ELSEVIER

Observations on the relations of some physico-chemical features and DVM of *Paradiaptomus africanus* in Lakes Bishoftu-Guda and Hora-Arsedi, Bishoftu, Ethiopia

Brook Lemma

Department of Biology Education, College of Education, Addis Ababa University, P.O. Box 1913 Code 1110, Addis Ababa, Ethiopia

Abstract

Bishoftu-Guda and Hora-Arsedi are two crater lakes found in close proximity with each other in a locality known as Bishoftu, 50 km south of Addis Ababa, capital city of Ethiopia. The main objective of this study was to measure some physico-chemical features and discuss their relations with the dial vertical migration (DVM) behavior of *Paradiaptomus africanus*, the dominant macrozooplankton in both lakes. By depth measurements of dissolved oxygen and temperature showed that there is persistent stratification in these lakes. Secchi depth was shallow and the water chemistry as shown from conductivity and chemical analysis were comparable between the two lakes. These data were compared with previous reports to bring out the overall limnological scenario of the two lakes. Then, the relations of these data to the DVM of *P. africanus* in both lakes were discussed. It was found out that DVM of *P. africanus* occurred in Lakes Bishoftu-Guda and Hora-Arsedi mostly within a range of about 3 m very likely for two reasons, namely avoidance of solar radiation and ultimately vertebrate visual predation. However, the depth of DVM of *P. africanus* was found to be very shallow probably due to high water turbidity that provided this calanoid sufficient refuge by daylight from both dangers, while at the same time *P. africanus* remained in warm and oxygen-rich waters. Temperature was not much of a factor affecting DVM as it remained above 19 °C at all depths. As this study was conducted over limited time frames, seasonal studies regarding changes in physico-chemical parameters, plankton, vertebrate predators and human interference were recommended so that the information so gathered could be used in the management of the study lakes.
© 2008 Elsevier GmbH. All rights reserved.

Keywords: DVM; Tropical lakes; Crater lakes; *Paradiaptomus africanus*; Calanoids; Ethiopia

Introduction

The role of zooplankton migration in the study of the trophic status of fresh waters has been investigated since the time of Weismann (1887). It is still highly debated in the literature. There is controversy in ironing out the true causes of zooplankton migration ranging from the long time co-evolution of predators along with their preys (O'Brien, 1987) to the identification of various cues that trigger the migrations of the same (Lampert, 1989; Han and Straškraba, 2001). This amounts to the movement of tons and tons of fish food (Frank and Widder, 1997; Bradford-Grieve et al., 2001) at specific periods within 24 h of a day to regions of water systems

that are quite illusive for predators to reach but with considerable costs for the migrating zooplankton (Lampert, 1993, 1989). One such studied group of zooplankton are the copepods, particularly the large-sized ones, the calanoids. There is a considerable amount of literature on this sector of the zooplankton that are known to have quite speedy reaction to changes in cues (Masson et al., 2001; Lemma, 2004) and in detecting the behavior of predators that have co-evolved with them (O'Brien, 1987). It is then generally accepted that zooplankton stay in the cold dark deeper water column during the day to ultimately avoid visual predation mostly by planktivorous fishes and migrate towards the warm food-rich surface water at night using nightfall as their refuge (McLaren, 1974; Zaret and Suffern, 1976; Stich and Lampert, 1981; Dagg et al., 1989). A considerable amount of both field and experimental evidences have accumulated to support this phenomenon as described by the generally accepted predator-evasion hypothesis (Stich and Lampert, 1981; Gliwicz, 1986; Hays et al., 1994). It is also argued that there are other cues that trigger the same behavior in zooplankton such as ultraviolet radiation (UVR) (Alonso et al., 2004), temperature (Ramos-Jiliberto and Zuñiga, 2001), oxygen limitation (Besiktepe, 2001; De Robertis, 2002), availability and competition for food (Pearre, 2000), wind action (Lemma, 2004), prey size (Hays et al., 1994; Cuker and Watson, 2002), conductivity (Roman et al., 2001) and others. Further readings dealing with different aspects of the causes of dial vertical migration (DVM) can be made in such publications as Perticarrari et al. (2004); Shimode and Shirayama (2004); Aguilera et al. (2006); Nomura (2006); Tsui (2006); Blachowiak-Samolyk et al. (2006).

The main objectives of this study were (i) to see the relationship of some physico-chemical parameters to DVM of *P. africanus* in the study lakes, (ii) to reflect if DVM of *Paradiaptomus africanus* (syn. *Lovenula africana*) occurs in deep tropical lakes and (iii) if possible to bring out some similarities and differences between the scenarios recorded in temperate and tropical fresh waters.

Materials and methods

The study sites

The study sites, namely Lakes Bishoftu-Guda and Hora-Arsedi, are located in an area known as Bishoftu (Debre Zeit) about 50 km south of Addis Ababa and make part of a volcanic region with seven crater lakes collectively known in the literature as the Bishoftu Crater Lakes. These lakes are found at an altitude of 1860 m above sea-level and longitude of 39°00′E and latitude 09°00′N, within very short distance from each other (Fig. 1) (see also Prosser et al., 1968). They are accessed by all-weather roads and with very close proximity to the capital city and quite convenient accommodations in the town of Bishoftu. This situation has attracted limnologists to study these lakes over the past 60 or more years. In earlier literature, Lake Bishoftu-Guda is known as L. Pawlo (Paulo) or Babogaya while Lake Hora-Arsedi is known as L. Biete-Mengest or simply Hora. These transliterations in names of some lakes and towns are prevalent in Ethiopia in recent years in relation to the changes in social order that gave recognition to regional administrations that uphold the respective cultures and languages, a phenomenon felt early on in the 1980s by Wood and Talling (1988). Limnologists should therefore pay special attention to these changes of names so that they can keep good track of the history of lakes.

L. Bishoftu-Guda and Hora-Arsedi have steep slopes with very small catchment areas and no inflowing rivers or streams. They are fed by runoffs during the rainy seasons and by underground inflows, in which case L. Hora-Arsedi happens to be the terminal lake (Wood and Talling, 1988; Kebede et al., 2001; Lemma, 2008a). Some of the morphometric features of the two lakes are given in Table 1.

The plankton communities of the two lakes show slight variation. The phytoplankton in L. Bishoftu-Guda tends to be dominated by Cyanophyceae while that of L. Hora-Arsedi is dominated by Chlorophyceae
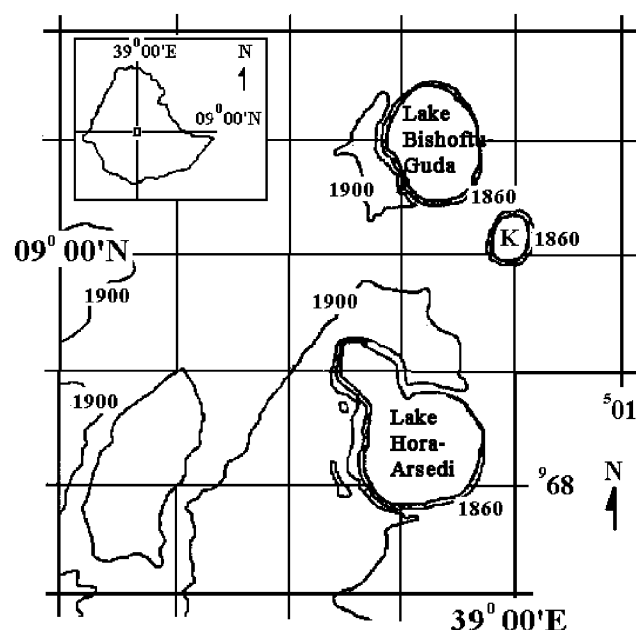

Fig. 1. Locations of Lakes Bishftu-Guda and Hora-Arsedi. The inset in the map of Ethiopia represents the enlarged area of the study sites (map after the topographic sheet of the Ethiopian Mapping Agency, Addis Ababa, with a scale of 1:50,000).

