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DIEL VERTICAL MIGRATION OF ZOOPLANKTON IN A HYPERTROPHIC SHALLOW TEMPERATE LAKE, GERMANY

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ABSTRACT: Zooplankton as important links in the food web of aquatic ecosystems have been studied extensively. In current literature their diel vertical migration (DVM) is a highly discussed issue. In this investigation DVM by zooplankton is studied in a hypertrophic shallow lake in Germany. The objectives of the study were to see if DVM by zooplankton occurs in shallow lakes such as Lake Dagowsee, the possible overlap in DVM of *Leptodora kindtii*, an invertebrate predator, and zoopankton, and the effect of wind action on DVM. It was found out that DVM of zooplankton occurs in Lake Dagowsee despite the limited range of depth for migration, wind action can influence DVM and *L. kindtii* poses a complex situation in relation to DVM behaviour of zooplankton in Lake Dagowsee. Finally, further studies are suggested with regard to DVM variation between different species, size and hybrid groups of Daphnids, and identification of the light sensitive range that can cue DVM of zooplankton and *L. kindtii* in temperate and tropical waters.

Key words/phrases: ***Daphnia* spp., *Diaphanosoma brachyurum*, *Eudiaptomus gracilis*, Lake Dagowsee, zooplankton**

INTRODUCTION

The study on zooplankton has always attracted the attention of limnologists due to their key role in the food web as links between the primary producers and the vast spectrum of invertebrate and vertebrate predators that prey upon them. This ecological niche of zooplankton has also made them key actors in their top-down grazing effect (trophic cascade) that plays pivotal roles in biomanipulation for lake restoration purposes (Carpenter and Kitchell, 1993). Consequently limnologists have not spared efforts to know more and manage zooplankton better in their natural settings for sustainable use of aquatic systems.

In this regard one major step was made when zooplankton seemingly drifting with water current have been known to systematically navigate in aquatic systems guided by various internal conditions and environmental cues with which they have intimately evolved through time. This has been mostly observed in the diel migration patterns of zooplankton for over a century now (Weismann, 1887). In general diel vertical migration (DVM) is a phenomenon that involves most zooplankton species and occurs in both marine and freshwaters (Sekino and Yamamura, 1999). As per the generally accepted predator avoidance hypothesis, zooplankton stay in the cold dark deeper water column during the day to avoid visual predation mostly by fishes and migrate towards the warm food-rich surface water at night using nightfall as their refuge (Zaret and Suffern, 1976; Stich and Lampert, 1981). In so doing zooplankton perform some trade-off by avoiding visual predation during the day and stay in the colder, oxygen and food limited deeper strata reducing their metabolic activities. In other words, upward migration into surface waters at nightfall is nutritionally and thermally favourable but a dangerous environment for zooplankton, while downward migration at daybreak is demographically disadvantageous that must be accepted by the same in order to be safe from visual predation (Lampert, 1993). Hence, the reports made by Weismann (1887) stimulated a milestone change in the understanding of zooplankton since it is a question dealing with tons and tons of migratory microscopic animals that serve as essential links in the food web of aquatic systems. Thus other studies made through the years included Russell (1927), McLaren (1963), Hutchinson (1967), Enright (1977), Enright and Honegger (1977) followed by many others after the 1980s.

The major influencing factors for zooplankton diel migration were predator avoidance (Zaret and Suffern, 1976; Stich and Lampert, 1981; Gliwicz, 1986; Lampert, 1993; Masson *et al.*, 2001; Rhode *et al.*, 2001), chemical cues (Enright and Honegger, 1977; Lampert, 1993; Pijanowska, 1993; Lass *et al.*, 2000; Masson *et al.*, 2001), solar or ultraviolet radiation (Vuorinen *et al.*, 1999; Leech and

Williamson, 2001; Rhode *et al.*, 2001), light (Ringelberg, 1993; 1999; Jensen *et al.*, 1999; Han and Straškraba, 2001), availability of and competition for food (Duval and Geen, 1976; Masson and Pinel-Alloul, 1998; Pearre, 2000), dissolved oxygen (LaRow, 1970; Duval and Geen, 1976; Masson and Pinel-Alloul, 1998; Besiktepe, 2001), temperature (Enright and Honegger, 1977; Ramos-Jiliberto and Zúñiga, 2001), stratification (Masson and Pinel-Alloul, 1998) prey size (Luo *et al.*, 1996; Lass *et al.*, 2000; Robertis *et al.,* 2000; Kornilovs *et al.*, 2001; Cuker and Watson, 2002), pigmentation of zooplankton (Enright, 1977; Rhode *et al.*, 2001), internal conditions or endogenous rhythms (McLaren, 1974; Enright and Honegger, 1977; Sekino and Yamamura, 1999), wind action or turbulence (Stavn, 1971; Patalas and Salki, 1992; Vuorinen *et al.*, 1999; Masson and Pinel-Alloul, 1998; Luo *et al.*, 2000; Masson *et al.,* 2001), diel timing and seasonal effects (Zaret and Suffern, 1976; Enright and Honegger, 1977; Vuorinen *et al.*, 1999; Thompson and Allen, 2000; Masson *et al.,* 2001), turbidity (Masson and Pinel-Alloul, 1998; Roman *et al.*, 2001), salinity (Roman *et al.*, 2001) and generally the effect of combinations of multiple physico-chemical and biological forces (Masson and Pinel-Alloul, 1998; Masson *et al.,* 2001).

