# DIEL VERTICAL MIGRATION OF *DAPHNIA BARBATA* IN A SHALLOW TROPICAL LAKE, ETHIOPIA

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**ABSTRACT:** Diel vertical migration (DVM) has rarely been studied in tropical fresh waters such as in Ethiopia, East Africa. However, its understanding is pivotal in lake ecosystem management as fresh waters are the means of all sorts of livelihood for populations in the tropics. It was therefore necessary to study various aspects of the ecology of these waters where zooplankton take their share. As a result DVM of *Daphnia barbata* was studied in two consecutive years to reflect on the tropical DVM scenario by sampling the lake by daylight and darkness using traps to collect water from various depths. The results showed that normal DVM takes place in Lake Kuriftu with ascent of *D. barbata* at dusk and descent at dawn. This behavior is discussed in light of tropical high water temperatures from top to bottom, dissolved oxygen stratification and other related parameters and comparisons have also been made with classical temperate lake scenarios with recommendations for future work for the sake of sustainable use of tropical freshwater ecosystems.

Key words/phrases: African lakes, Ethiopia, Lake Kuriftu, shallow lakes, tropical lakes

## INTRODUCTION

The ecological niche zooplankton occupy has made them key actors in their top-down grazing effect (trophic cascade) that plays pivotal role 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 (Brook Lemma, 2004). 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 evolved through time (Brook Lemma, 2004). One such aspect of zooplankton navigation is their diel vertical migration (DVM) studied since the time of Weismann (1887) to date. DVM is still highly debated in the literature with prominent articles such as those by Stich and Lampert (1981); Gliwicz (1986); Lampert (1993); Lampert *et al.* (2003); Brook Lemma (2004); Kessler and Lampert (2004); Tsui (2006); Blachowiak-Samolyk *et al.* (2006), and many others. Most of these studies were conducted in temperate lakes and oceans. Information on zooplankton DVM from tropical waters is apparently lacking.

Unlike temperate lakes that are closed by ice cover in winter, tropical freshwater systems are known to be open throughout the year due to the non-limiting nature of temperature, and hence zooplankton are exposed to apparently non-stop visual predation particularly by fishes throughout the year. Tropical fishes on their part have versatile feeding behavior (Fernando, 1994; Kornilovs *et al.*, 2001; Gliwicz, 2005) where there are species that prey upon macrozooplankton when they are available at certain seasons and shift to other modes of feeding, ranging as far as directly grazing on phytoplankton at other seasons of the year (*e.g.*, *Oreochromis niloticus*) (Nilssen, 1984; Fernando, 1994; Brook Lemma *et al.*, 2001). Lake Kuriftu as described in Brook Lemma (1997) and Brook Lemma *et al.* (2001) presented the ideal scenario in which *Daphnia barbata* flourished despite the presence of planktivores and the year-round predation pressure by simply finding their refuge in the highly turbid water of the lake with Secchi depth of only 20 cm in 2001 (Brook Lemma *et al.*, 2001). Furthermore, it should be stated that the predation impact of *O. niloticus* is enhanced in tropical waters by the frequent reproductive capacity of the fish and the consequent predation impact of high biomass of 0+ fishes on daphnids (see Flik, 2000).

This work therefore was set out to firstly study if DVM by macrozooplankton takes place in tropical freshwater systems as described by the above-cited authors, particularly according to the generally

accepted visual predator avoidance hypothesis. Secondly, it was also interesting to see if DVM takes place in such shallow turbid tropical lakes where mixing is as frequent as the passage of day and night, which may imply that there is no need of performing DVM (particularly ascending to the surface in dark hours) if food, oxygen, adequate temperature, *etc.* are available at all levels of the water strata of such lakes.

### The study site

Lake Kuriftu is an artificial lake originally formed by diverting seasonally running waters into an empty crater over 30 years ago. At present it is a well-established lake with a maximum depth of 6 meters and surface area of 0.4 km² (Brook Lemma, 1997; Brook Lemma *et al.*, 2001) (Fig. 1). The specific location of the lake (39°00'E and 09°00'N; at an altitude of 1860 m above sea-level) is some 50 km south of Addis Ababa in a locality known as Babogaya found in the outskirts of the town of Bishoftu (previously known as Debre Zeyt) (Fig. 1). This region is well known in the literature for its crater lakes such as Lakes Hora-Kilole, Hora-Arsedi (BeteMengist), Bishoftu-Guda (Babogaya or Pawlo) and Hora-Hoda (Arenguade).

## MATERIALS AND METHODS

Routine in-depth measurements of water temperature, dissolved oxygen and conductivity were recorded by day and night at 0.5 meters intervals from the surface down up to the sediment from a central sampling station of about 6 meters depth. During the day hours Secchi depth was measured using a metal disk of 20 cm diameter with black and white quarters.