(Table 2). Occasional blooms of dinophytes, particularly *Peridinium* spp. can be expected following fresh external nutrients and organic matter loads by way of runoffs. Such instances have also implications on the zooplankton structure where water turbidity as refuge and blooming of grazeable phytoplankton as source of adequate food can stimulate the reappearance of cladocerans as recorded by Lemma et al. (2001) in L. Kuriftu located between these two study lakes (Fig. 1). Zooplankton are largely represented by a wide range of rotifers in both lakes, the dominating genus being *Brachionus*, followed by some copepods and particularly the calanoid *P. africanus* (syn. *Lovenula africana*) (Table 2). If at all cladocerans such as the three cladoceran species in L. Hora-Arsedi (Table 2) appear at certain seasons, they happen to be very small in size and short lived due to the intense predation pressure they face from vertebrate predators.

L. Bishoftu-Guda is inhabited by two cichlid fishes, namely, *Oreochromis nitoticus* and *Tilapia zillii* and by one clariid fish, namely, the African catfish *Clarias gariepinus,* while L. Hora-Arsedi is inhabited by *O. nitoticus* only (Fassil, 2007). According to Lemma (2008b) the feeding habits of *O. niloticus*, generally characterized as grazer, is also well known to selectively feed on macrozooplankton like daphnids if and when they are available at certain seasons. *T. zillii* is a macrophyte feeder while *C. gariepinus* is known for its omnivorous habit that tends to be more carnivorous at large sizes.

Sampling procedures

Routine by depth measurements of water temperature, dissolved oxygen and conductivity were recorded by day and night at 1 m intervals from the surface down close to the sediment from centrally located sampling stations of about 50 and 25 m depth in Lakes Bishoftu-Guda from 23. to 26.03.2001 and from 28.02. to 02.03.2002 and Hora-Arsedi from 23. to 26.2003 and from 22. to 24.03.2004, respectively. During the daylight hours Secchi depth transparency was measured by

Table 1. Some of the morphometric features of Lakes Hora-Arsedi and Bishoftu-Guda (Prosser et al., 1968; Wood and Talling, 1988)

Parameters	L. Hora-Arsedi	L. Bishoftu-Guda
Surface area (km^2)	1.03	0.58
Maximum depth (m)	38	65
Mean depth (m)	17.5	38
Volume (km^3)	0.018	0.022

Table 2. Phytoplankton and zooplankton communities of Lake Bishoftu-Guda and L. Hora-Arsedi (Baxter et al., 1965; Kebede et al., 1986; Wood and Talling, 1988; Green, 1986; Green and Mengistou, 1991; Lemma, 1997, 2008b)

L. Bishoftu-Guda		L. Hora-Arsedi	
Phytoplankton	Zooplankton	Phytoplankton	Zooplankton
Cyanophyceae	Cladocera	Chlorophyceae	Cladocera
Microcystis aeroginosa		µ-*Algae*	*Daphnia barbata*
Oscillatoria sp.	Copepoda	*Oocystis* spp.	*Diaphanosoma* sp.
	Paradiaptomus africanus	*Scenedesmus dimorphus*	*Ceriodaphnia* sp.
	(syn. *Lovenula africana*)		
Bacillariophyceae	*Afrocyclops gibsoni*	*Scenedesmus* spp.	*Alona* sp.
A few diatoms		*Gloeocystis* sp.	
	Rotifera		Copepoda
	Asplanchna sieboldi	Dinophyceae	*Mesocyclops* sp.
	Brachionus calyciflorus		*Thermocyclops* sp.
	B. urceolaris		*Paradiaptomus africanus*
			(syn. *Lovenula africana*).
	B. angularis	Bacillariophyceae	Rotifera
	B. caudatus	*Eunotia* sp.	*B. calyciflorus*
	Filinia longiseta	*Navicula* sp.	*B. dimidiatus*
	Lepadella patella		*Polyarthra* sp.
	Hexarthra jenkinae	Cyanophyceae	*Filinia* sp.
	Lecane closterocera	*Limnothrix* sp.	*Asplanchna* sp.
	Polyarthra vulgaris		*Keratella* sp.
		Cryptophyceae	*Lecane* sp.
		Cryptomonas sp.	*Hexarthra* sp.
		Rhodomonas sp.	

lowering a metal disc of 20 cm diameter with black and white quarters.

Zooplankton were collected using Schindler-Patalas Trap of 15 L capacity equipped with 55 μm mesh. This was operated from approximately central stations to collect zooplankton from 0, 3, 10, 20, 30, 40 and 50 m depths in Lake Bishoftu-Guda and from 0, 3, 10, 15, 20 and 25 m depths in Lake Hora-Arsedi by daylight and dark hours at approximately 6 h intervals on the dates specified above. Zooplankton samples were stored in 250 mL plastic bottles fixed with 4% sugar–formalin solution. Identification, counting and length measurements of the calanoids from among the assemblages of zooplankton 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 *P. africanus* of 30–40 individuals from each sample was used to calculate bio-volume of the animals from simple geometric models as a measure of biomass (Børshiem and Andersen, 1987; Lemma, 2004).

Water samples were collected with HydroBios 2-L capacity sampler from the above-designated depths of the two lakes. In the case of Lake Bishoftu-Guda the samples collected from the depths of 0, 3, 6, 16, 30 and 50 m on 23.03.2001 were analyzed separately while the samples collected by the same sampler from Lake Hora-Arsedi on 23.06.2002 were pooled together in buckets properly rinsed with lake water. From this pooled and homogenized sample, 1-L sub-samples were taken in opaque plastic bottles with tight screw caps for water chemical analysis. The samples in both cases were immediately deep frozen until analysis was conducted within 1 week. All the analyses were conducted at the National Soils Research Center of the Ethiopian Agricultural Research Organization, Addis Ababa, by using methods described in Greenberg and Franson (1981) and Pawels et al. (1992).

Results

By depth measurements of temperature and dissolved oxygen clearly showed that the lakes were stratified during these periods of sampling (Figs. 2–5). In L. Bishoftu-Guda distinct thermal discontinuity has been observed where the thermocline extending up to 15 m during the period of 22.–23.03.2001. It was shallower (up to 10 m) during the period of 28.02.–23.03.2002 (Fig. 2). Water column below 15 and 10 m at L. Bishoftu-Guda represented the hypolimnion with minimum temperature of 19 °C.

In L. Hora-Arsedi the surface water was obviously more heated as compared with the water immediately below, probably owing to its shallowness in comparison
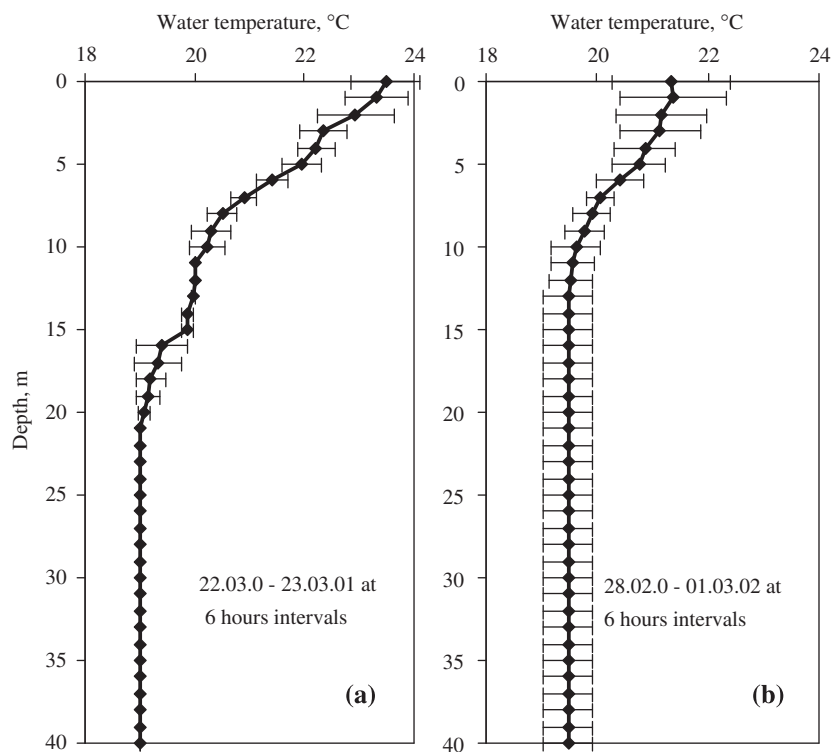