In light of the aforementioned general purpose of investigating DVM of zooplankton, the objectives of this study were to gather (i) baseline data on the DVM of zooplankton in the shallow hypertrophic Lake Dagowsee, Germany, (ii) to see the relations between DVM patterns of zooplankton and the cladoceran predator *Leptodora kindtii* and (iii) to see the effect of wind turbulence on DVM of zooplankton in the same lake. In due course, this line of investigation is anticipated to lead to a better understanding of zooplankton that are important links in the aquatic food web and to contribute some knowledge in the effort of extending the survival of macrozooplankton for biomanipulation purposes in both temperate and tropical lakes.

DESCRIPTION OF THE STUDY SITE

Lake Dagowsee, a hypertrophic lake (Koschel *et al.*, 1990), is located at 13^0 04′ E and 53^0 08′ N at an altitude of 60.2 m above sea-level very close to Lake Stechlin of the Baltic Lake District in one of Germany's well-known natural conservation areas (See figure drawn to scale in Brook Lemma *et al.*, 2001). This lake has a surface area of 0.3 km^2, a maximum depth of 9.5 m, mean depth of 5 m and volume of 8.2 x 106 m^3, with conductivity of 340 µS cm^{-1}, pH range of 7.2 – 9.2 and PO_4-P concentration of 114 mgL^{-1} (Brook Lemma *et al.*, 2001). The eutrophication of Lake Dagowsee dates back to the 1960s when breeding of carp and ducks was carried out in it (Koschel *et al.*, 1990). This was interrupted as one of the first and major restoration measures taken in 1972. Soon after, other ecological studies have been conducted on this lake (See Dittrich *et al.*, 1993 and Brook Lemma, 1997; Brook Lemma *et al.,* 2001) to restore the lake for the safe use of its fishery resources and summer recreation.

MATERIALS AND METHODS

Routine depth measurements of temperature and dissolved oxygen have been made at 0.5 m intervals from the surface down to the sediment. Water transparency was measured during daylight hours using a standard white painted Secchi disc of 20 cm diameter. Meteorological data for the days of sampling were collected from the Deutsche-Wetter Dienst (DWD), Neuglobsow, Germany.

Zooplankton samples were collected at three occasions, specifically on 12–13. 06.; 26–27. 06. and 10–11. 07. 2002 each time at a six-hour interval to complete a diel cycle. The samples were taken using a Schindler-Patalas Trap of 15 liters capacity equipped with 55 µm mesh to capture small zooplankton. This was operated from a centrally located station (9 m deep) at five different depths of 0 m, 2 m, 4 m, 6 m and 8.5 m. The samples were stored in 250 ml plastic bottles fixed with 4% sugar-formalin solution. Zooplankton identification, counting and length measurements were made from at least three homogenized 10 ml samples in a sedimentation chamber under an inverted Olympus microscope at a magnification of 8x1.5x4 (Kasprzak *et al.,* 1993). Mean body lengths of 30 to 40 individuals of *Daphnia* spp., *Diaphanosoma brachyurum* and *Eudiaptomus gracilis* from each sample were used to calculate cell volume from simple geometric models as a measure of biomass (Børsheim and Andersen, 1987).

RESULTS

Temperature and dissolved oxygen depth measurements recorded at the three sampling dates at six-hour intervals were averaged with standard deviations as shown in Figs 1 and 2. With the exception of midnight, transparency of lakewater measured at 6, 12 and 18 hours of each sampling day were averaged and the results are illustrated in Fig. 3.

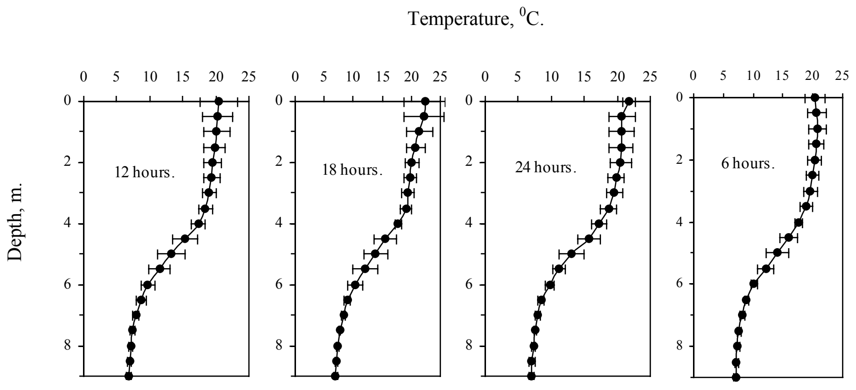

Fig. 1. Mean temperature depth profiles with standard deviation measured on 12–13. 06., 26–27. 06. and 10–11. 06. 2002, Lake Dagowsee.

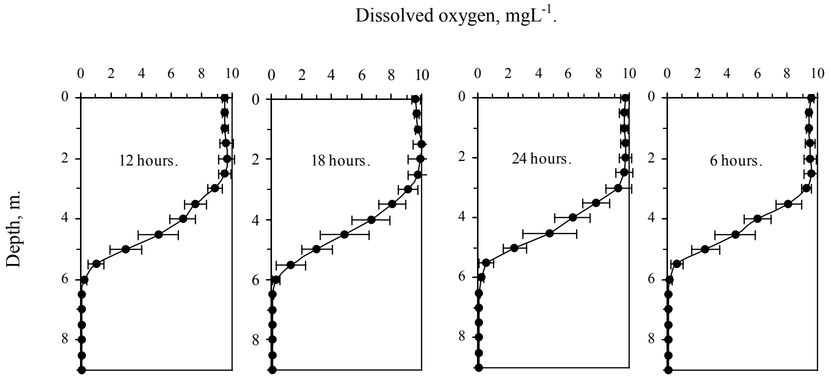

Fig. 2. Mean dissolved oxygen depth profiles with standard deviation measured on 12–13. 06., 26–27. 06. and 10–11. 06. 2002, Lake Dagowsee.