Zooplankton were collected using Schindler-Patalas volume sampler of 15 liters capacity equipped with 55 µm mesh. This was operated from a central station to sample zooplankton from 0 m, 2 m and 5 m of the water column by day and night at approximately 5 to 6 hours intervals. Zooplankton samples were stored in 250 ml plastic bottles fixed with 4% sugar-formalin solution. *D. barbata* counting and length measurements were made from at least three homogenized 10 ml sub-samples in a sedimentation chamber under inverted microscope (Kasprzak *et al.*, 1993). Mean body length of *Daphnia barbata* of 30 to 40 individuals from each sample were used to calculate bio-volume from simple geometric models as a measure of biomass (Børsheim and Anderson, 1987; Brook Lemma, 2004).
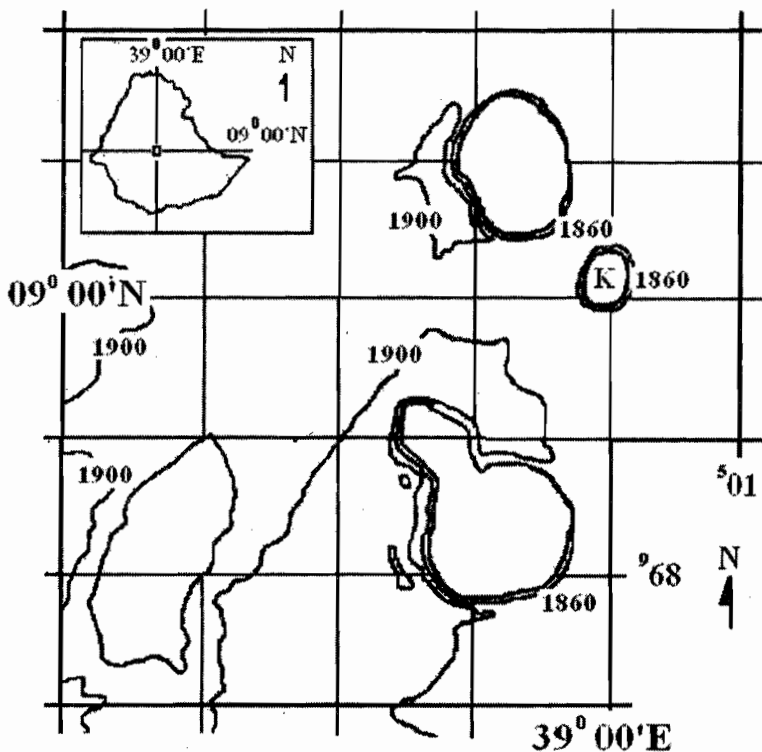


Fig. 1. Location of the study site with Lake Kuriftu indicated by the letter K and two crater lakes (to the north Lake Bishoftu-Guda and to the south Lake Hora-Arsedi). The figures by the lakes indicate their altitude above sea-level. The inset shows lake location in Ethiopia (Modified from 1975 map of the Ethiopian Mapping Agency, Addis Ababa, scale 1:50 000).

During the first sampling on 26.03.2001 water samples were collected from the surface and close to the sediment at 6 meters in opaque one-liter bottles with tight screw caps for water chemical analysis. The samples were immediately deep-frozen until analysis within one week. All the analyses were conducted at the National Soil Research Center of the Ethiopian Agricultural Research Organization, Addis Ababa, using the methods described by Greenberg and Franson (1981) and Pawels *et al.* (1992).

## RESULTS

Temperature, dissolved oxygen and conductivity (the latter at second sampling period) depth measurements were recorded at 0.5 m intervals from a central sampling station and averaged with standard errors as shown in Figs 2, 3 and 4. With the exception of night sampling periods, transparency measurements of lakewater were taken by day and averaged (Fig. 5).
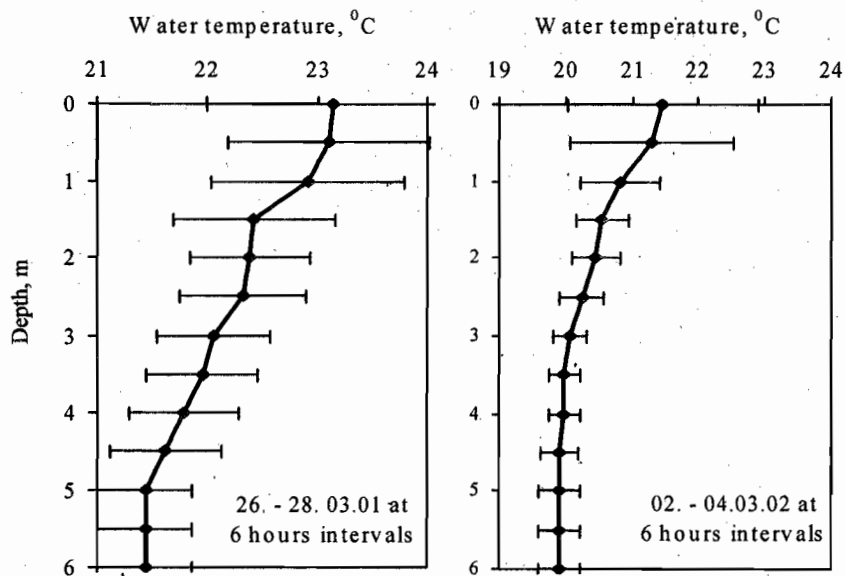


Fig. 2. Depth profile of water temperature from 10 and 9 observations in 2001 and 2002, respectively, with standard error bars, Lake Kuriftu.
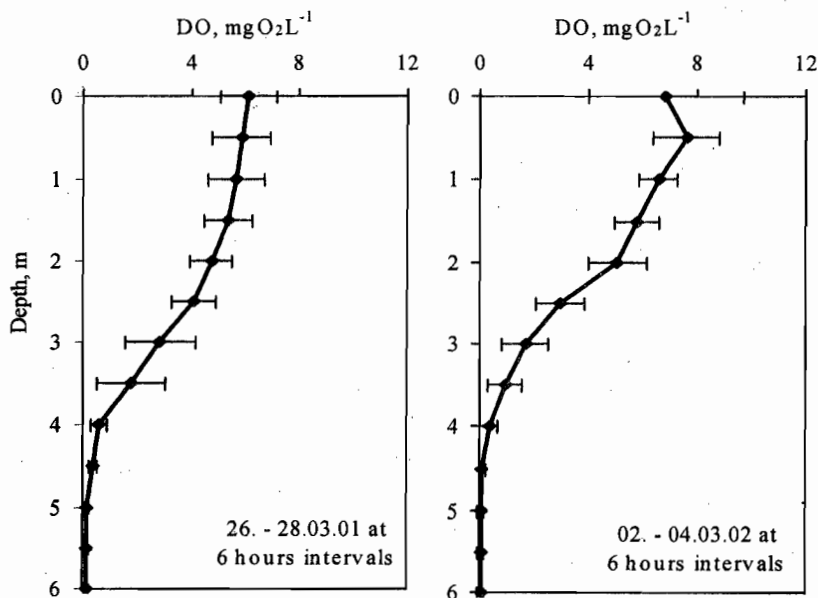


