).

	11-12 June	15-16 July	20-21 August
10 <sup>3</sup> Females m <sup>-2</sup>	72 ± 16	73 ± 21	59 ± 8
10 <sup>3</sup> Males m <sup>-2</sup>	0	0.22 ± 0.11	5.2 ± 1.3
10 <sup>3</sup> Eggs m <sup>-2</sup>	16 ± 11	9 ± 3	27 ± 2
Eggs per ovigerous female	7.6 ± 1.4	3.4 ± 0.2	4.3 ± 0.1

July and 6 °C in August. The population structure was no longer dominated by smallest individuals (Fig. 7). Few males were present in July, but in August they formed 8% of the population (Table 2). In July and August, diel vertical migration of *D. longispina* was still evident (Fig. 8), but less striking than in June. The vertical distributions of juveniles suggested a shift towards twilight migration. Large females did not show any synchronized vertical migration and again they occurred in deeper water than juveniles. Particularly large females were found near the oxycline (Fig. 8) and many of them were ovigerous (Fig. 11). The difference in temperature between the epilimnetic and deep water maxima of *D. longispina* was 6-7 °C in July and 2.5-4.5 °C in August depending on the time of the day.

All vertical distributions of *Daphnia longispina* showed a bimodality (although slight in June)

(Fig. 8) indicating asynchronous vertical migration (Pearre, 1979). Bimodality was strikingly evident in the mean daily vertical distribution (Fig. 11) irrespective of different vertical migrations between June and late summer. However, it could not be observed in the vertical distribution of ovigerous females which showed a tendency to avoid surface water layers. In spite of that, in June most ovigerous females were in the epilimnion. Later in summer the situation was more or less reversed and most ovigerous females occurred in the lower part of the oxic water column.

In June in 1985 (Fig. 6) and 1986 (Figs. 8, 12) the vertical migrations of *Daphnia longispina* and *Chaoborus* larvae were similar. Taking into account the large variations and some inconsistency in the diel distributions (Fig. 6), this was particularly striking. The larvae were small (only 2-3 mm long) and their density was high (800 ind. m<sup>-2</sup>). In July *Chaoborus* larvae were mostly large (8-11 mm long), and their density had decreased to about 270 ind. m<sup>-2</sup>. Although *D. longispina* in late summer changed its migration behaviour (Fig. 8), *Chaoborus* continued nocturnal vertical migration. In late summer they seemed to continue the same behaviour, but their density was so low (170 ind. m<sup>-2</sup>) that the number of animals counted in samples makes the interpretation uncertain.