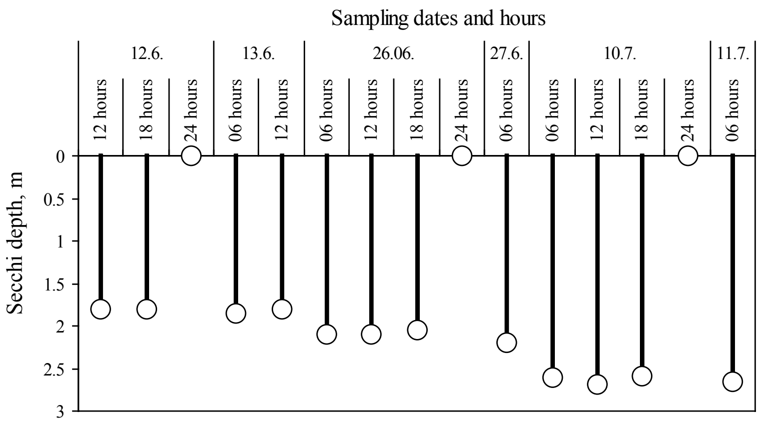

Fig. 3. Secchi depth measurements in year 2002, Lake Dagowsee.

With regard to zooplankton that inhabit Lake Dagowsee, *Daphnia cucullata*, *D. hyalina*, *Diaphanosoma brachyurum*, *Ceriodaphnia* sp., *Eudiaptomus gracilis*, and a number of copepods were recorded in the samples collected. These were found to be similar to previous work by Brook Lemma (1997) and Brook Lemma *et al.* (2001). Identification and head counts of *Leptodora kindtii* caught in the trap were also made at the same time.

The biomass of *Daphnia* spp. as a group has been calculated (Fig. 4), while that of other zooplankton, such as, *Diaphanosoma brachyurum* (Fig. 5), *Eudiaptomus gracilis* (Fig. 6) and *Leptodora kindtii* (Fig. 7) was calculated separately by species. Using the weather data collected from DWD, Fig. 8 has been constructed to see the influence of wind action (turbulence) on zooplankton migration.

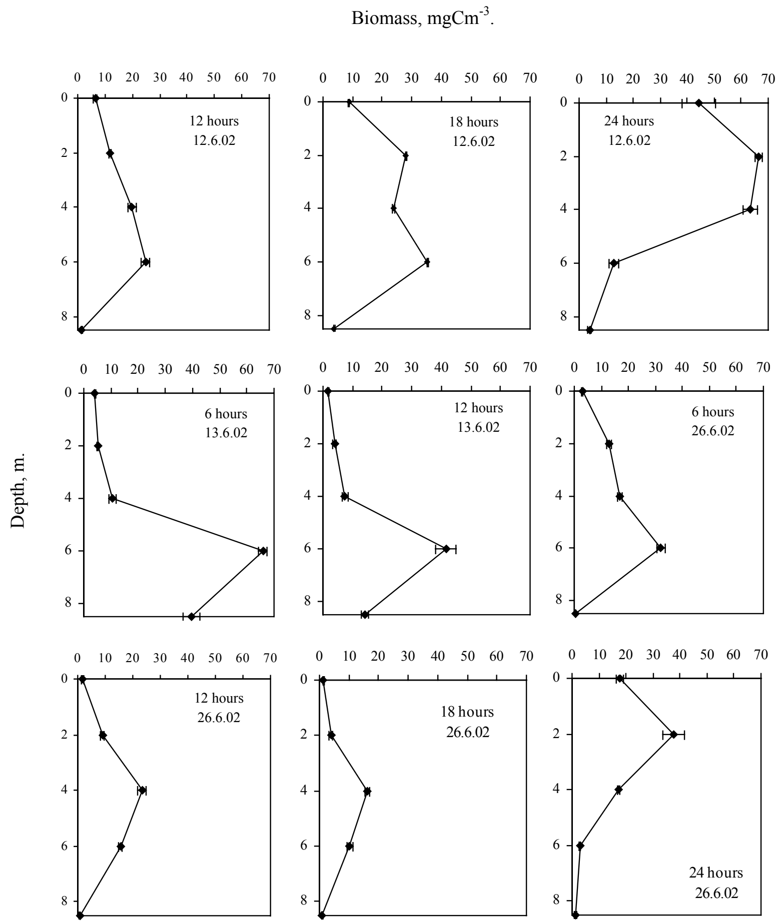

Fig. 4a. Diel vertical distribution of *Daphnia* spp., Lake Dagowsee (June 12,13 and 26, 2002).

