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PRIMARY RESEARCH PAPER

Diel Vertical Migration of zooplankton in a eutrophic bay of Lake Victoria

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Abstract We studied the Diel Vertical Migration (DVM) of several zooplankton taxa and an important zooplanktivore *Rastrineobola argentea* in a eutrophic bay of Lake Victoria for a total of 3 months during wet and dry seasons. Zooplankton were sampled twice a month at full moon and new moon. The zooplankton community of this lake was numerically dominated by cyclopoid copepods (>80%) of which 80% were juveniles. The composition of zooplankton was not significantly different ($P > 0.05$) for the different sampling months (November 2000, March 2001 and July 2001), but total zooplankton abundance was significantly lower ($P < 0.05$) in July (dry season) than during March or November (wet seasons). DVM behaviour was observed in some of the zooplankton groups including *Tropocyclops* spp., *Thermocyclops* spp., *Thermodiaptomus galeboides* and *Diaphanosoma excisum*. In these groups, we also observed that they were significantly ($P < 0.05$) more abundant at full moon than at new moon in some months, a pattern not seen in non-DVM groups. The amplitude of migration tended to be higher at new moon than full moon for all DVM zooplankton but not significantly so ($P > 0.05$). The zooplanktivore *R. argentea* exhibits typical DVM behaviour, perhaps to avoid visual predation itself, but it also increases the predation pressure on zooplankton in deeper waters. Feeding times for *R. argentea* peak just after dusk and dawn. For the copepod calanoid *T. galeboides*, there was a strong relationship ($P < 0.05$) between the amplitude of migration and midday (12:00) water transparency, suggesting that these zooplankton may have descended deeper on days with higher water transparency. In the absence of temperature and food gradients but with predation pressure from a migrating zooplanktivore, the depth of descent of zooplankton may be well associated with water transparency.

Keywords Lake Victoria · Zooplankton · Diel Vertical Migration · Murchison Bay

Introduction

Zooplankton constitute a major link between primary production and higher trophic levels in aquatic ecosystems. An intriguing behaviour of zooplankton is their vertical movement within a water column known as Diel Vertical Migration (DVM). Zooplankton move to deeper, darker and sometimes even anoxic waters during daytime and move upwards to

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surface waters during night time. The reverse movement also occurs with some zooplankton moving upwards during the day and moving downwards during the night, and some zooplankton may not exhibit migratory behaviour at all.

It has been widely accepted that predation plays a key role in DVM of zooplankton. The predator avoidance hypothesis (Zaret & Suffern, 1976) suggests that DVM is a way for zooplankton to avoid visual predators like fish. 'Normal' migration behaviour is to move to the dark hypolimnion during daytime (Lampert, 1993), and to move back to the epilimnion at night when the threat of predation by visual predators is reduced, and because the epilimnion is assumed to have a more favourable environment with a higher concentration or quality of food as well as warmer temperatures (Lampert et al., 2003). However, the assumption that the epilimnion has warmer temperatures and a higher concentration and quality of food has been challenged. Williamson et al. (1996) argue that in fresh water and marine systems with strong temperature gradients and deep-water chlorophyll maxima, the DVM patterns for zooplankton are altered. In such situations, zooplankton are assumed to occupy depths with the highest food abundance (Jakobsen & Johnsen, 1987a), but also with the most optimal temperature conditions (Gliwicz & Pijanowska, 1988). In the absence of predation, zooplankton will distribute themselves in a water column according to the availability of food resources (Lampert et al., 2003), with other factors like competition (Larsson, 1997) contributing to their distribution to maximize fitness. The choice for an optimal habitat may therefore be a function of several factors including temperature, food availability and predation (Beklioglu et al., 2008).

Change in light intensity is the proximate cue for DVM (Ringelberg et al., 1991). At dawn and dusk, light intensity changes rapidly and correlations exist between the measured descent and ascent velocities of zooplankton and the rate of the relative increases and decreases in light intensity, respectively (Ringelberg & Flik, 1994). Lunar periodicity may also act to modify the effect of change of light intensity on DVM. The tendency for zooplankton to migrate upwards following a full moon might be less than on the nights following a new moon because of an increased risk of predation by visual hunters (Gliwicz, 1986).

Conditions of year-round predation from fish, insects and insect larvae, as well as algal blooms in eutrophic tropical lakes (Fernando, 1994), may further modify DVM behaviour of zooplankton, especially in shallow lakes that experience constant mixing all year round and have uniform temperature and food gradients (vonSperling, 1997). Zooplankton in such circumstances would be expected to reside in deeper waters all the time to avoid visual predation and would not ascend as expected (Gliwicz & Pijanowska, 1988) since the advantage of acquiring better resources (e.g. food) and conditions (e.g. temperature) may not necessarily be strong enough. Gliwicz & Pijanowska (1988) concluded that the absence of food gradients or better food quality in upper strata and absence of thermal stratification can affect the occurrence of DVM in zooplankton and that the depths in which zooplankton descend is related to the water transparency.