Vertical migrations and distributions of bacte-

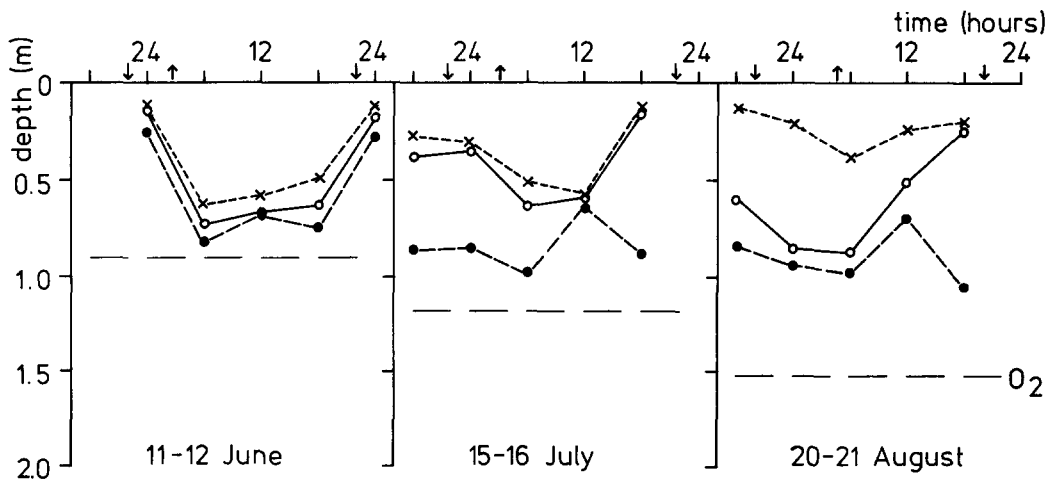


Fig. 11. The mean vertical positions of different size classes of *Daphnia longispina* in diel samples in 1986. Circles - All animals; Dots - > 1.5 mm long animals; Crosses - < 1 mm long animals. The broken line shows the oxygen limit.