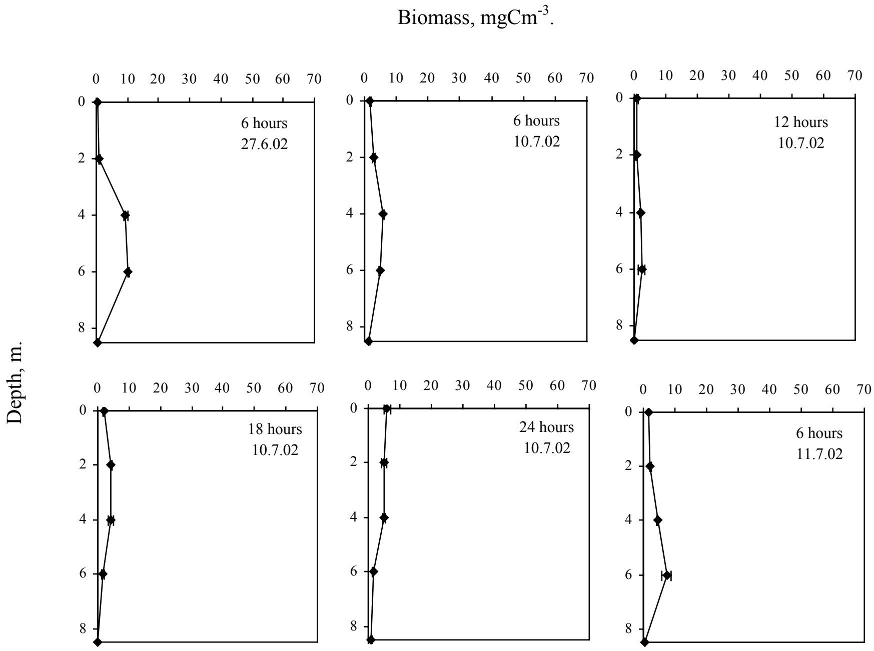

Fig. 4b. Diel vertical distribution of *Daphnia* spp., Lake Dagowsee (June 27, July 10 and 11, 2002).

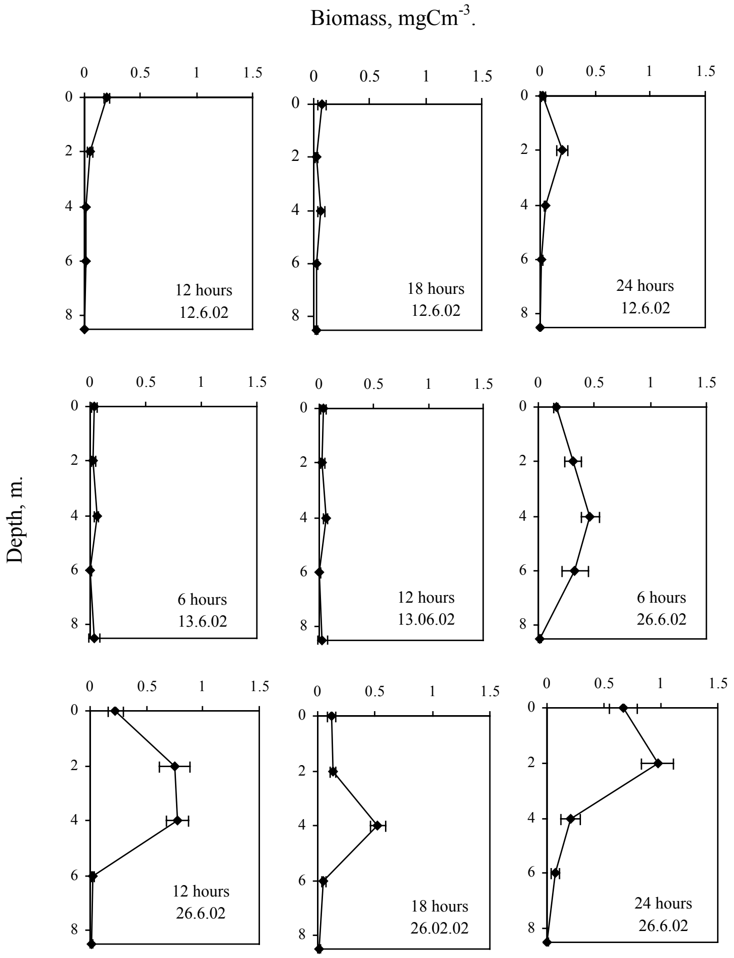

Fig. 5a. Diel vertical distribution of *Diaphanosoma brachyurum*, Lake Dagowsee (June 12, 13 and 26, 2002).

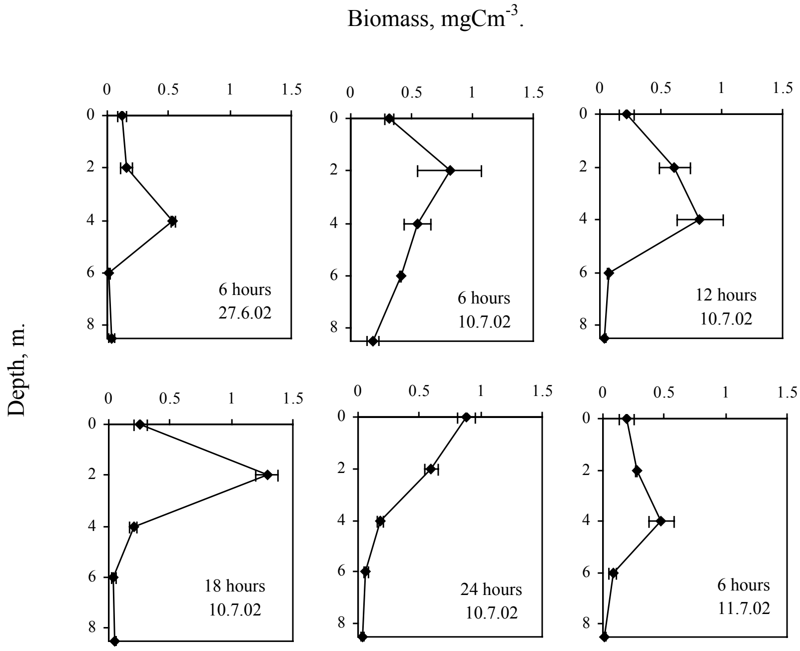

Fig. 5b. Diel vertical distribution of *Diaphanosoma brachyurum*, Lake Dagowsee (June 27, July 10 and 11, 2002).