Fig. 3. Depth profile of dissolved oxygen from 10 and 9 observations in 2001 and 2002, respectively, with standard error bars, Lake Kuriftu.
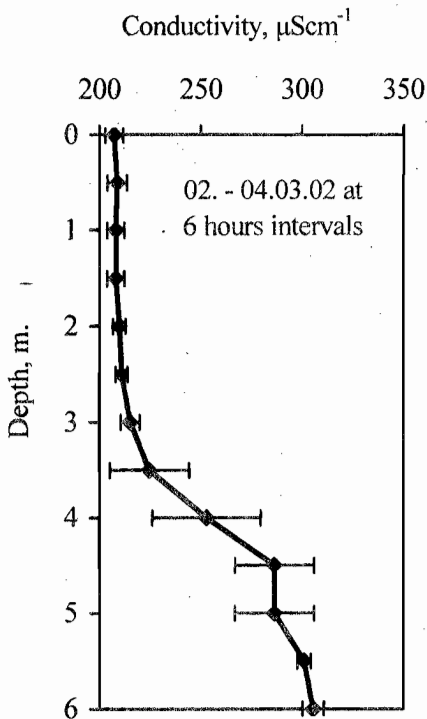
Conductivity, μScm$^{-1}$



Fig. 4. Depth profile of conductivity from 10 and 9 observations in 2001 and 2002, respectively, with standard error bars, Lake Kuriftu.
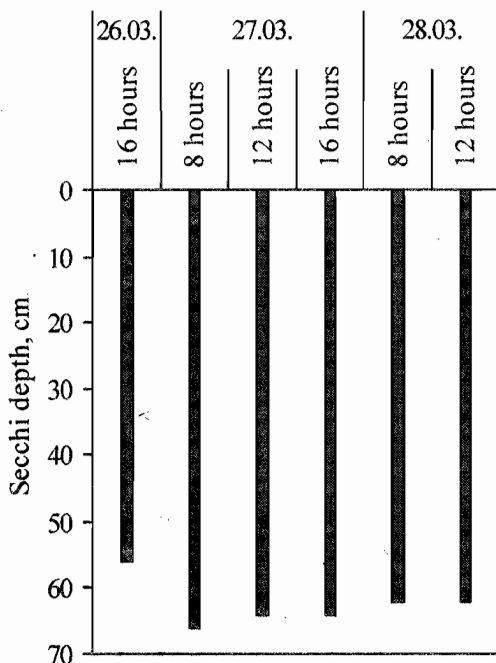


Fig. 5. Mean Secchi-disk depth profile measured at daylight hours, Lake Kuriftu.

Biomass of *Daphnia barbata* sampled at daylight and night hours from different depths are shown in Fig. 5. Over the six days of sampling period,

three days in 2001 and another corresponding three days in 2002, it was recorded that daphnids migrated to the surface by night with a biomass range of 20–29 mgCm$^{-3}$ during the first sampling from 26 to 28 March 2001 and 400–600 mgCm$^{-3}$ during the second sampling from 02 to 04 March 2002. The highest biomass of daphnids during dark hours for each of the respective sampling days was limited to the upper 2 m of water column, while their biomass progressively decreased below that depth. The reverse was recorded during daylight at 9, 12 and 18 hours, as the case may be, when daphnids were concentrated in deeper waters at about 2 m and below (Figs 6 and 7). As in the studies of temperate lakes, the mean body lengths of the individuals indicate that the large bodied *D. barbata* perform most of the normal DVM, while the small-bodied ones either remain at the surface or perform reverse DVM (Fig. 8a). The only discrepancy to normal DVM was observed on 03.03.2002 at 21 hours where large-bodied individuals were found at all depths of sampling (Fig. 8b).

## DISCUSSION

Temperature in this shallow lake was not limiting at all depths of the water column where it has remained above 20°C during the study period (Fig. 2a and b). This is quite different to the scenario in temperate lakes where water temperature varied from 23°C at the surface to about 4°C at 8.5 m (*e.g.,* Brook Lemma, 2004; Park *et al.,* 2004) affecting the growth rates of daphnids to significant levels (Ringelberg, 1999; Ramos-Jiliberto and Zúñiga, 2001; Park *et al.,* 2004). This apparently allows tropical daphnids to circumvent those physiological trade offs encountered in temperate waters that could arise due to reduced temperature at their descent during moon or daylight hours.