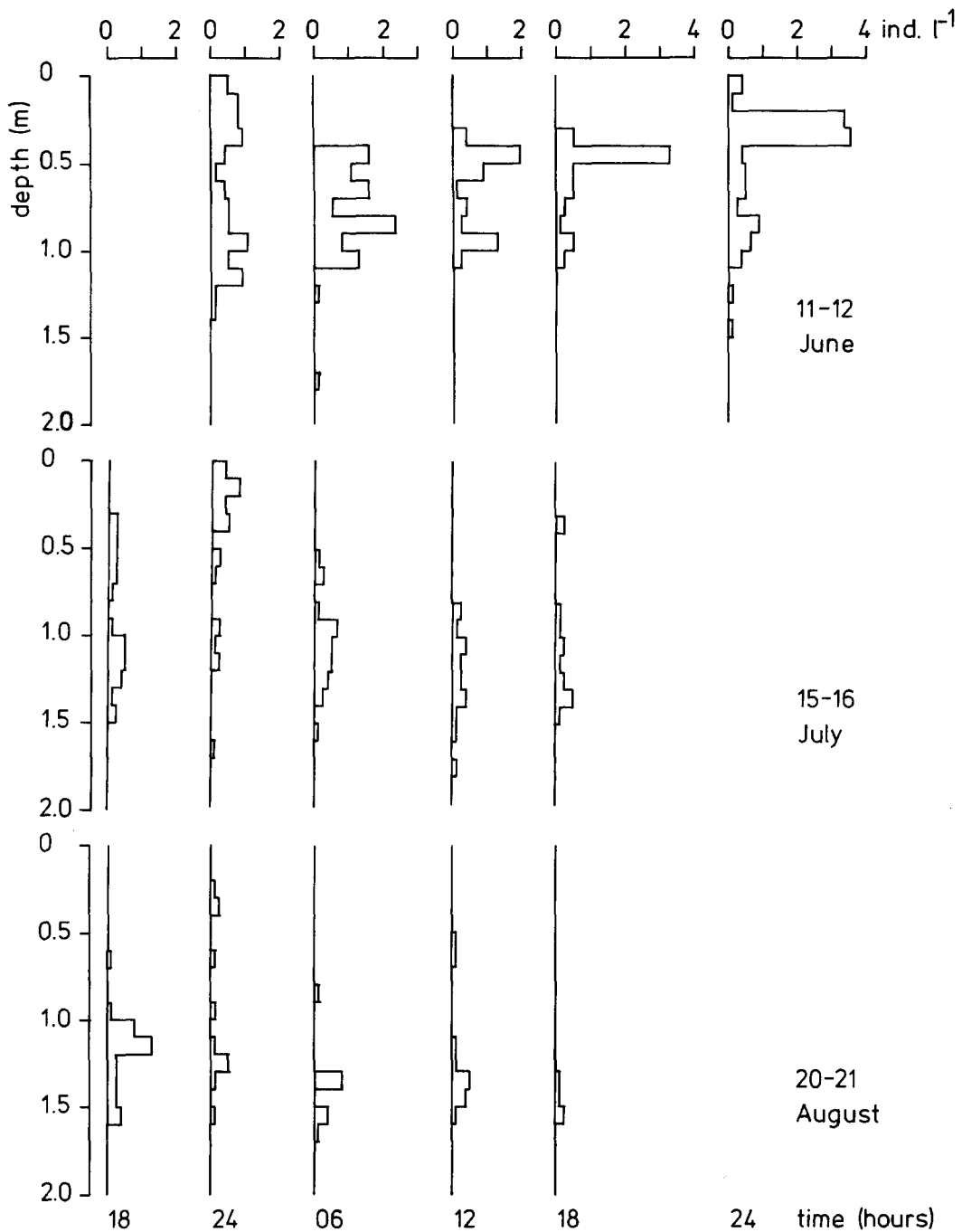


Fig. 12. Diel vertical distributions of *Chaoborus* sp. in the summer 1986. The broken horizontal lines indicate the oxygen limit.

ria and phytoplankton were studied using the same samples (Arvola *et al.*, 1991). During all three sampling periods in 1986, bacteria and algae were most abundant throughout the day in the upper hypolimnion (Fig. 13; Table 3). Small

algae, *Chlamydomonas* sp. and *Scourfieldia cordiformis*, were particularly abundant near the deep water maximum of *Daphnia longispina*. The vertical migrations of algae are reported in more detail by Arvola *et al.* (1992).

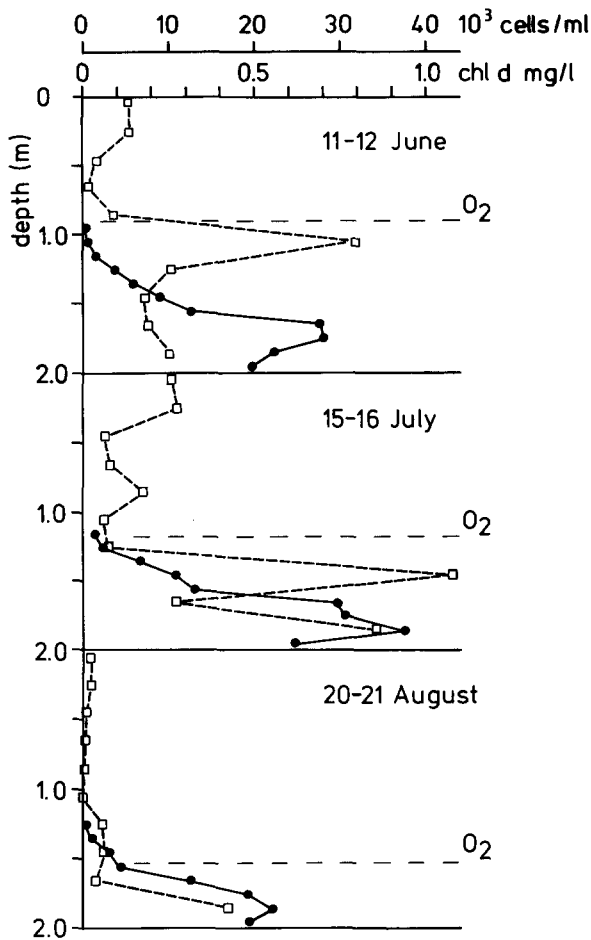


Fig. 13. Vertical distributions of phyto- and bacterioplankton at noon in Mekkojärvi in 1986. Squares – Density of phytoplankton; Dots – Concentration of bacteriochlorophyll *d*.

Vertical traps showed that *Daphnia longispina* can visit the upper anoxic hypolimnion at least 0.5 m below the oxycline. The results of successive periods showed high variation in the numbers of animals caught (Fig. 14) and hence the visit rates of animals at various depths cannot be reliably estimated. Most of the animals caught were large females while in the whole population most individuals were small (Fig. 15). The latter looked pale and contained less than 10% haemoglobin in their dry mass (Fig. 16), but large animals were dark brown and their haemoglobin concentration was up to one third of dry mass.