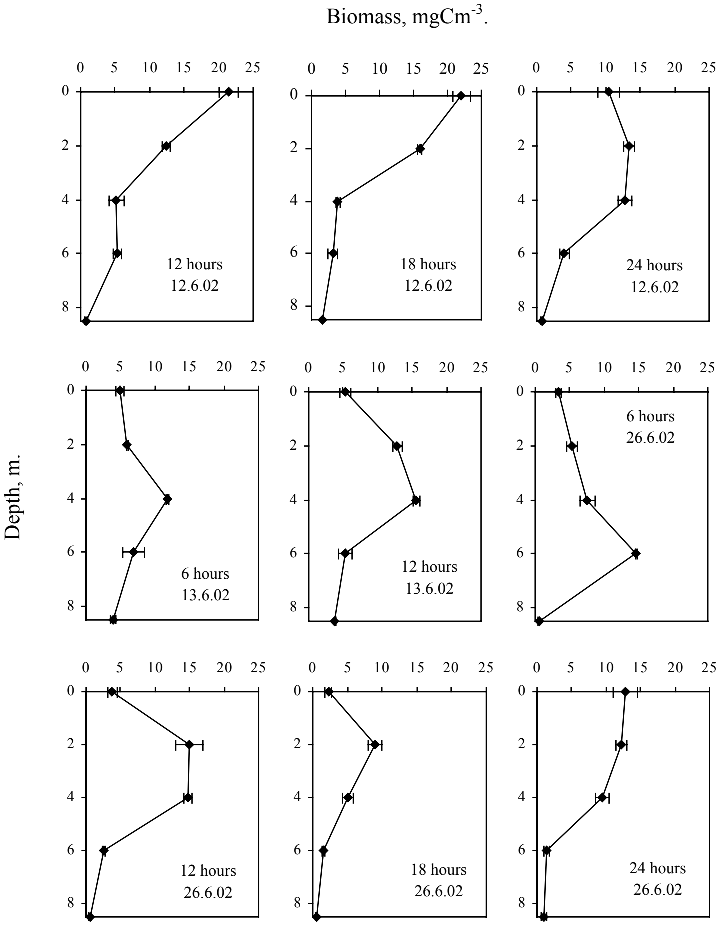

Fig. 6a. Diel vertical distribution of *Eudiaptomus gracilis*, Lake Dagowsee ((June 12, 13 and 26, 2002).

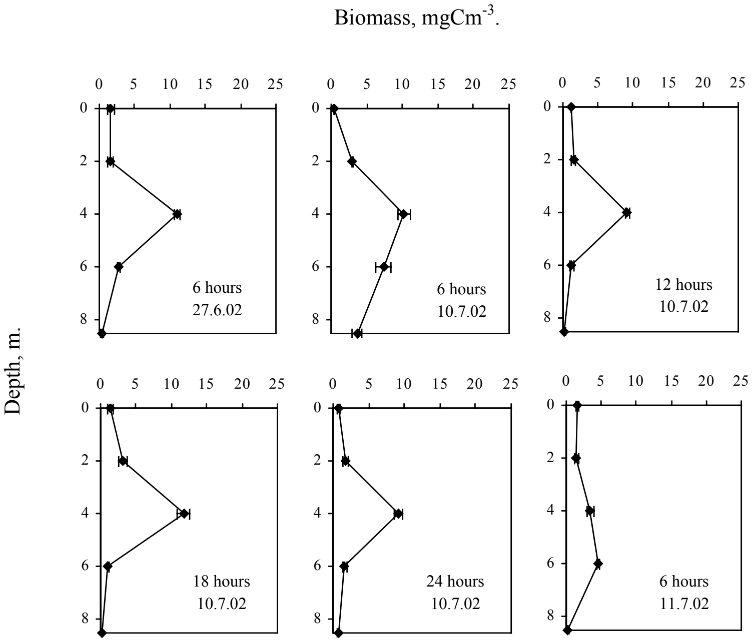

Fig. 6b. Diel vertical distribution of *Eudiaptomus gracilis*, Lake Dagowsee (June 27, July 10 and 11, 2002).