The wide range in the standard error bars for water temperature particularly during the first sampling period (26.–28. 03 2001) may indicate that there was substantial air temperature variation between the daylight and dark hours of the sampling days, coupled with some mixing at least in the upper half of the water column of Lake Kuriftu (Fig. 2). Despite the shallowness of the lake, mixing did not seem to reach the deepest layer of 6 m as seen from the unchanged anoxic situation and relatively higher conductivity of water columns below 3.5 or 4 m during the study periods (Figs 3 and 4).
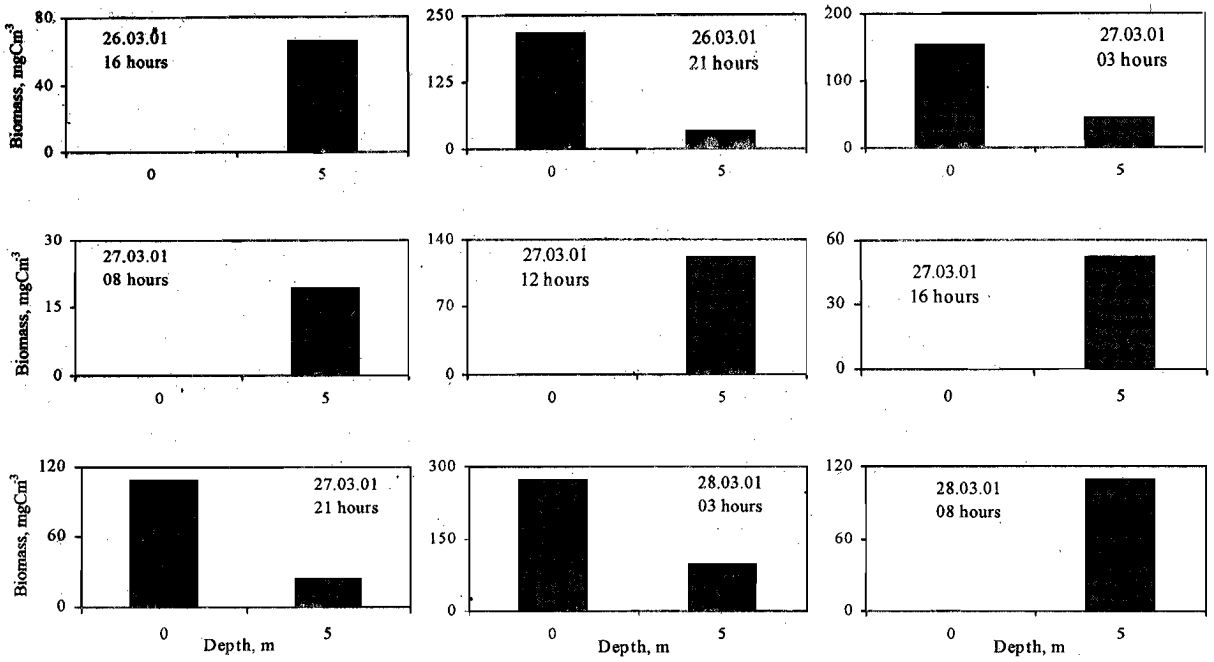
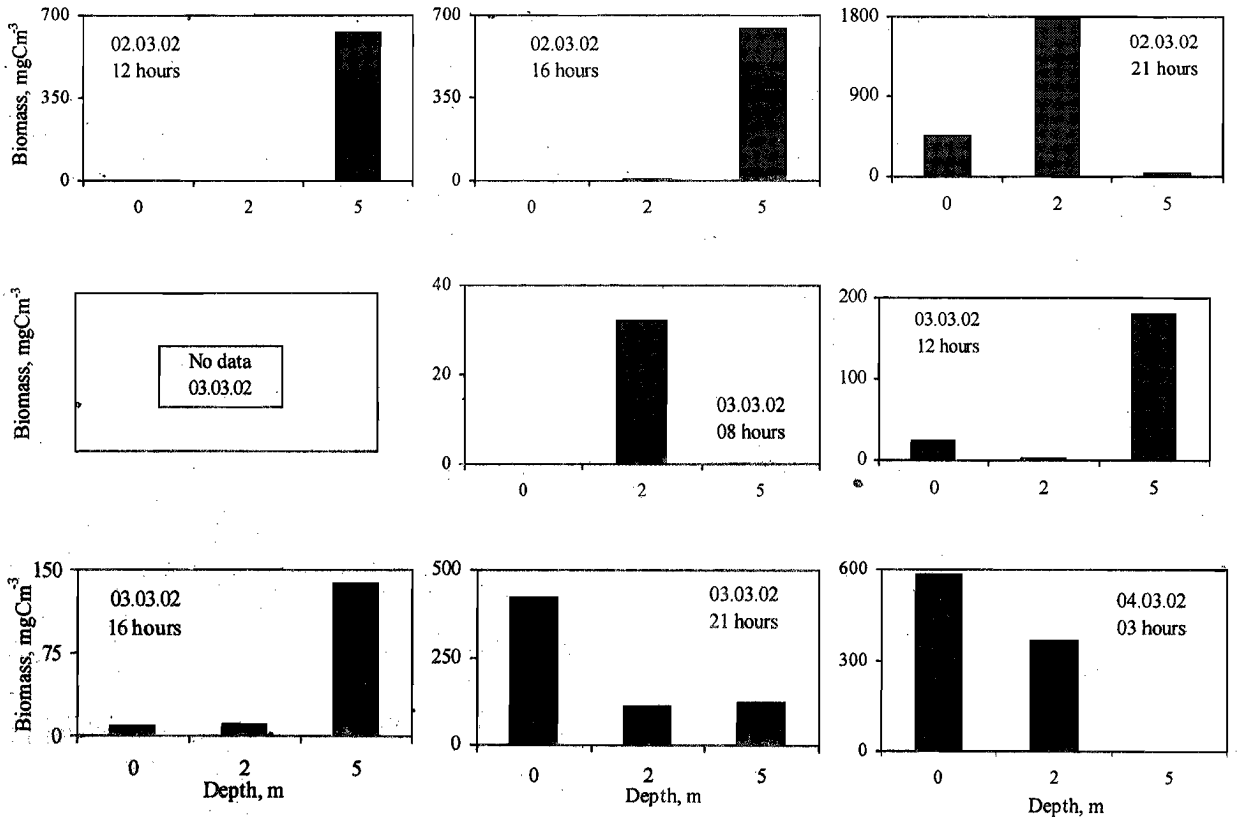Fig. 6. Diel vertical distribution of *Daphnia barbata* in 2001, Lake Kuriftu.