Fig. 2. Temperature depth profile at Lake Bishftu-Guda from (a) 22.–3.03.2001 and (b) 28.02.2002–01.03.2002. Error bars show variations in temperature between the cool nights and the warm-day hours.
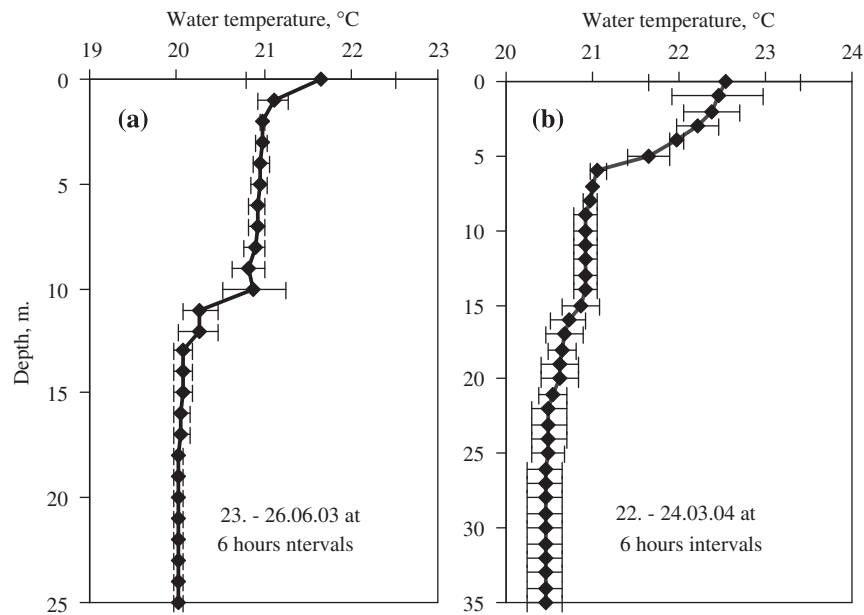
Fig. 3. Temperature depth profile at Lake Hora-Arsedi from (a) 23.–26.06.2003 and (b) 22.–24.03.2004. Error bars show variations in temperature between the relatively cool nights and the warm-day hours.
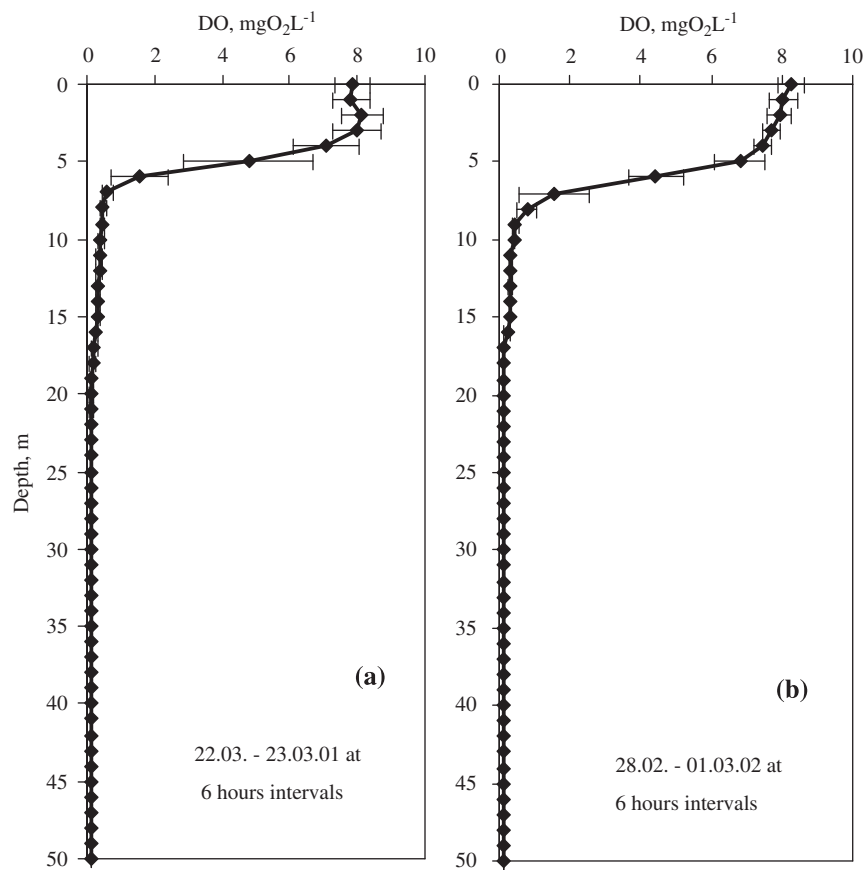

Fig. 4. Dissolved oxygen depth profile at Lake Bishoftu-Guda from (a) 22.–23.03.2001 and (b) 28.02.2002–01.03.2002. Error bars show variations in dissolved oxygen the relatively cool nights and the warm-day hours.
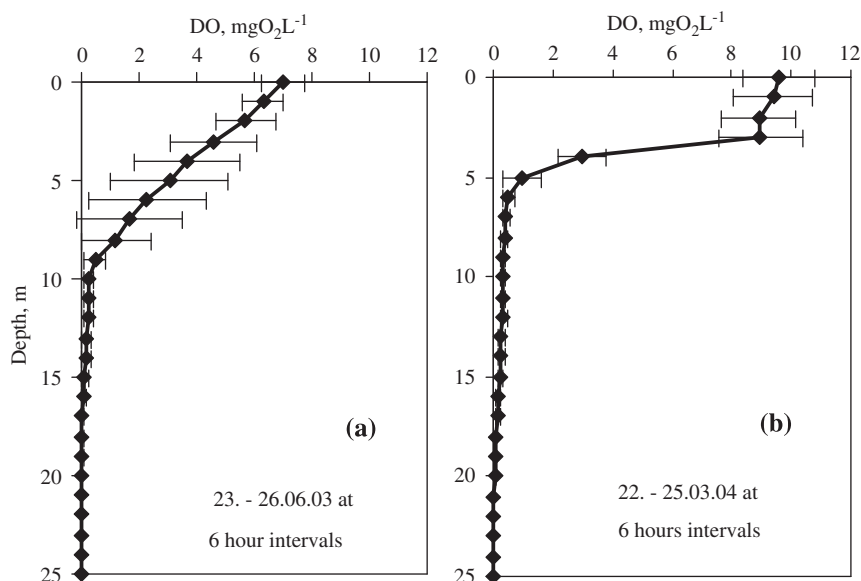
Fig. 5. Dissolved oxygen depth profile at Hora-Arsedi (a) 23.–26.06.2003 and (b) 22.–24.03.2004. Error bars show variations in dissolved oxygen the relatively cool nights and the warm-day hours.

to the depth of Lake Bishoftu-Guda (Fig. 3). The surface maximum reached 22.7 °C and the observed thermal discontinuity was similar to that of L. Bishoftu-Guda. In L. Hora-Arsedi multiple thermoclines of small variations in temperature were recorded (Fig. 3).