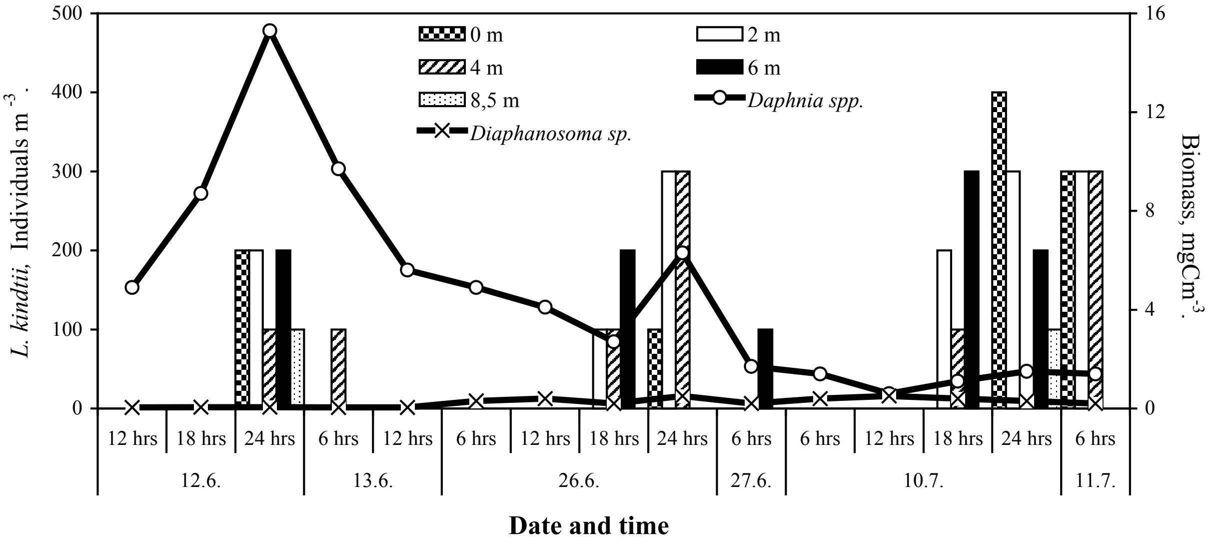

Fig. 7. Diel vertical distribution of *Leptodora kindtii*, as compared to total biomass of *Daphnia* spp. and *Diaphanosoma brachyurum* in year 2002, Lake Dagowsee.

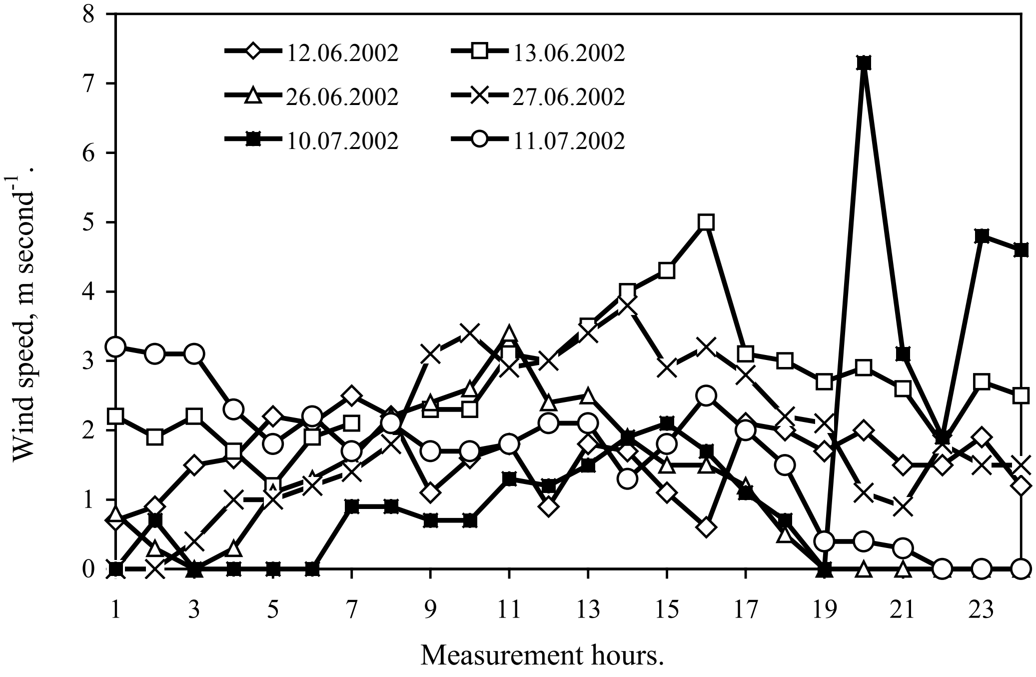

Fig. 8. Wind speed on the sampling dates in Lake Dagowsee area.

Over the three-day sampling period (12–13. 06.; 26–27. 06. and 10–11. 07. 2002) it was recorded that Daphnids migrated to the surface at midnight (24 hours) with a biomass range of 66.5, 37.6 and 5.9 mgCm^{-3} in the respective days. The highest biomass of daphnids for each of the respective sampling days was limited to the upper 4 m water column, while their biomass progressively decreased below that depth. The reverse was recorded during daylight at 6 and 12 hours, when daphnids were concentrated in deeper waters below 4 m with concentrations of 65.9, 32.1 and 7.4 mgCm^{-3} in the respective sampling days. At other hours of sampling daphnids seemed to be more evenly distributed in the water column as they migrate on their way up or down. *D. brachyurum* seemed to show similar patterns as the daphnids at midnight and daylight hours. The biomass recorded at midnight for the respective sampling days were 0.2, 1.0 and 0.9 mgCm^{-3}. Unlike the daphnids, the migration range of *D. brachyurum* seemed to be limited to the upper 4 m of the water column. The calanoid *E. gracilis* had maximum concentrations of 13.4, 12.8 and 0.8 mgCm^{-3} during midnight, although the low concentration on the last sampling date is accounted for in the discussion along with the weather data collected from DWD, Neuglobsow. *L. kindtii*, commonly found in such hypertrophic shallow lakes (Palmer *et al*., 2001), also showed diel migration pattern by appearing in the upper water column during the night. Its maximum concentrations at 0 m, 2 m and 4 m depths were recorded as 200, 300 and 400 individuals m^{-3} of lakewater in the respective depths and sampling days. *L. kindtii* seemed to disappear from the water column between 6 and 18 hours, as there were apparently no individuals caught in the trap during this period.