In August 1985 we determined chlorophyll extracted from *Daphnia longispina* collected from

Table 3. Mean daily biomass ( $\text{g m}^{-3}$ ) of algae and bacteria in the upper water layers of Mekkojärvi in 1986. Cell volumes were converted to carbon using factors 0.2 and  $0.38 \mu\text{m}^{-3}$  for algae and bacteria, respectively.

	Algae		Bacteria		Alga + bacteria	
	0–1 m	1–2 m	0–1 m	1–2 m	0–1 m	1–2 m
11–12 June	0.19	0.55	0.44	3.21	0.63	3.77
15–16 July	0.69	2.91	0.69	3.92	1.67	6.83
20–21 August	0.31	0.21	0.56	1.99	0.86	2.20

0.5 m depth to assess possible feeding on photosynthetic bacteria. Although located on the tail of the high haemoglobin absorption curve, a clear absorption peak was observed at 653 nm, which coincides with the absorption maximum of bacteriochlorophyll *d* and indicates that the animals had ingested photosynthetic bacteria.

## Discussion

Diel vertical distributions observed in nature are often difficult to interpret. Water masses at the sampling site may move, the distribution of organisms is generally patchy and the efficiency of sampling may vary according to weather conditions. In addition to sampling problems, the vertical migration behaviour itself may change due to rather small changes in the environment. Hence it is very tedious to collect and count enough samples to get statistically unambiguous results. In Mekkojärvi we demonstrated horizontal variation in the distribution of *Daphnia longispina*, and the results indicated some regularity in the distribution rather than random patchiness. This probably resulted from the low turbulence and the absence of waves in this small and sheltered lake. Similarly the diel vertical samples taken with the high resolution sampler showed no major irregularities in the distributions of *D. longispina*. Thus, although no replicate samples were counted, the smooth vertical distributions shown by the pooled samples seem to provide a reasonable basis for the interpretation of the results.

In very small lakes horizontal migrations are certainly realistic in terms of the swimming speed

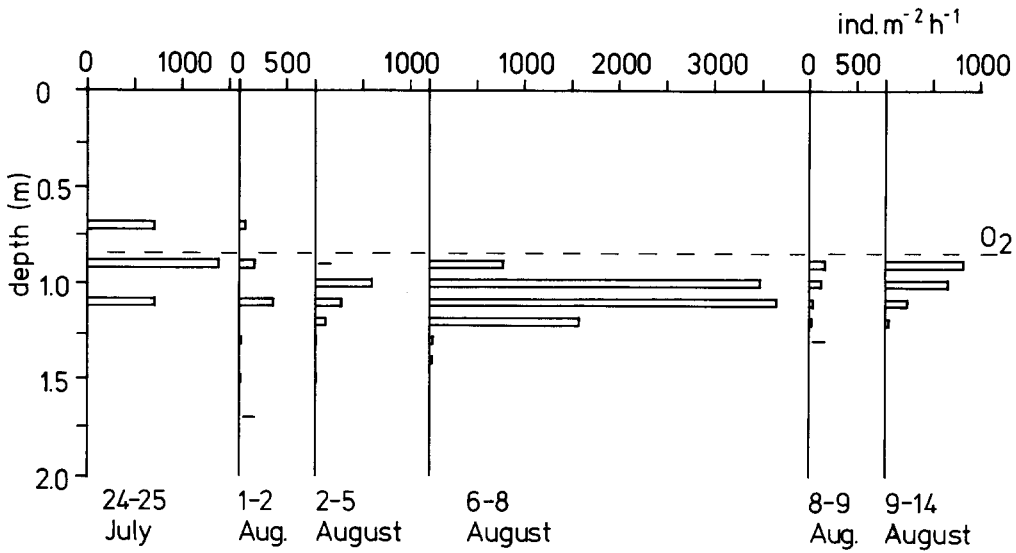


Fig. 14. The catches of *Daphnia longispina* in traps suspended near or below the oxycline.