Fig. 7. Diel vertical distribution of *Daphnia barbata* in 2002, Lake Kuriftu.
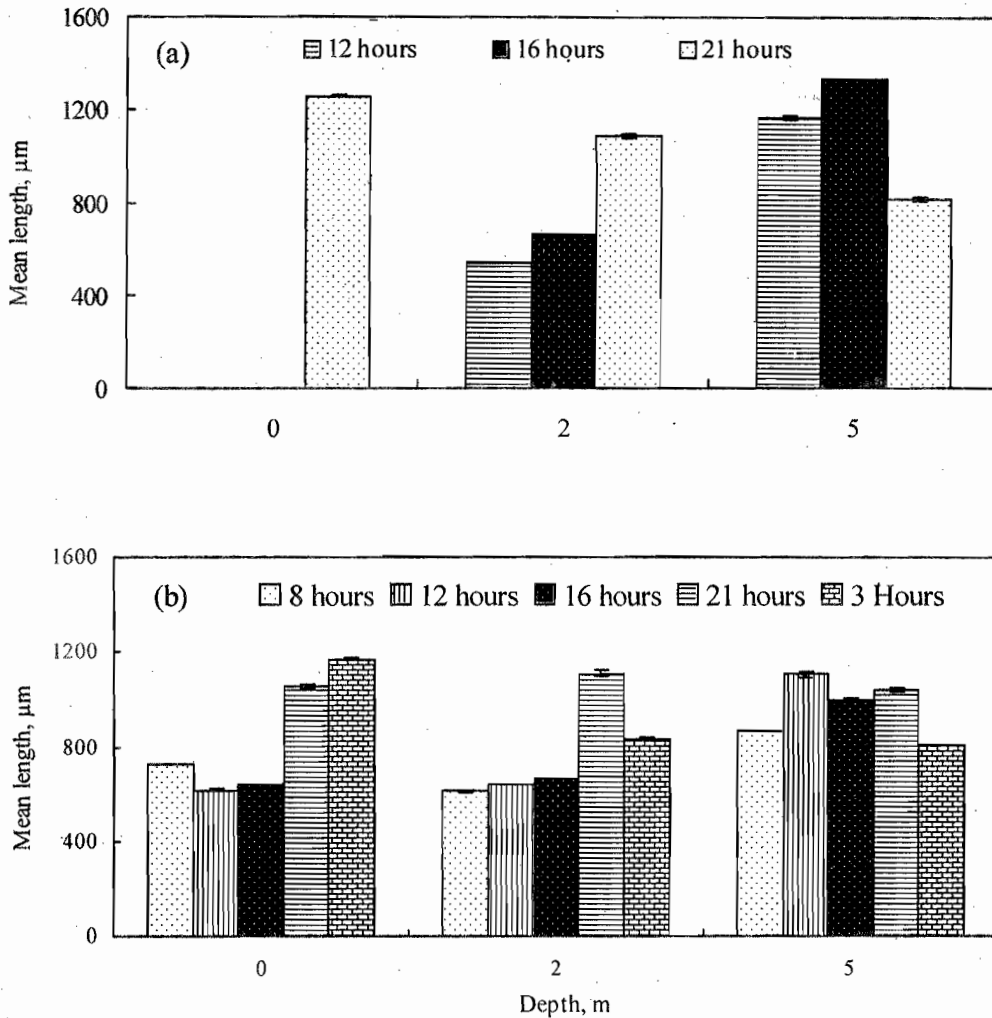
Fig. 8. Mean body length of *Daphnia barbata* recorded from samples collected from different depths and sampling hours with standard error bars (a) on 02.03.2002 and (b) on 03 and 04.03.2002, Lake Kuriftu.

Firstly, there were differences in *D. barbata* biomass during the two sampling periods with biomass in the first sampling of 2001 lower than the second one in 2002 (Figs 6 and 7). Although the sampling period in 2001 and 2002 were in the same month with a difference of only about three weeks, variations of such nature are pretty normal to expect, as each year has its own uniqueness in rainfall, nutrient input and recycling, solar radiation, *etc.* properties. Secondly, it seems reasonable to suggest that even by 2 m water depth, the water column was sufficiently dark to minimize visual predation by fish to an acceptable level for daphnids to bargain for access to quantitatively and qualitatively better food as indicated by the shallow Secchi depth of not more than 67 cm (Fig. 5). At other hours of sampling (between 16 to 21 hours and 3 to 8 hours), daphnids were likely to be more evenly distributed in the water column as they migrate on their way up or down, respectively. Thirdly, this study has shown that normal DVM occurs in Lake Kuriftu with ascent of *D. barbata* at dusk to the surface and descent to the bottom at dawn (Figs 6 and 7). Fourthly, unlike water temperature, dissolved oxygen apparently disappears by 4 m depth in Lake Kuriftu (Figs 3a and b) presenting itself as parameter of trade off *D. barbata* should bear to minimize the risk of predation, as experienced by daphnids in temperate lakes (see also LaRow, 1970; Duval and Geen, 1976; Masson and Pinel-Alloul, 1998; Besiktepe, 2001; Liu *et al.*, 2003). Starting 3 m depth and then beyond (up to 6 m), the conductivity started to slightly increase from about 200 μScm⁻¹ to about 285 μScm⁻¹ at 6 m depth (Fig. 4). Although the exact effect of increased salinity on *D. barbata* in

Lake Kuriftu is not known (Fig. 4 and Table 1), there is every reason to believe that freshwater daphnids prefer as dilute and as less turbid water as possible to maintain a homeostatic internal biological conditions and continue to proliferate successfully maintaining normal DVM (see also Masson and Pinel-Alloul, 1998; Masson *et al.,* 2001; Roman *et al.,* 2001; Liu *et al.,* 2003).