Dissolved oxygen did not show much variation in the case of L. Bishoftu-Guda during both sampling periods (22.–23.03.01 and 28.02.–01.03.2002) (Fig. 3). The upper 4 to 5 m had about $8 \, mgO_2 \, L^{-1}$, which suddenly dropped to about $0.5 \, mgO_2 \, L^{-1}$ by 7 or 8 m depth. The lake was apparently anoxic below 15 m. During the first sampling period (23.–26.06.2003) L. Hora-Arsedi showed a similar trend as that of L. Bishoftu-Guda, but varied at the second sampling period (22.–25. 03.2004) (Fig. 4). At this lake, dissolved oxygen sharply and progressively decreased from the surface up to 10 m during the second sampling period (Fig. 4b). This is most likely linked with the temperature instability of the epilimnion as described above (see Fig. 3), and probably the effect of seiche as caused by wind action.

Conductivity was slightly higher at the surfaces of both lakes (Figs. 6 and 7), probably due to higher surface water temperature that might have lent itself to higher chemical activity. Below 4 or 5 m, conductivity tended to be lower due to cooler and calmer waters. However, conductivity below 15 m was much higher in L. Bishoftu-Guda as substances slowly sink; water tended to be more stable and concentrated than the waters of upper columns. A similar but less pronounced scenario is also observed at L. Hora-Arsedi probably owing to its relative shallowness.
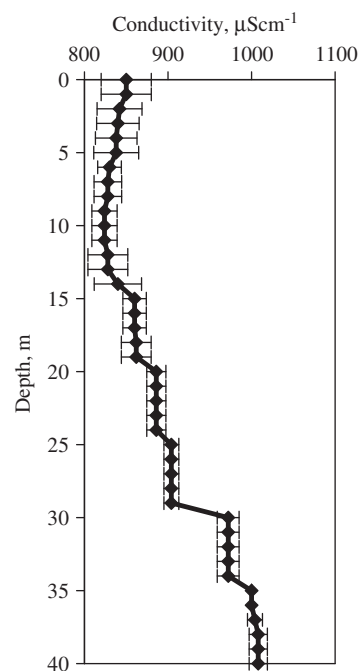

Fig. 6. Conductivity depth profile at Lake Bishoftu-Guda for the periods of 22.–23.03.2001 and 28.02.2002–01.03.2002. Error bars show variations in conductivity in the relatively cool nights and the warm-day hours.

Secchi disc transparency was deeper by almost two to three folds (140–160 cm) in L. Bishoftu-Guda than in L. Hora-Arsedi (47–68 cm) (Figs. 8 and 9). These two crater lakes found in close proximity with each other
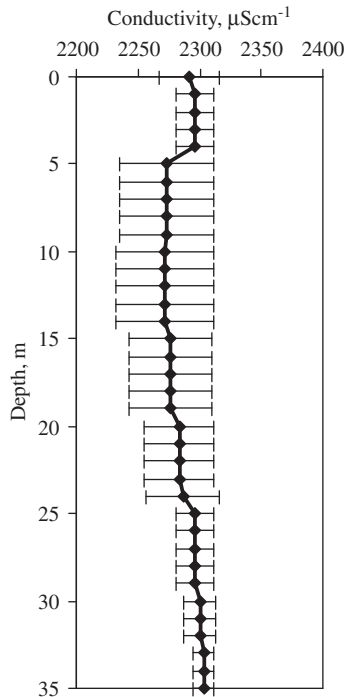
Conductivity, μScm⁻¹

Fig. 7. Conductivity depth profile Lake Hora-Arsedi for the periods of 23.06.2003–26.06.2003 and 22.03.2004–24.03.2004. Error bars show variations in conductivity in the relatively cool nights and the warm-day hours.

and described in the literature as having a lot of limnological similarities were experiencing different levels of turbidity caused by suspended matters of both organic and inorganic nature.

Water chemical analyses data conducted on samples collected from various depths of L. Bishoftu-Guda is given in Table 3. Important nutrients such as inorganic phosphate, nitrate and ammonium ions were very low in quantity at various depths, decreasing to trace levels at some depths. In L. Hora-Arsedi, where water chemical analysis was done from pooled samples (Table 4), conductivity and total dissolved solids were twice as much as those of L. Bishoftu-Guda.

In all zooplankton samples of Lakes Bishoftu-Guda and Hora-arsedi, no daphnids were found. The copepod *P. africanus* was found to be the dominant macro-zooplankton in both lakes.

P. africanus showed DVM patterns in both studied lakes by ascending at dusk or dark hours and descending into deeper waters by daylight (Figs. 10 and 11). The migration range of this species extended up to 15–20 m in both lakes (Figs. 10 and 11). This depth for L. Hora-Arsedi was already at or near the sediment while it was about one-third of the maximum depth of L. Bishoftu-Guda. In both lakes the maximum biomass of *P. africanus* during daylight hours was measured at a depth of 3 m. Beyond this depth the biomass

thinned out finally diminishing to almost total absence by 15 up to 20 m. At nightfall and through most of the dark hours of the day, *P. africanus* tended to stay at the water surface.

Discussions

The data on temperature–depth profile of L. Bishoftu-Guda are in agreement with a study conducted between 1965 and 1966 by Wood et al. (1976) who described the thermal features for the period of March as having "round shouldered form" with multiple thermoclines that gradually deepened the epilimnion up to 15 m. This has very likely occurred during this study period mainly due to repeated warming up and cooling of surface waters in a matter of a day or a few days. In L. Hora-Arsedi as well the thermocline varied from 13 m during 23.–26.06.2003 and up to 22 m during 22.–25.03.2004 (see also Wood et al., 1976). Talling (1963) described such tropical situations as peculiarly mobile and asymmetric form of stratification. Although stratification was clearly observed in both lakes, the temperature differences between surface and bottom waters were very low (surface maximum of 22 °C and bottom minimum of 19 °C). This was a difference of only 3 °C, which is typical for tropical lakes (Talling, 1963; Beadle, 1981). What this amounts to is that within a temperature difference of 3 °C, the water columns of the two lakes had developed sufficient density differences that could enable them to withstand wind action and remain stratified. Talling (1963); Wood et al. (1976) and Beadle (1981) agree that change of density with temperature is greater at higher than at lower temperatures. Such a scenario is unimaginable in temperate lakes where summer stratification can only occur with 15 °C or more water temperature differences between the epilimnion and the hypolimnion (e.g. Lemma, 2004).