of *Daphnia* (e.g. Hutchinson, 1967; Gerritsen, 1982). In Mekkojärvi the horizontal migration of *Daphnia longispina* was not as clear as found by Davies (1985) for *D. hyalina lacustris* which, in daytime, moved towards the shoreline. He explained horizontal migration as an avoidance of fish predation in open water. Although the shoreline avoidance observed in Mekkojärvi is seemingly opposite to the results of Davies, it can also be explained by predation, because in the middle of the lake there was no fish predation, whereas invertebrate beetle as well as heteropteran (*No-*

*tonecta* sp.) predators were visibly much more abundant near the shoreline.

*Daphnia* populations frequently occur in anoxic or nearly anoxic water (e.g. Sorokin, 1966; Mazumder & Dickman, 1989; Prepas & Rigler, 1978; Murtaugh, 1985) and their ability to synthesize haemoglobin is common. The presence of haemoglobin has been proposed as an adaptation to unpredictable environments where the oxygen concentration may suddenly drop to lethally low levels (e.g. Heisey & Porter, 1977; Weider & Lampert, 1985). This explanation is unlikely for

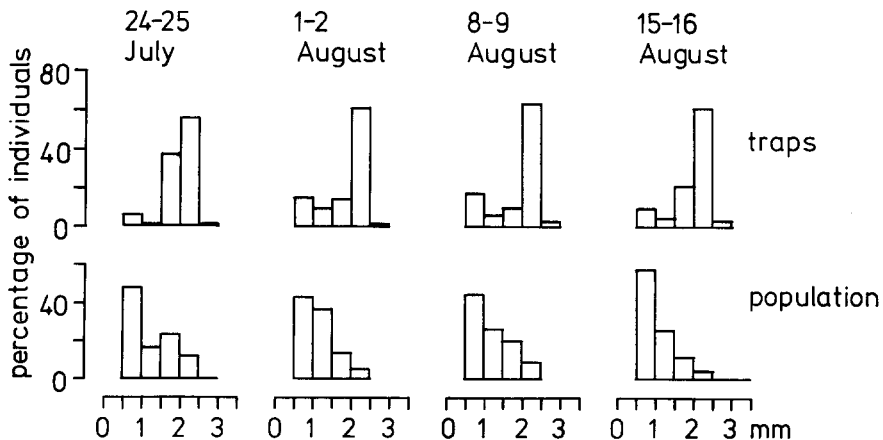


Fig. 15. Size distributions of *Daphnia longispina* population in Mekkojärvi and in the catches caught by the vertical traps.

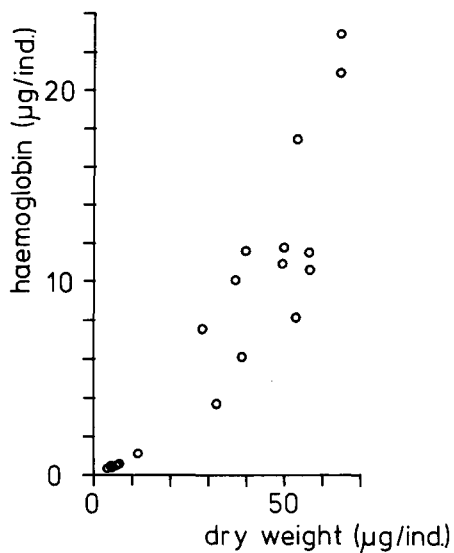


Fig. 16. The haemoglobin content as a function of the size of *Daphnia longispina*.

Mekkojärvi where the summer stratification of oxygen is stable. During 6 summers of study we have never seen any sign of mixing of water that would turn the epilimnion anoxic. In Mekkojärvi the haemoglobin concentrations were about ten times higher than those observed in the experiments of Weider & Lampert (1985) and Kring & O'Brien (1976), manifesting the importance of the ability to tolerate low oxygen concentration. Similarly high values have been reported only for *Daphnia* overwintering in very poorly oxygenated water (Landon & Stasiak, 1983) and for *D. pulex* (Engle, 1985) in a pond without vertebrate predators.