DISCUSSION

The temperature pattern in Lake Dagowsee was similar to previous records (Brook Lemma, 1997; Brook Lemma *et al*., 2001) with distinct stratification where the epilimnion extended up to 3 m depth and the hypolimnion was below 6 m (Fig. 1). Temperature declined in the metalimnion (3 to 6 m) from an average epilimnetic temperature of 21.25 ^{0}C to about 10°C at the upper limit of the hypolimnion. Temperature in the hypolimnion decreased very slowly from 10°C to around 6 ^{0}C. There was a clear temperature difference of at least 14 ^{0}C between the surface and the bottom 9 m. Likewise, dissolved oxygen in Lake Dagowsee showed stratification that more or less corresponded to the temperature pattern in terms of depth profile (Fig. 2). The epilimnion maintained dissolved oxygen concentration of around 10 mgO$_2$L^{-1}, the metalimnion decreased from 10 mgO$_2$L^{-1} to below 1 mgO$_2$L^{-1} and the hypolimnion was anoxic with oxygen closing up to nil below 6 m. Transparency as measured by Secchi disc ranged from 1.8 m to about 2.4 m in Lake Dagowsee (Fig. 3). When this was compared to previous Secchi depth measurements of 2.85 m - 4.75 m for Lake Dagowsee (Brook Lemma, 1997; Brook Lemma *et al*., 2001), the present situation is much shallower for the season indicating that clarity as a measure of water quality has deteriorated in this lake.

These three factors are known to have important impacts on zooplankton migration. The warm, oxygen and food rich surface waters are advantageous when visited by zooplankton and the cold, oxygen and food poor waters below 6 m are metabolically unfavorable at periods when zooplankton shelter themselves from predation at this depth (Zaret and Suffern, 1976; Gliwicz, 1986; Lampert, 1993; Masson *et al*., 2001; Rhode *et al*., 2001). Conversely, with less clarity in water, zooplankton get better refuge from vertebrate visual predation in the upper strata of the water column as recorded in Lake Kuriftu (Brook Lemma *et al*., 2001). Consequently, it can be said that with increasing turbidity and shallower Secchi depth, light will not provide the proper intensities to cue vertical migration behavior that can be induced by photoperiod (Roman *et al*., 2001).

In Lake Dagowsee the migration of daphnids to the surface during the night and their sinking to deeper waters during daylight can actually be attributed to the effect of light. By such behavior zooplankton are known to use resources very efficiently while at the same time playing it safe from predation by vertebrates (McLaren, 1963; 1974; Enright, 1977; Gliwicz, 1986), and guaranteeing the continuity of their species. Zooplankton by staying in the dark for 24 hours (in deeper waters by daylight), they avoid visual predation by vertebrates. For this activity, they pay the price of staying in the cold, food and oxygen poor depths of Lake Dagowsee enduring hunger and metabolic sacrifices as a trade-off for staying alive and maintain their generations, as described in the hypothesis of avoidance of visually oriented predation (Zeret and Suffern, 1976; Stich and Lampert, 1981; Neill, 1990; De Meester *et al*., 1995). However, this behavior is paradoxical if one looks at the DVM of *L. kindtii* in Lake Dagowsee, which assumes similar DVM behavior as daphnids (Fig. 4) and prey upon daphnids and other zooplankters (Palmer *et al*., 2001). This invertebrate predator presumably follows such migration pattern to avoid vertebrate visual predation by daylight (Liu *et al*., 2002). For daphnids the trend of natural selection in Lake Dagowsee is apparently to select the better of two evils, whereby they avoid the stronger vertebrate visual predation and endure the consequences of the weaker invertebrate predation in the dark, which the invertebrate predator launches apparently by way of chemical cues. Incidentally, vertebrate predation is known to be stronger from the experience of many tropical waters where year-round vertebrate predation has completely wiped out daphnids (Fernando 1994, Brook Lemma *et al.*, 2001). In temperate waters daphnids use DVM to avoid vertebrate visual predation, somehow survive invertebrate predation and reappear each year in early spring, although the trend of natural selection with daphnids is to avoid all forms of predation pressures as much as possible. This was observed by Masson and Pinel-Alloul (1998) who stated that zooplankton in Lake Geai, Quebec uniquely evolved inverse DVM to avoid invertebrate predation by *Chaoborus* sp. in the absence of vertebrate visual predation. In Lake Dagowsee, the price daphnids pay for migrating along with the invertebrate predator is observed when populations of *L. kindtii* increases and that of daphnids declines as summer progresses (Fig. 4, see also Palmer *et al.*, 2001). Another aspect of *L. kindtii* DVM is that it tends to migrate up the water column earlier at dusk and down later at dawn than daphnids, as observed in the last two sampling periods (Figs 1 and 4; see also Palmer *et al.*, 2001; Liu *et al.*, 2002). This indicates that *L. kindtii* protected by its transparent body from vertebrate visual predation (DeBernardi and Giussani, 1975) occupies strategic time and space, to await for zooplankton on their way up and down, making it an efficient predator with positive returns for the catch effort it expends.