Large bodied, gravid females and most likely older individuals of *D. barbata* have shown normal DVM as shown in Fig. 8a and b. This is in agreement to the findings in temperate freshwater systems (*e.g.,* Liu *et al.,* 2003 and Brook Lemma, 2004). The presence of smaller cladocerans such as *Diaphanosoma* spp. and *Ceriodaphnia* spp. in Lake Kuriftu previously reported by Brook Lemma *et al.* (2001) were also observed during this study. In this study, the migration pattern of these small cladocerans was not investigated mainly due to their very low abundance and consequently minimal contribution to the energy flow. *Diaphanosoma* spp. and *Ceriodaphnia* spp. have probably been effectively out-competed by *D. barbata* which is generally accepted as a better and an efficient grazer (see also Flik and Vijverberg, 2003). On the other hand, however small is the biomass of *Diaphanosoma* spp. and *Ceriodaphnia* spp., they are likely to find refuge in their small sizes and hence may stay in the warm food-rich water column through most of the 24-hours of the day, performing little or no DVM (see also De Robertis *et al.,* 2000; De Robertis, 2002; Cerbin *et al.,* 2003). However, it is likely that they can be affected by the versatile feeding behavior of tropical fishes such as *Oreochromis niloticus* which can also filter-feed on *Diaphanosoma* spp. and *Ceriodaphnia* spp. along with phytoplankton on which this fish

species can successfully thrive (Elias Dadebo, 2001).

One other aspect of studying Lake Kuriftu may also be to give some reflections on its present trophic status as this could be linked to its zooplankton structure. In Lake Kuriftu the shallowness of its Secchi depth, high turbidity, high load of organic matter that comes in through run-off particularly during rainy periods, stirring of sediments by *C. carpio* that exports silt and nutrients into the upper water column, possibly high primary production by diverse phytoplankton assemblages (both accessible species that support macrozooplankton and non-accessible ones) and absence of dissolved oxygen at the bottom are likely to bring the status of this lake to eutrophiclevels (see also Mandaville, 2000; Gulati and van Donk, 2002). One important aspect of eutrophication that made conclusions here difficult to declare Lake Kuriftu as eutrophic is that soluble phosphate and nitrate were measured to be very low as shown in Table 1. One probable explanation for the low measurements of these two essential nutrients could be that the primary producers probably constantly assimilate them given the year-round openness of the lake (described above), adequate solar radiation and high temperature of the tropical environment. Considering the above, Lake Kuriftu may then be safely considered to be eutrophic from the point of uncontrolled external and internal nutrient loads (*e.g.,* by *Cyprinus carpio*), and the absence of any regulation of fish populations (*O. niloticus*). The former enhances the proliferation of ungrazeable phytoplankton, mostly Cyanobacteria and the latter wipe out *D. barbata* replacing the zooplankton community with microzooplankton such as *Ceriodaphnia* spp., *Diaphanosama* spp. and a wide range of rotifers.

**Table 1.** Water chemical analysis of samples collected from 0 and 6 meters on 26. 03. 2001 (*except $PO_3^{3-}$ and $NO_3^-$, **except $NH_4^+$ and TDS stands for Total Dissolved Solids), Lake Kuriftu.

| Sampling depth | Anions | Values (meqL$^{-1}$) | Sampling depth | Cations | Values (meqL$^{-1}$) |
|---|---|---|---|---|---|
| 0 m | $CO_3^{2-}$ | 0.30 meqL$^{-1}$ | 0 m | $Na^+$ | 0.33 meqL$^{-1}$ |
| 6 m | $CO3^{2-}$ | 0.00 meqL$^{-1}$ | 6 m | $Na^+$ | 0.29 meqL$^{-1}$ |
| 0 m | $HCO^{3-}$ | 1.40 meqL$^{-1}$ | 0 m | $K^+$ | 0.12 meqL$^{-1}$ |
| 6 m | $HCO^{3-}$ | 1.65 meqL$^{-1}$ | 6 m | $K^+$ | 0.11 meqL$^{-1}$ |
| 0 m | $Cl^-$ | 0.05 meqL$^{-1}$ | 0 m | $Ca^{2+}$ | 0.88 meqL$^{-1}$ |
| 6 m | $Cl^-$ | 0.05 meqL$^{-1}$ | 6 m | $Ca^{2+}$ | 1.40 meqL$^{-1}$ |
| 0 m | $SO_4^{2-}$ | 0.51 meqL$^{-1}$ | 0 m | $Mg^{2+}$ | 1.64 meqL$^{-1}$ |
| 6 m | $SO_4^{2-}$ | 0.31 meqL$^{-1}$ | 6 m | $Mg^{2+}$ | 0.80 meqL$^{-1}$ |
| 0 m | $NO_3^-$ | 0.009 meqL$^{-1}$ | 0 m | $NH_4^+$ | 0.01 meqL$^{-1}$ |
| 6 m | $NO_3^-$ | 0.004 meqL$^{-1}$ | 6 m | $NH_4^+$ | 0.09 meqL$^{-1}$ |
| 0 m | $PO_4^{3-}$ | 0.09 mgL$^{-1}$ | | | |
| 6 m | $PO_4^{3-}$ | 0.16 mgL$^{-1}$ | | | |
| 0 m (Sum) | Anions* | 2.26 meqL$^{-1}$ | 0 m (Sum) | Cations** | 2.97 meqL$^{-1}$ |
| 6 m (Sum) | Anions* | 2.01 meqL$^{-1}$ | 6 m (Sum) | Cations** | 2.60 meqL$^{-1}$ |
| 0 m | TDS | 260 mgL$^{-1}$ | 6 m | TDS | 240 mgL$^{-1}$ |