High haemoglobin concentration may yield several advantages for *Daphnia*. Weider & Lampert (1985) found *Daphnia pulex* to be able to regulate oxygen consumption across a wide range of oxygen concentrations down to a level of 0.5–1 mg O<sub>2</sub> l<sup>-1</sup>. In Mekkojärvi, *D. longispina*, with an order of magnitude higher haemoglobin concentration, was probably able to tolerate even lower concentrations. Evidently a low oxygen level provides an even better refuge from predators than darkness alone. Analogous to Mekkojärvi, Hanazato *et al.* (1989) found *D. longispina* to escape fish predation by retreat into the anoxic

water of Lake Yonoko. With high haemoglobin filtering rates are also higher (Fox *et al.*, 1951; Kring & O'Brien, 1976). Thus even in the aerobic epilimnion the feeding rate of haemoglobin rich *D. longispina* can be 2–3 times higher than in the absence of haemoglobin. Therefore animals remaining a long time in deep water without feeding might still be able to collect as much food as their counterparts, without haemoglobin, living continuously in the epilimnion. Haney (1985) observed higher filtering rates of several cladoceran species at night than in daytime and this was most pronounced in large individuals. Although there is no information about the haemoglobin level in those species, his results suggest that vertically migrating animals may in general be able to compensate for the time spent in deeper water, perhaps with low food concentration, by more intensive filtering. Combined with high feeding rate, vertical migration, irrespective of whether it is synchronous or not, may then provide a scanning mechanism through the water column to detect and rapidly utilize the most favourable food patches. If haemoglobin-containing animals are such superior filter feeders and they do not have essential costs from vertical migration, any advantages of vertical migration are amplified. This raises the question of why cladocerans everywhere do not take advantage of the benefits of high haemoglobin concentration. Kring & O'Brien (1976) and Engle (1985) suggested the higher visual predation of pigmented animals as the most probable explanation. In the very brown water of Mekkojärvi, the high visibility of strongly pigmented animals is less disadvantageous.

Lampert (1989) concluded that vertical migration may not evolve without light dependent mortality (visual predation) of zooplankton. Ohman (1990) has extended the predation hypothesis by differentiating between visual and nonvisual predation and was able to explain large variation in diel migration behaviour of the same species ranging from reversed vertical migration to the typical nocturnal one. When mortality by visually hunting predators is dominating, nocturnal migration is adopted, but when mortality is mainly caused by nonvisually hunting predators (e.g.

predatory zooplankton) reversed migration may be adopted. In Mekkojärvi, *D. longispina* had to adjust its behaviour to meet mortality caused by two predators with different behaviour, *Notonecta* sp. and *Chaoborus* sp. larvae. Dodson (1988) found that the chemical stimulus from these predators caused completely different behaviour of several *Daphnia* species. Contact with the stimulus from the visual predator, *Notonecta* (e.g. Dodson & Havel, 1988; Dodson, 1989) leads into the sinking of *Daphnia* within less than one hour, while the presence of *Chaoborus* causes escape upwards. In June, *Notonecta* sp. was likely the main predator, because *Chaoborus* larvae were probably too small to prey on *D. longispina* (Moore, 1988; Vanni, 1988). Therefore the identical diel migration patterns of *Chaoborus* and *D. longispina* do not conflict with the predation avoidance hypothesis. Later in summer *Chaoborus*, which continued to migrate nocturnally, got larger and, in spite of its lower abundance, became an important predator of small *D. longispina* and may have forced them to shift from nocturnal migration towards twilight and asynchronous migration. Large individuals were probably not affected by *Chaoborus* larvae. The increase in the size of *Notonecta* and increase in temperature may explain the change in their behaviour. The lack of information of the numbers and feeding of *Notonecta* sp. in Mekkojärvi does not allow more detailed explanation of the results.