Although during most of the study periods the thermal stratification of the two lakes was much affected by the formation of multiple thermoclines, this is not much reflected on dissolved oxygen stratification at both study periods of L. Bishoftu-Guda and during the second sampling period of L. Hora-Arsedi (Figs. 4a and b, and 5b). The multiple thermocline scenario of water temperature is probably reflected on records of the first dissolved oxygen measurements of L. Hora-Arsedi (Fig. 5a). Generally, these results are in agreement with the report made by Prosser et al. (1968) on dissolved oxygen stratification of the Bishoftu Crater Lakes. Conductivity reported without specific depths of measurement for Lakes Bishoftu-Guda and Hora-Arsedi by Prosser et al. (1968) and Wood and Talling (1988) were 1000 and 2340 μS cm⁻¹, respectively, which are comparable to the present records of 850 μS cm⁻¹ at the surface and 1000 μS cm⁻¹ at 40 m at L. Bishoftu-Guda (Fig. 6)
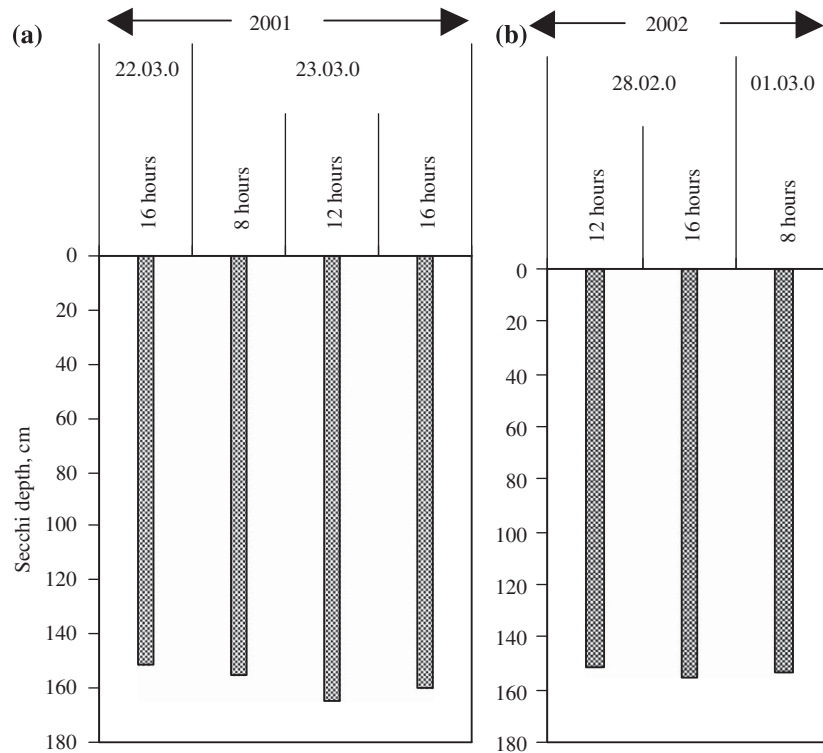
Fig. 8. Secchi disk transparency measurements at Lake Bishoftu-Guda from (a) 22.–23.03.2001 and (b) 28.02.2002–01.03.2002, both at daylight hours.
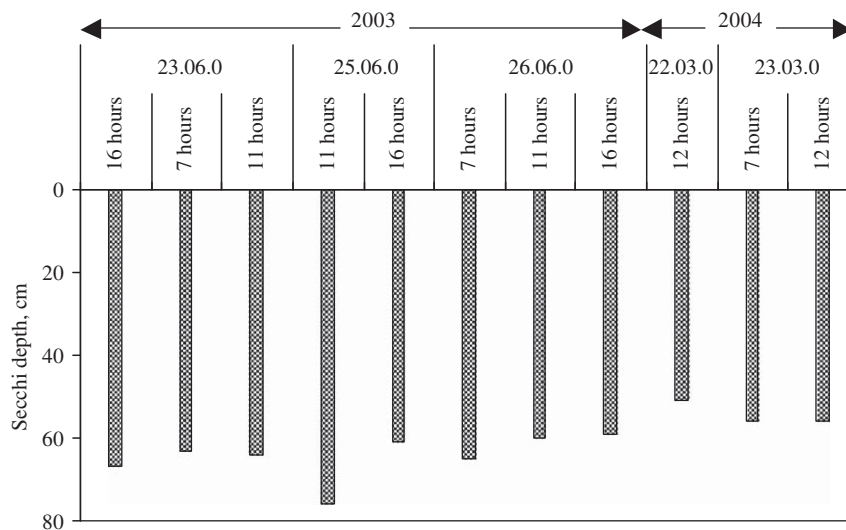

Fig. 9. Secchi disk transparency measurements at Lake Hora-Arsedi from for the periods of 23.–26.06.2003 and 22.–24.03.2004, both at daylight hours.

and $2300 \, \mu S \, cm^{-1}$ at the surface and at 35 m, with slight decrease to about $2200 \, \mu S \, cm^{-1}$ between 5 and 25 m at L. Hora-Arsedi (Fig. 7).

Secchi depth reports on these lakes are hard to find in the literature. This study finds L. Hora-Arsedi (Z_{SD} range of 45–78 cm) (Fig. 9) to have much shallower Secchi depth than L. Bishftu-Guda (Z_{SD} range of 140–160 cm), indicating that it has a lot more suspended matter of organic and inorganic nature in its water column than in L. Bishoftu-Guda (Fig. 8). The possible reason for such a difference for lakes that are found in such close proximity could be that L. Hora-Arsedi is more exposed to untreated waste inflow from the town of Bishoftu than L. Bishoftu-Guda and that

Table 3. Water chemical analysis of samples collected from 0 to 50 m on 22.03.2001 (*except PO_3^{3-} and NO_3^-, **except NH_4^+ and TDS stands for total dissolved solids), Lake Bishoftu-Guda

Depth (m)	CO_3^- (meq L^{-1})	HCO_3^- (meq L^{-1})	Cl^- (meq L^{-1})	SO_4^{2-} (meq L^{-1})	NO_3^- (mg L^{-1})	PO_4^{3-} (mg L^{-1})	Sum of anions* (meq L^{-1})	Na^+ (meq L^{-1})	K^+ (meq L^{-1})	Ca^{2+} (meq L^{-1})	Mg^{2+} (meq L^{-1})	NH_4^+ (mg L^{-1})	TDS (mg L^{-1})	Sum of cations** (meq L^{-1})
0	2.70	2.55	0.06	4.09	0.004	0.01	9.40	2.33	0.37	0.84	3.72	0.31	960	7.26
3	3.00	4.20	0.11	3.51	0.004	0.01	10.82	4.97	0.72	0.80	3.92	0.03	680	10.41
6	2.90	4.30	0.11	2.28	Nil	Nil	9.59	4.97	0.76	0.60	4.64	0.03	640	10.97
16	2.60	4.60	0.11	2.68	0.002	Nil	9.99	4.58	0.62	0.68	4.36	0.03	760	10.24
30	1.90	5.99	0.10	2.79	0.014	0.17	10.79	2.84	0.45	0.68	4.72	0.19	780	8.69
50	1.70	5.49	0.10	2.08	0.004	0.10	9.37	2.52	0.42	0.60	4.52	0.31	680	8.06
Total anions							59.96	Total cations						55.63

L. Hora-Arsedi is a lot more exposed to human interference because of a historic recreation center located at its shores. Besides, the plant cover of the crater rim of this lake has been much affected by people collecting firewood that exposed the top soil to be eroded by wind and runoffs that follow torrential rains of the tropics.

With regard to the water chemistry of the two lakes, NO_3^-, PO_4^- and K^+ compounds are found in trace amounts in both lakes. This could be due to the year round availability of light and high temperature in the tropics that keeps the metabolic process of phytoplankton pretty active which then take up nutrients quite quickly throughout the year, of course very much unlike the freezing winters of temperate lakes. There has been slight decrease in calcium ions concentration from the surface down, while the reverse was the situation with magnesium ions, particularly in L. Bishoftu-Guda where by depth vertical chemical analysis was done. It is very likely that primary production activity could have been high during noon hours when the water samples were collected, and which in turn could have very likely raised the pH. This combination of events apparently causes calcium ions to precipitate, and whose place could be taken up by magnesium ions that came into solution. From the experiences obtained at this lake and at Lake Alemaya (Lemma, 1995), it is safe to assume a similar scenario can be observed in L. Hora-Arsedi where water chemical analysis was conducted from pooled samples due to shortages in resources.

There are considerable differences in the concentrations of anions, cations and TDS of the study lakes (Tables 2 and 3), where Lake Bishoftu-Guda tends to be less concentrated than L. Hora-Arsedi. The similarities in origin, history and close proximity of the two lakes obscure the underlying differences of the two lakes and hence the exact causes for water chemistry variations, as one expects similarity rather than differences. It is however important to note that these lakes are connected by underground water flow with L. Hora-Arsedi being the terminal recipient of groundwater inflow from all other crater lakes of the region to which the possibility of continuous and persistent concentration of solutes in this lake can be attributed (Kebede, 1999; Kebede et al., 2001). Among the cations, for instance, the appreciably high concentration of 25.11 meq L^{-1} Na^+ in L. Hora-Arsedi as compared with a maximum of 4.97 meq L^{-1} at 3 and 6 m depths in L. Bishoftu-Guda could be attributed to the topographic position of L. Hora-Arsedi.