It is generally accepted that Secchi depth is subject to seasonal variation due to patterns of rainfall, runoff rates, external and internal nutrient load and proliferation of phytoplankton that affect active visual predation (Liu *et al.*, 2003). In Lake Kuriftu, although the improvement of water turbidity, as seen from changes in Secchi depth from 20 cm in 2001 (Brook Lemma *et al.*, 2001) to 67 cm in this study, is much desired, improvement in turbidity alone to bring about water clarity such as by improving land cover of the watershed (unlikely to come by in present day Ethiopian environmental scenario) is very likely to expose daphnids to year-round predation. That would very likely lead to the breakdown of macrozooplankton populations that are needed for removal of phytoplankton and their replacement by microzooplankton such as rotifers and proliferation of less competent and undesired filamentous algae particularly Cyanobacteria. Such a scenario would then bring about a much worse water quality deterioration that will be quite difficult to reverse. It is therefore further suggested that any watershed management to control runoff and loading of Lake Kuriftu with s ilt, p articulate organic matter and nutrients should be coupled with the study and management of zooplankton and fish structures (mainly dominated by *O. niloticus* and *C. carpio* that stir the sediment in search of benthic organisms) (see also Brook Lemma *et al.*, 2001; Gulati and van Donk, 2002).

Furthermore since Lake Kuriftu located in the outskirts of Bishoftu town is prone to excessive selective fishing of market-size *O. niloticus* (leaving behind small-sized *O. niloticus* and the benthos feeder species) and excessive water use, such studies as zooplankton and their DVM may contribute to a better understanding of the ecosystem so as to use the lake sustainably and avert scenarios experienced at Lake Haramaya (previously known in the literature as Lake Alemaya) in Eastern Ethiopia (Brook Lemma, 1994; 2003a and b).

This work on DVM on a tropical shallow lake is hoped to stimulate research on migration behavior of zooplankton in tropical aquatic ecosystems so as to bring out the differences and similarities of DVM in temperate and tropical waters. Such tropical studies particularly become interesting to compare the effects of by-depth variable parameters such as seston quality and quantity, visual predation, dissolved oxygen, solar radiation, *etc.* on DVM, where temperature is non-limiting at all depths. Long-term information gathered from such DVM studies when coupled with other aquatic investiga-

tions can provide adequate knowledge towards a better understanding of the food web in shallow tropical lakes and the interaction of such water systems to living and non-living factors of the watershed, as lakes are not independent entities but part of the story of the watershed, communities in it and even global atmospheric and climate changes (see also Brook Lemma, 1997; Gulati and van Donk, 2002).

## REFERENCES

1. Besiktepe, S. (2001). Diel vertical migration and herbivory of copepods in south-western part of the Black sea. *J. Mar. Syst.* **28**:281–301.

2. Blachowiak-Samolyk, K., Kwasniewski, S., Richardson, K., Dmoch, K., Hansen, E., Hop, H., Falk-Peterson, S. and Mouritsen, L.T. (2006). Arctic zooplankton do not perform diel vertical migration (DVM) during periods of midnight sun. *Mar. Ecol. Prog. Ser.* **308**:102–116.

3. Børsheim, K.Y. and Anderson, S. (1987). Grazing and food size selection by crustacean zooplankton compared to production of bacteria and phytoplankton in a shallow Norwegian mountain lake. *J. Plankton Res.* **9**(2):367–379.

4. Brook Lemma (1994). Changes in the limnological behavior of a tropical African explosion crater lake: Lake Hora-Kilole, Ethiopia. *Limnologica* **24**(1):57–70.

5. Brook Lemma (1997). Der Einfluss zooplanktonfressender Fische auf die Grossenfraktionen des Phytoplanktons und die Primärproduktion in gemässigten und tropischen Seen. PhD dissertation, TU Dresden, 177 pp.

6. Brook Lemma (2003a). Aquatic habitats and biodiversity changes of two Ethiopian lakes. In: *"Wetlands and Aquatic Resources: Status, Challenges and Prospects"*, Ethiopian Biological Society Conference, pp. 27–31, Addis Ababa University, Addis Ababa, 12–13 February 2003.

7. Brook Lemma (2003b). Ecological changes of two Ethiopian lakes as caused by contrasting human interventions. *Limnologica* **33**:44–53.

8.  Brook Lemma (2004). Diel vertical migration of zooplankton in a hypertrophic shallow temperate lake, Germany. *SINET: Ethiop. J. Sci.* **27**(1):33–44.

9.  Brook Lemma, Benndorf, J. and Koschel, R. (2001). Fish predation pressure on and interactions between cladocerans: Observations using enclosures in three temperate lakes (Germany) and one tropical lake (Ethiopia). *Limnologica* **31**:209–220.

10. Carpenter, S.R. and Kitchell, J.F. (1993). Cascading trophic interactions. In: *The Trophic Cascade in Lakes*. (Carpenter, S.R. and Kitchell, J.F., eds). Cambridge University Press, Cambridge, 385 pp.

11. Cerbin, S., Balayla, D.J. and Van de Bund, W.J. (2003). Small-scale distribution and diel vertical migration of zooplankton in a shallow lake (Lake Naardermeer, the Netherlands). *Hydrobiologia* **491**:111–117.

12. De Robertis, A. (2002). Size-dependent visual predation risk and the timing of vertical migration: An optimization model. *Limnol. Oceanogr.* **47**(4):925–933.

13. De Robertis, A.D., Jaffe, J.S. and Ohman, M.D. (2000). Size-dependant visual predation risk and the timing of vertical migration in zooplankton. *Limnol. Oceanogr.* **45**(8):1838–1844.

14. Duval, W.S. and Geen, G.H. (1976). Diel feeding and respiration rhythms in zooplankton. *Limnol. Oceanogr.* **21**(6):823–829.