In addition to predation, food (e.g. Bohrer, 1980; Walls *et al.*, 1990) is another probable ultimate cause of vertical migration. Among modifying factors, temperature and light are certainly important (Hutchinson, 1967). At high latitudes the seasonal course of illumination and the length of the day might explain the apparent shift from typical nocturnal vertical migration in Mekkojärvi in June towards twilight migration in late summer. In midsummer of high latitudes, midnight would be the most favourable time to avoid visual predation in the epilimnion and hence nocturnal migration would be a reasonable strategy. However, later in summer when nights are long, the time to be able to avoid visual predators is longer and allows avoidance of nonvisual preda-

tors without sacrificing too much feeding time. Thus twilight migration would have been the optimum behaviour to minimize temporal overlap with nocturnally migrating *Chaoborus* as well as visual predators. However, because the change in the light climate between June and July sampling was slight, light cannot alone explain the change in the migration behaviour. In late summer the need for more frequent feeding in the epilimnion and asynchronous migration, as indicated by the bimodal distributions of *Daphnia longispina* (Pearre, 1979) might have followed the ca. 5 °C rise in hypolimnetic temperature at the depth of the deep population maximum. This may have increased the metabolism of *D. longispina* so much that at least part of the population may not have been able to follow the diel light cycle in its vertical migration, but was forced to have more frequent feeding forays in the epilimnion. Asynchronous vertical migration is, particularly when combined with such short distances as present in Mekkojärvi, also effective to reduce epilimnetic predation.

In the conditions prevailing in Mekkojärvi, asynchronous migration might be particularly probable, because the migration over short distances requires insignificant energetic cost (Hutchinson, 1967: 785). That would also allow larger scale of variation in the behaviour of animals. Short scale asynchronous migration can take place at a frequency allowed by the swimming speed of animals. For *D. longispina* the time required for one vertical cycle is only of the order of minutes which is of the same order as the reaction time of *Daphnia* to the stimulus from its predators (Dodson, 1988). In large lakes the respective distance is much larger and hence the time required to swim between two vertical localities might dictate that the possible frequency of visits to near surface layers is not far from the diel solar cycle. Under such conditions any other factors coupled with the light cycle can more easily lead to synchronous diel vertical migration.

Pearre (1979) suggested that asynchronous migration is most probable with surplus food. The biomasses of algae and bacteria in the epilimnion of Mekkojärvi seem to support this hypothesis

(Table 2), but the high variation between the day and night results of algae and bacteria (Arvola *et al.*, 1991) and the uncertainty of volume-to-carbon conversion factors for reliable summation of algal and bacterial biomasses do not allow unambiguous conclusions. On the other hand, small and large *D. longispina* may differ in their ability to eat bacteria (Kankaala, 1988) and the availability of food may be highly size specific. The size distribution and egg ratio of *D. longispina* in fact indicate that in late summer the food availability was somewhat worse. However, in June large individuals were derived from ehippia and their egg ratio may not be comparable with individuals derived from parthenogenetic eggs. Under high grazing pressure, such as in Mekkojärvi, biomasses of food organisms might be misleading in the estimation of food availability, but knowledge of food production would be needed. It has been shown that with enough food *Daphnia longispina* may migrate vertically, but when food is scarce hunger forces it to feed all the time in the epilimnion irrespective of predation (Dagg, 1985; Johnsen & Jakobsen, 1987). However, De Meester & Dumont (1989) obtained opposite results and concluded that the vertical daytime distribution cannot be ascribed to a physiological adaptation alone, but that genetic differences are also significant.