Zooplankton inhabiting L. Bishoftu-Guda and Hora-Arsedi are given in Table 2. At the time of the present study rotifers were highly abundant and cladocerans were not encountered. On the other hand, copepods were largely represented by the Calanoids, particularly by *P. africanus*. The disappearance of the cladocerans,

particularly the daphnids and the cyclopoid copepods; and the dominance of the rotifers can be attributed to the predation pressure of the vertebrates, particularly the cichlid fishes and juvenile clariids. These fishes selectively prey upon the large sized ones and those that have relatively slow reaction time (e.g. daphnids) to the dangers of predation (Lieschke and Closs, 1999). This phenomenon creates ecological gap where the less competitive and small sized zooplankton, mostly the rotifers, dominate in these two lakes (Lemma et al., 2001). *P. africanus* is known to overcome such pressures of vertebrates mainly due to their fast reaction and rapid movements (Masson et al., 2001; Lemma, 2004).

From this study it was inferred that adaptation to migration by *P. africanus* into deeper waters by daylight and approaching surface waters in the dark was prevalent. However, unlike many reports particularly on calanoids of marine systems (e.g. Dagg et al., 1989;

Table 4. Water chemical analyses of pooled samples collected from 0 to 20 m on 23.03.2004, Lake Hora-Arsedi

Cations	meq L^{-1}	Anions	meq L^{-1}	Anions	meq L^{-1}
Ca^{2+}	1.36	Cl$^-$	2.92	NO$_3^-$	Trace
Mg^{2+}	4.68	SO$_4^{2-}$	7.00	PO$_4^{3-}$	0.01
K$^+$	1.90	CO$_3^{2-}$	4.95	TDS (mg L^{-1})	1580
Na$^+$	25.11	HCO$_3^-$	13.94		
Sum	33.05	Sum	28.81		

TDS stands for total dissolved solids.

Tarling et al., 2000; Shimode and Shirayama, 2004) the depth of migration was limited to the upper 20 m with the highest concentration being at about 3 m in both study lakes (Figs. 10 and 11), while there was still warm temperature of 19 °C way down up to the sediments of both lakes. Here then emerged two questions as what the reasons could be for this shallow depth of migration.

Firstly, *P. africanus* migration into deeper waters by daylight hours could be to avoid the deleterious effects of the tropical solar radiation (Leech et al., 2005a, b), which could have ultimately served the predator avoidance behavior of these calanoids of both lakes. Secondly, this migration of calanoids by day light down to 3 m and returning to the surface by darkness is too shallow when compared with the experiences gathered from freshwater and marine systems (LaRow, 1970; Duval and Geen, 1976; Masson and Pinel-Alloul, 1998; Besiktepe, 2001; Liu et al., 2003) which state that migrations up 100 m depth and more have been recorded. This could probably be explained by the facts that waters below 3 m start to show drastic decrease in dissolved oxygen finally approaching nil at 5–8 m and below (Figs. 4 and 5). Another factor is the shallow Seechi depths (Figs. 8 and 9) that indicated the lakes are so much turbid that by 3 m depth calanoids are already protected from the deleterious effects of solar radiation and have found sufficient refuge from visual predation of vertebrates and still reap the benefits of staying in reasonably upper waters. Leech et al. (2005a) suggested that copepods and rotifers that avoid solar radiation
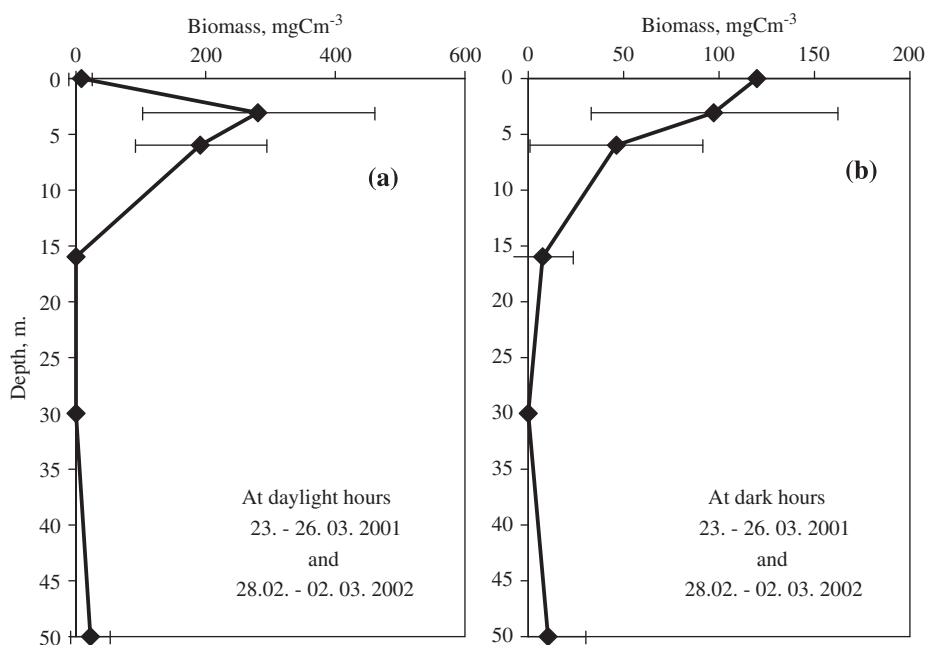

Fig. 10. *Paradiaptomus africanus* biomass measurements by depth at Lake Bishoftu-Guda (a) at daylight hours and (b) at dark hours both for the periods of 22.–23.03.2001 and 28.02.2002–01.03.2002 (number of observations = 12). Error bars indicate the variations in biomass during the different sampling hours.
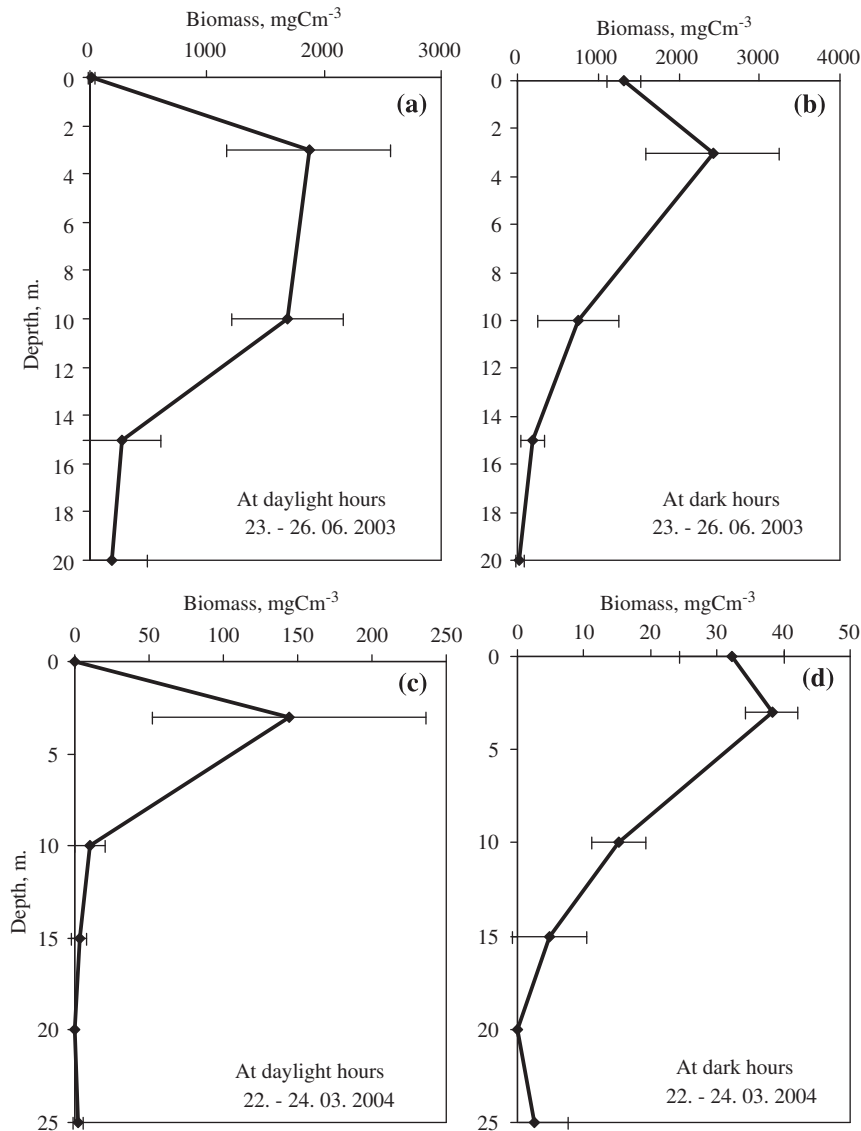
Fig. 11. *Paradiaptomus africanus* biomass measurements by depth at Lake Hora-Arsedi (a) at daylight hours and (b) at dark hours both for the periods of 23.–26.06.2003 and 22.–24.03.2004 (number of observations = 16). Error bars indicate the variations in biomass during the different sampling hours.