Having said this, it must be obvious that all daphnids do not perform DVM by virtue of being daphnids. In Lake Dagowsee, closer observation of DVM by daphnids has revealed that those that migrate most are the large-sized individuals and gravid females (Fig. 9; see also Lampert, 1993 and Besiktepe, 2001), while the juvenile and small daphnids stay in the upper water column by daylight, what Cuker and Watson (2002) referred to as inverse DVM. These small-sized or stunted daphnids find refuge from vertebrate predation in their smallness (Slusarczyk, 1997; Brook Lemma *et al.*, 2001) and benefit by staying in the warm, food and oxygen rich surface waters, as described by the size efficiency hypothesis (Brooks and Dodson, 1965; Kerfoot and Sih, 1987; Gliwicz, 1994). DVM therefore seems to be an evolutionary trend that gradually unfolds as the age and sizes of daphnids increases. Therefore DVM of zooplankton is not considered as a fixed behavior but flexible (Lampert, 1993), as observed (i) in their direct DVM in the presence of vertebrate predation, (ii) inverse DVM in the absence of vertebrate predation but presence of invertebrate predation and (iii) variation of DVM in different size groups and species types (Stich and Lampert, 1981).

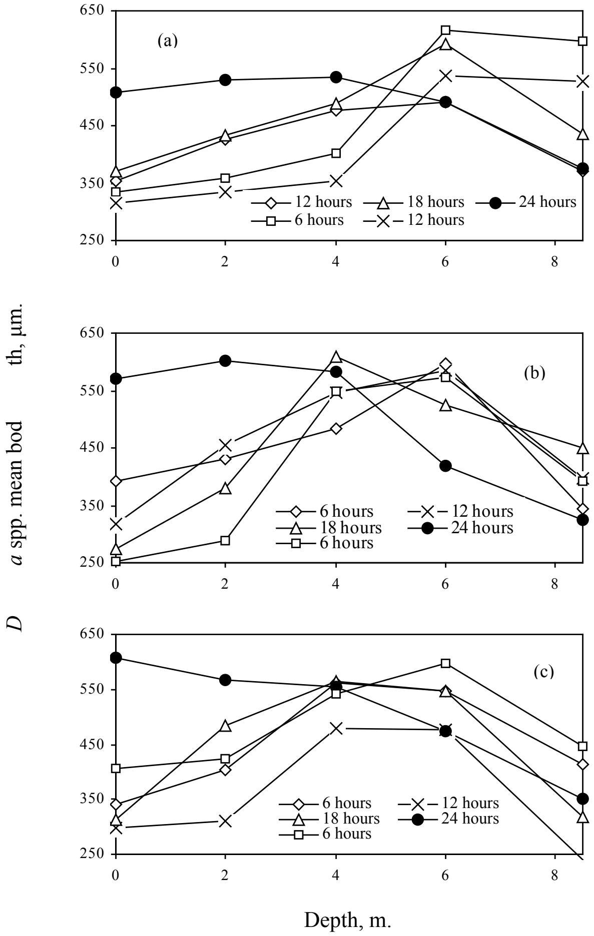

Fig. 9. Mean body length of *Daphnia* spp. on (a) 12–13. 06. (b) 26–27. 06. and (c) 10–11. 07. 2002, Lake Dagowsee.

DVM of *D. brachyurum* became more pronounced as summer progressed and their population started to increase (Fig. 5; See also Brook Lemma, 1997). On 12 .06., 26. 06. and 10.07.02 at 24 hours *D. brachyurum* increasingly migrated to the surface. During daylight it seemed to retreat to deeper waters mostly down to about 4 or 5 m, while the daphnids migrated to 6 m and below. Given the small size of *D. brachyurum* it is apparently logical to assume that it can escape the visual predation effect of vertebrates by retreating to reasonable subdued light situation of 4 or 5 m depth of turbid Lake Dagowsee and still benefit from warmer waters with richer food and oxygen supply rather than going into deeper, colder and anoxic waters with limited amount of food. This seems to be in agreement with the logical conclusion that the largest daphnids migrate most, while the juvenile, small and stunted ones stay in upper waters.

Similarly, DVM behavior of *E. gracilis* has been recorded in Lake Dagowsee, except on 10.07.02 at 24 hours. At this time *E. gracilis* migrated into deeper waters. The explanation for this behavior was the sudden change in the climate of Lake Dagowsee area at that sampling period when the wind speed changed from 0 m second^{-1} at 19 hours to 7.5 m second^{-1} at 20 hours and then to 5 m second^{-1} at 24 hours (Fig. 8). As shown in the same figure all the sampling hours were under relative quietness except at this night when a sudden strong windstorm struck the lake. Given the fast reaction and speed of *E. gracilis* (Masson *et al.*, 2001), it migrated into deeper waters of 4 m depth under this circumstance. *E. gracilis* has also been observed to react quickly by migrating to the surface when during daylight heavy cloud cover followed with rain shower came and the water column was subject to subdued light, such as at 12 and 18 hours of 12.06.02 (Fig. 6), while still daphnids and *D. brachyurum* remained below, as they have slow reaction time (Lieschke and Closs, 1999).

In Lake Dagowsee zooplankton showed DVM induced mainly by light but with the apparent purpose of avoiding vertebrate visual predation. The predation by invertebrates posed a complex situation in the evolution of DVM behavior in zooplankton and warrants further research. Investigations should also be directed into the variation in DVM between different size-groups of daphnids and daphnid species. Zooplankton DVM induced by light can be further investigated in tropical waters where solar radiation and length of daylight are more or less constant through most of the year. Instead of expressing the timing of downward migration as dawn and upward migration as dusk, investigations should be conducted to find out the most probable minimum light intensity required to cue DVM reactions in zooplankton for the conditions of a specific lake. Further, using this minimum light intensity required to cue DVM, it may be possible to develop light intensity index in relation to Secchi disc measurements for various lake conditions. If such knowledge is acquired it may be possible to initiate zooplankton migration for any specific purpose, be it to ensure their continued existence through the seasons or use them in accordance with the trophic cascade hypothesis for lake restoration management practices.

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