15. Elias Dadebo (2001). Reproductive biology and feeding habits of some fish species in Lake Chamo, Ethiopia. PhD Thesis, School of Graduate Studies, Addis Ababa University, Addis Ababa, Ethiopia, 109 pp.

16. Fernando, C.H. (1994). Zooplankton, fish and fisheries in tropical freshwaters. *Hydrobiologia* **272**:105–123.

17. Flik, B.J.G. (2000). Size selective feeding of 0+ perch during a period of diel vertical migration of *Daphnia*. *Verh. Internat. Verein. Limnol.* **27**:3019.

18. Flik, B.J.G. and Vijverberg, J. (2003). Contrasting migration behavior of *Daphnia pulicaria* and *D. galeata* x *hylina*, in avoidance of predation by 0+ perch (*Perca fluviatilis*). *Hydrobiologia* **491**:289–299.

19. Gliwicz, M.Z. (1986). Predation and the evolution of migration in zooplankton. *Nature* **320**:746–748.

20. Gliwicz, M.Z. (2005). Food web interactions: why are they reluctant to be manipulated? *Verh. Internat. Verein. Limnol.* **29**:73–88.

21. Greenberg, A.E. and Franson, A.H. (1981). *Standard Methods for the Examination of Water and Wastewaters*, 15th edition. American Public Health Association (APHA), Washington.

22. Gulati, R.D. and van Donk, E. (2002). Lakes in the Netherlands, their origin, eutrophication and restoration: state of the art review. *Hydobiologia* **478**:73–106.

23. Kasprzak, P., Krienitz, L. and Koschel, R. (1993). Changes in the plankton of Lake Feldberg Haussee (Germany, Meklenburg-Vorpomern) in response to biomanipulation. *Arch. Hydrobiol.* **128**:149–168.

24. Kessler, K. and Lampert, W. (2004). Depth distribution of *Daphnia* in response to a deep-water algal maximum: The effect of body size and temperature gradients. *Freshwat. Biol.* **49**:392–401.

25. Kornilovs, G., Sidrevics, L. and Dippner, J.W. (2001). Fish and zooplankton interaction in the Central baltic Sea. *ICES J. Mar. Sci.* **58**:579–588.

26. Lampert, W. (1993). Ultimate causes of diel vertical migration of zooplankton: New evidence for the predator-avoidance hypothesis. *Arch. Hydrobiol. Beih. Ergebn. limnol.* **39**:79–88.

27. Lampert, W., McCauley, E. and Manly, B.F.J. (2003). Trade-offs in the vertical distribution of zooplankton: ideal free distribution with costs? *Proc. R. Soc. Lond. B.* **270**:765–773.

28. LaRow, E.J. (1970). The effect of oxygen tension in the vertical migration of *Chaoborus* larvae. *Limnol. Oceanogr.* **15**:357–362.

29. Liu, S.H., Sun, S. and Han, B.P. (2003). Diel vertical migration of zooplankton following optimal food intake predation. *J. Plankton Res.* **25**(9):1069–1077.

30. Mandaville, S.M. (2000). Soil and water conservation society of Metro Halifax. Synopsis In: *Eutrophication of Lakes and Effects of Global Warming, Acid Deposition & UV-B penetration.* Dartmouth NS Canada B2Y 3Z6. 57 pp.

31. Masson, S. and Pinel-Alloul, B. (1998). Spatial distribution of zooplankton biomass size fractions in a bog lake: Abiotic and (or) biotic regulations? *Can. J. Zool.* **76**:805–823.

32. Masson, S., Angeli, N., Guillard, J. and Pinel-Alloul, B. (2001). Diel vertical migration and horizontal distribution of crustacean zooplankton and young of the year fish in a sub-alpine lake: An approach based on high frequency sampling. *J. Plankton Res.* **23**(10):1041–1060.

33. Nilssen, J.P. (1984). Tropical lakes–Functional ecology and future development: The need for a process oriented approach. *Hydobiologia* **113**:231–242.

34. Park, S., Chandra, S., Müller-Navarra, D.C. and Goldman, C.R. (2004). Diel and vertical variability of seston food quality and quantity in a small subalpine oligomesotrophic lake. *J. Plankton Res.* **26**(12):1489–1498.

35. Pawels, J.M., van Ranst, E., Varloo, M. and Ze, A.M. (1992). Mannual de laboratoire de pedologie. Methode d'analyses de sols et de plantes, equipment, gestion de stocks de verrerie et de

produits chimiques. Publications Agricoles -28. A.G. Building Place du Champ de Mars 5. Boite 57; 1050 Bruxelles, Royaume de Belgique.

36. Ramos-Jiliberto, R. and Zúñiga, L.R. (2001). Depth selection patterns and diel vertical migration of *Daphnia ambigua* (Crustacea: Cladocera) in Lake El Plateado. *Resista Chilena de Historia Natural* **74**:573–585.

37. Ringelberg, J. (1999). The photobehaviour of *Daphnia* spp. as a model to explain diel vertical migration in zooplankton. *Biol. Rev.* **74**:397–423.

38. Roman, M.R., Holliday, D.V. and Sanford, L.P. (2001). Temporal and spatial patterns of zooplankton in the Chesapeake Bay turbidity maxium. *Mar. Ecol. Prog. Ser.* **213**:215–227.

39. Stich, H.B. and Lampert, W. (1981). Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature* **291**:396–398.

40. Tsui, N. (2006). Vertical migration of marine copepods in the Galapegos Islands in relation to size and colour. http://course.washington.edu/ocean444/secondDraft/Tsui.pdf.

41. Weismann, A. (1887). Das Tierleben im Bodensee. *Schr. Ver. Geschichte Bodensee Umgebung* **7**:1–31.