Mazumder & Dickman (1989) made direct determinations of the feeding rate of *Daphnia* spp. on photosynthetic bacteria in meromictic Crawford lake in Ontario and found good evidence that *Daphnia* do feed on those organisms. In contrast, Murtaugh (1985) suggested that in the Canadian Roi lake the organisms at the chemocline and in deeper water were not heavily exploited by zooplankton. In Mekkojärvi the deep living *Daphnia longispina* population was able to penetrate into anoxic water and was potentially able to utilize the dense community of food organisms living near the oxycline. Populations of *Scourfieldia cordiformis* and *Chlamydomonas* sp. (Fig. 13; Arvola *et al.*, 1992) and photosynthetic bacteria (Arvola *et al.*, 1992; Kuuppo-Leinikki & Salonen, 1992) represented, together with heterotrophic bacteria, higher biomass per volume than

is available in the epilimnion (Table 2). In support of the hypothesis of utilization of organisms in anaerobic layers, we were able to detect bacteriochlorophyll *d* in *D. longispina* caught in the epilimnion at 0.5 m depth. Although we could probably avoid any passive contamination of animals at sampling, our method did not yield any quantitative estimate about the importance of photosynthetic bacteria as a food. Similarly the importance of algae living in anoxic water cannot be quantified, but the near proximity of the vertical distributions of algae and *D. longispina* and the ability of the latter to visit anoxic water might allow grazing on the deep water algal population.

Among other alternatives to explain the diel vertical migration of *Daphnia longispina*, metabolic advantages (McLaren, 1963) are often considered inconclusive (Stich & Lampert, 1984; Kerfoot, 1985). However, although vertical migration would yield not instantaneous growth advantage, the lifetime reproduction may become higher and make it possible to maintain higher population density than in nonmigrating, but faster growing populations. In Mekkojärvi, large *D. longispina*, often carrying eggs, clearly preferred deeper and colder water than did the small ones (for other *Daphnia* species see also Murtaugh, 1985; Buchanan & Haney, 1980). With vertical migration between cold and warm water the population would also be able, to some extent, to regulate its food consumption and reduce the effects of starvation (Geller, 1986; 1989) under fluctuating food level. *Daphnia* in general seems to possess life history parameters which allow rapid exploitation of favourable periods although its responses may not always be optimal over a short time scale (Porter *et al.*, 1983; Threlkeld, 1987). Increased growth potential and regulation of food consumption might be particularly advantageous in small headwater lakes where the terrestrial influence is not buffered by the large volume of the epilimnion, but cause frequent nutrient input pulses markedly affecting the nutrient status. As a consequence algal populations, generally composed of small, fast growing species, also develop temporal maxima. The duration of such events are typically not compatible with the length of the life cycle of large



zooplankton species such as *Daphnia longispina*. In strongly fluctuating environments, a sufficiently dense population of large reproducing *D. longispina* individuals can also obtain an advantage over competing herbivores.

Migrations represent a versatile behaviour by animals to cope with a multitude of different factors distributed unevenly in time and space. Consequently diel migration is a complex behaviour which combines optimised reactions to various constraints encountered by zooplankton. Along with temperature, feeding and avoidance of predation are certainly among the most important factors affecting vertical migrations. Because rather small differences in some parameters – e.g. about 10% in mortality (Vuorinen, 1987; Ohman, 1990) – may have a significant effect on the success of species depending on its behaviour, all ultimate reasons for vertical migration are seldom self evident. A few aspects seem to deserve more emphasis in future studies of vertical migrations. First, more efforts should be taken to study vertical migration of individuals rather than populations. Although that is very difficult, the results should be more unequivocally explainable. Such studies would also yield a better basis to take into account possible individual solutions and genetic shifts in the population along with varying environmental conditions. Second, one should take into account that diel migrations of plankton probably play an essential role in the functioning of the whole ecosystem. Therefore large and intensive efforts with many factors including not only information about the numbers of single migrating species, but also the metabolic rates of animals as well as their food, are needed to more thoroughly understand the migrations of zooplankton. Migrations are dynamic responses to the environment (Ohman, 1990) and such behaviour is an essential part in studying the structure and function of the ecosystems.

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