remain in the epilimnion, which apparently is the case in these two lakes. It would have been a supplementary advantage if depth profiles of light quantum were measured in Lakes Bishoftu-Guda and Hora-Arsedi to support the amount of darkness suggested by Secchi depth measurements (see Shimode and Shirayama, 2004). Selection of the appropriate light intensity to reduce the risk of predation be it at a depth of 3 m as in L. Bishoftu-Guda and Hora-Arsedi or in much deeper waters as in marine systems (e.g. 150 m in Dabob Bay, Washington, Dagg et al., 1989) or avoiding severe tropical radiation could be a natural selection mechanism which such animals as *P. africanus* developed through evolution (Masson and Pinel-Alloul, 1998).

An additional probable reason for the shallow migration depths could be the chemically dense environment below 20 m as seen in the high conductivity measurements of the lakes (Figs. 6 and 7). There is every reason to believe that freshwater macrozooplankton prefer as dilute and as less turbid water as possible to maintain a homeostatic internal biological conditions and continue to proliferate successfully maintaining at the same time normal DVM (see also Masson and Pinel-Alloul, 1998; Masson et al., 2001; Roman et al., 2001; Liu et al., 2003; Lemma, 2006). These scenarios of dissolved oxygen, Secchi depth and conductivity would be too costly for *P. africanus* to migrate beyond the depths attained in the study lakes and hence these macrozooplankton remained mostly at around 3 m

depth and decreasingly extending up to 20 m. This depth distribution by *P. africanus* might have created the condition for a quick ascent at dawn to surface waters and quick descent at daybreak to deeper waters and at the same time obtain the desired protection from visual predation of vertebrate predators and/or avoidance of solar radiation. This behavior is apparently assisted by the short reaction time and quick movement of *P. africanus* (Lieschke and Closs, 1999; Masson et al., 2001; Lemma, 2004).

Although thermal stratification was observed in both study lakes with surface water ranging in temperature between 21 and 24 °C and bottom waters were at 19 °C, *P. africanus* did not seem to face metabolic disadvantages because of decreased temperature by migrating into deep waters. This is quite exceptional to the scenario observed in temperate lakes, where summer temperatures varied between surface water temperatures of 24 °C to 6–7 °C at even 9 m in Lake Dagow, which was exposing calanoids and daphnids to severe temperature limitations (Lemma, 2004). The fact, however, remains that these small temperature differences between surface and bottom waters in Lakes Bishoftu-Guda and Hora-Arsedi have caused appreciable vertical density differences and prolonged stratification that resulted in the differences that were recorded in terms of dissolved oxygen, conductivity and some of the variations in water chemistry. Hence, remaining mostly at 3 m depth gave *P. africanus* the added advantage of staying in oxygen-rich depth while at the same obtaining protection from both radiation and visual predation. In addition to evasion of visual predation and avoidance of solar radiation, macrozooplankton such as *P. africanus* may have added advantages by swimming into deeper waters by daylight to prevent their population from being drifted to shallow shore areas by onshore tidal currents, as these animals were largely distributed in the central parts of the study lakes where they can freely exercise their fast reactions and rapid movements away from danger of predation, radiation and even winds (Lieschke and Closs, 1999; Masson et al., 2001; Shimode and Shirayama, 2004; Lemma, 2004).

Having established the diel migration pattern of *P. africanus*, it should be logical to think that feeding activity as well followed a diel rhythm where these organisms conduct their maximum feeding and other metabolic activities during the dark hours at surface waters where plankton are available in the desired quantity and diversity (with apparently sufficient tropical night temperatures at the surface) and feed comparatively less during the daylight hours in deeper waters where food is relatively scanty (Tarling et al., 2000). This way dangers of predation and exposure to lethal solar radiations are minimized so long as *P. africanus* remains in the dark be it at the surface at night or in deep waters in the daylight hours or simply 24 h of a day.

Another aspect of tropical lakes such as Bishoftu-Guda and Hora-Arsedi is the absence of invertebrate predators such as *Chaoborus* sp. and *Leptodora* sp. or any other organism that could have filled their environmental niche. These predators along with the more vulnerable daphnids that are relatively slow reacting to visual predation are wiped out by the year-round vertebrate predation in tropical waters (Fernando, 1994; Lemma et al., 2001).

In general, this work has brought out the DVM pattern of *P. africanus* in two tropical crater lakes, where avoidance of deleterious tropical solar radiation and/or the widely accepted predator evasion are apparently at work. This DVM pattern observed with *P. africanus* operated in Lakes Bishoftu-Guda and Hora-Arsedi in such environmental conditions where temperatures are high from surface to bottom, high turbidity, formation of anoxic scenarios in deep waters, bio-chemical activities are presumed to be high mainly due to high water temperature throughout the year, and predation pressure is potentially persistent throughout the year owing to the openness of lakes in the tropics, i.e. absence of air temperatures at or below the freezing point as in temperate lakes. Temperature probably played no significant role in DVM and the vertical migration ranges exhibited by *P. africanus* in tropical waters as compared with temperate lakes scenarios. It is, however, recommended that seasonal studies over a number of years should be conducted to correlate DVM of *P. africanus* biomass cycles and their vertical migration with population dynamics of phytoplankton and zooplankton species and seasonal variations in visual predators inhabiting Lakes Bishoftu-Guda and Hora-Arsedi, the light climate conditions and the seasonal cycles in internal and external nutrient loads.

Acknowledgments

reviewers have made significant contributions towards the improvement of this paper.

References

Aguilera, X., Crespo, G., Declerck, S., de Meester, L., 2006. Diel vertical migration of zooplankton in tropical high mountain lakes (Andes, Bolivia). Pol. J. Ecol. 54 (3), 453–464.

Alonso, C., Rocco, V., Barriga, J.P., Battini, M.A., Zagarese, H., 2004. Surface avoidance by freshwater zooplankton: field evidence on the role of ultraviolet radiation. Limnol. Oceanogr. 49 (1), 225–232.

Baxter, R.M., Prosser, M.V., Talling, J.F., Wood, R.B., 1965. Stratification in tropical African lakes at moderate altitude (1500 to 2000 m). Limnol. Oceanogr. 10, 511–520.

Beadle, L.C., 1981. The Inland Waters of Tropical Africa, second ed. Longman Inc., New York.

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

Blachowiak-Samolyk, K., Kwasniewski, S., Richardson, K., Dmoch, K., Hansen, E., Hop, H., Falk-Peterson, S., 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.

Børshiem, K.Y., Andersen, 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.

Bradford-Grieve, J.M., Nodder, S.D., Jillet, J.B., Cirrie, K., Lassey, K.R., 2001. Potential contribution that the copepod Neocalanus tonsus makes to downward carbon flux in the Southern ocean. J. Plankton Res. 23 (9), 963–975.

Cuker, B.E., Watson, M.A., 2002. Diel vertical migration of zooplankton in contrasting habitats of Chesapeake Bay. Estuaries 25 (2), 296–307.

Dagg, M.J., Frost, B.W., Walser, W.E., 1989. Copepod diel mogration, feeding, and the vertical flux of pheopigments. Limnol. Oceanogr. 34 (6), 1062–1071.

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

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

Fassil, D., 2007. Some aspects of the biology of Oreochromis niloticus Linn. In: Lakes Hora and Babogaya and Tilapia zillii, Grev. (Pisces: Cichlidae in Lake Babogaya, Ethiopia). M.Sc. Thesis, Faculty of Science, Department of Biology, Addis Ababa University, Ethiopia.

Fernando, C.H., 1994. Zooplankton, fish and fisheries in tropical fisheries. Hydrobiologia 272, 105–123.

Frank, T.M., Widder, E.A., 1997. The correlation of down-welling irradiance and staggered vertical migration patterns of zooplankton in Wilkinson Basin, Gulf of Maine. J. Plankton Res. 19 (12), 1975–1991.

Gliwicz, M.Z., 1986. Predation and the evolution of migration in zooplankton. Nature 320, 746–748.

Green, J., 1986. Zooplankton associations in some Ethiopian crater lakes. Freshwater Biol. 16, 495–499.

Green, J., Mengistou, S., 1991. Species density and community structure of Rotifera in a salinity series of Ethiopian inland waters. Hydrobiologia 209, 95–106.

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

Han, B-P., Straškraba, M., 2001. Control mechanisms of diel vertical migration: theoretical assumptions. J. Theor. Biol. 210, 305–318.

Hays, G.C., Proctor, C.A., John, A.W.G., Warner, A.J., 1994. Interspecific differences in the diel vertical migration of marine copepods: the implications of size, color and morphology. Limnol. Oceanogr. 39 (7), 1621–1629.

Kasprzak, P., Krienitz, L., Koschel, R., 1993. Changes in the plankton of Lake Feldberg Haussee (Germany, Mecklenburg-Vorpommern) in response to biomanipulation. Arch. Hydrobiol. 128 (2), 149–168.

Kebede, S., 1999. Hydrology and hydrochemistry of Bishoftu Crater Lakes (Ethiopia): hydrogeological, hydrochemical and oxygen isotope modeling. M.Sc. Dissertation, Faculty of Science, Department of Earth Sciences, Addis Ababa University.

Kebede, E., Humber, D., Belay, A., 1986. The explosion crater lakes of Debrezeyt. WALIA: J. Ethiop. Wildl. Nat. Hist. Soc. 9, 11–15.

Kebede, S., Ayenew, T., Umer, M., 2001. Application of isotope and water balance approaches for the study of the hydrological regime of the Bishoftu Crater Lakes, Ethiopia. SINET: Ethiop. J. Sci. 24 (2), 151–166.

Lampert, W., 1989. The adaptive significance of diel vertical migration of zooplankton. Funct. Ecol. 3 (1), 21–27.

Lampert, W., 1993. Ultimate causes of diel vertebrate migration of zooplankton: new evidence for the predator-avoidance hypothesis. Arch. Hydrobiol. Beih. Ergebn. Limnol. 39, 79–88.

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

Leech, D.M., Williamson, C.E., Moeller, R.E., Hargreaves, B.R., 2005a. Effects of ultraviolet radiation on the seasonal vertical distribution of zooplankton: a database analysis. Arch. Hydrobiol. 162 (4), 445–464.

Leech, D.M., Padeletti, A., Williamson, C.E., 2005b. Zooplankton behavioral responses to solar radiation vary within and among lakes. J. Plankton Res. 27 (5), 461–471.

Lemma, B., 1995. Seasonal limnological studies on lake Alemaya: a tropical African lake, Ethiopia. Arch. Hydrobiol./Suppl. 107 (2), 263–285.

Lemma, B., 1997. Der Einfluss zooplanktonfressender Fische auf die Größenfraktionen des Phytoplanktons und die Primärproduktion in gemäßigten und tropischen Seen. Ph.D. Dissertation.

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

Lemma, B., 2006. Diel vertical migration of zooplankton in a shallow tropical lake, Ethiopia. SINET: Ethiop. J. Sci., accepted for publication

Lemma, B., 2008a. Long-term observations on contrasting water use scenarios of Lakes Haramaya and Hora-Kilole, Ethiopia (1986–2006). Int. Rev. Hydrobiol. Germany, submitted for publication.

Lemma, B., 2008b. Introduction to Lake Ecology, Aquaculture and Fisheries in Ethiopia. Haramaya University, in press.

Lemma, B., Benndorf, J., 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.

Lieschke, J.A., Closs, G., 1999. Regulation of zooplankton composition and distribution by a zooplanktivorous fish in a shallow, eutrophic floodplain lake in south east Australia. Arch. Hydrobiol. 146 (4), 397–412.

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

Masson, S., 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.

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

McLaren, I.A., 1974. Demographic strategy of vertical migration by a marine copepod. Am. Nat. 108 (959), 91–102.

Nomura, J., 2006. Diel variability in vertical distribution in high chlorophyll of the Galapagos Archipelago, Ecuador. ⟨http://students.washington.edu/jmnomura/figures.html⟩.

O'Brien, J.W., 1987. Planktivory by freshwater fish thrust and parry in the Pelagia. In: Kerfoot, W.S., Sih, A. (Eds.), Predation, Direct and Indirect Impacts on Aquatic Communities. University of New England, Hanover and London, pp. 3–16.

Pawels, J.M., van Ranst, E., Varloo, M., 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.

Pearre, S., 2000. Long-term changes in diel vertical migration behavior: more ups and downs. Mar. Ecol. Prog. Ser. 197, 305–307.

Perticarrari, A., Arcifa, M.S., Rodrigues, R.A., 2004. Diel vertical migration of copepods in a Brazilian lake: a mechanism for decreasing risk of Chaoborus predation? Braz. J. Biol. 64 (2), 289–298.

Prosser, M.V., Wood, R.B., Baxter, R.M., 1968. The Bishoftu Crater Lakes: a bathymetric and chemical study. Arch. Hydrobiol. 65, 309–324.

Ramos-Jiliberto, R., Zuñiga, L.R., 2001. Depth selection patterns and diel vertical migration of Daphnia ambigua (Crustacea: Cladocera) in Lake El Plateado. Rev. Chil. Hist. Nat. 74, 573–585.

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

Stich, H-B., Lampert, W., 1981. Predator evasion as an explanation of diurnal vertical migration by zooplankton. Nature 291, 396–398.

Shimode, S., Shirayama, Y., 2004. Diel changes in vertical distribution of copepods community in Tanabe Bay, Japan. J. Mar. Biol. UK 84, 607–615.

Talling, J.F., 1963. Origin of stratification in an African rift lake. Limnol. Oceanogr. 8, 68–78.

Tarling, G., Burrows, M., Mathews, J., Saborwski, R., Buchholz, F., Bedo, A., Mayzaud, P., 2000. An optimization model of the diel vertical migration of northern krill (Meganyctiphanes norvegica) in the Clyde Sea and the Kattegat. Can. J. Fish. Aquat. Sci. 57 (Suppl. 3), 38–50.

Tsui, N., 2006. Vertical migration of marine copepods in the Galapegos Islands in relation to size and color. ⟨http://courses.washington.edu/ocean444/SecondDraft/Tsui.pdf#search='zooplankton%20and%20and%202006'⟩.

Weismann, A., 1887. Das Tierleben im Bodensee. Schr. Ver. Geschichte Bodensee Umgebung 7, 1–31.

Wood, R.B., Prosser, M.V., Baxter, R.M., 1976. The seasonal pattern of thermal characteristics of four of the Bishoftu Crater Lakes, Ethiopia. Freshwater Biol. 6, 519–530.

Wood, R.B., Talling, J.F., 1988. Chemical and algal relationships in a salinity series of Ethiopian inland waters. Hydrobiologia 158, 29–67.

Zaret, T.M., Suffern, J.S., 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr. 21, 804–813.