In this study, we looked for evidence of DVM among several zooplankton groups in the inner Murchison Bay, Lake Victoria (Uganda), and relationships with the environmental parameters of dissolved oxygen, water temperature and water transparency. This study was carried out during 3 months—November 2000, March 2001 and July 2001—at lunar phases of full moon and new moon. The months of sampling lie within the short wet, long wet and long dry season, respectively. We also looked at the diel vertical distribution, diet and feeding habits of the most important zooplanktivore in Lake Victoria *Rastrineobola argentea* (Wanink et al., 2002) during May (wet season), June and July 2001 (dry season) following the zooplankton survey.

Methods

Study site

Lake Victoria is the world's largest tropical fresh water lake covering an area of 68,800 km^2. In the last 50 years the lake has undergone wide-scale eutrophication, characterised by a loss of deep-water oxygen (Hecky et al., 1994), dominance of bloom-forming cyanobacteria (Verschuren et al., 2002) and losses in fish biodiversity (Ogutu-Ohwayo, 1990). Murchison Bay of Lake Victoria is situated 8-km east of the capital city of Uganda, Kampala, and lies between latitude

00°15′N–00°18′N and longitude 32°33′E–32°41′E at an altitude of 1,135-m above sea level. The Bay is divided into two parts; the inner bay (18 km^2) and the outer bay (180 km^2) separated by a narrow section. Average depth of the inner bay is 3.2 m. The Bay and its catchment has an average annual precipitation of 1,400 mm and a bimodal precipitation pattern with peaks in April and September–October (wet seasons) with January–February and June–August (dry seasons) having minimum precipitation.

Data collection and analysis

Zooplankton sampling and measurement of environmental parameters were carried out on 11–12 November 2000 (full moon), 26–27 November 2000 (new moon), 9–10 March 2001 (full moon), 25–26 March 2001 (new moon), 5–6 July 2001 (full moon) and 20–21 July 2001 (new moon). A fishing survey to collect samples of the zooplanktivore *R. argentea* was carried out during three consecutive months in May, June and July of 2001.

Environmental variables

On each sampling occasion, dissolved oxygen and water temperature were measured at 1-m depth intervals from the surface (0 m) down to a depth of 17 m, using a YSI 85 dissolved oxygen and conductivity instrument. Water transparency was measured at 06:00, 12:00 and 18:00 using a 20-cm white secchi disc. Water samples for phytoplankton were collected at midday (12:00) during every sampling occasion, from the surface and at a depth of 10 m, using a 5 l water column sampler of a modified Ramberg type. From this 5 l sample, 200 ml were collected in a brown glass bottle and preserved by adding 5 ml of Lugol's solution. In the laboratory, the phytoplankton samples were analysed under inverted microscope using the Utermöhl technique (Brettum & Halvorsen, 2004).

Zooplankton

Samples were collected at several depth intervals (0–1 m, 1–2 m, 4–5 m, 7–8 m, 10–11 m, 13–14 m and 16–17 m) every 6 h (12:00, 18:00, 00:00, 06:00 and 12:00 the following day). Sampling for zooplankton was carried out at a single site (00°14.62′N; 32°38.59′E) at the narrow section of the bay which has several deep depressions of up to 22 m. At each depth, two replicate samples were taken using a 5 l water column sampler of a modified Ramberg type (but due to unavoidable circumstances only single samples were collected during the new moon in November and July). Samples were filtered through a 45-µm mesh net and fixed in 95% alcohol.

Total counts (all individuals in the sample) of zooplankton were made for each sample using a Sedgwick rafter cell and a stereo microscope. Identification was done up to species level for rotifers and for micro crustaceans where possible using standard identification keys (Fernando, 2002).

Fish (*Rastrineobola argentea*)

Fishing for the zooplanktivore *R. argentea* was carried out over a 24-h period at 4 h intervals (12:00—midday, 16:00—afternoon, 20:00—dusk, 00:00—night, 04:00—dawn and 08:00—morning).

Two monofilament, multimesh nylon gill nets, also known as Nordic survey nets (Appleberg et al., 1995) with 12 sections of 5.0, 6.25, 8.0, 10.0, 12.5, 15.5, 19.5, 24.0, 29.0, 35.0, 43.0 and 55.0 mm (unstretched) mesh, net depth 5 and 2.5 m length of each section, were used to sample *R. argentea* at a single site (9-m depth) a few hundred metres away from the zooplankton sampling site. (The site used for zooplankton sampling was too deep to allow us to cover the entire water column with the available fishing nets.) One gill net was set at the surface and the other on the bottom covering the whole water column. The gill nets were deployed for 30–45 min at each sampling time. Fish were removed from the gill nets and their body length (to the nearest 0.1 mm—standard length and total length—using vernier callipers) and fresh body weight (to the nearest 0.1 g using a spring balance) were measured. Identification and measurements were carried out using standard methods (Greenwood, 1966), while taking note of the position/location of the fish in the gill net and recording the mesh-size (we divided each net equally into two sections—top and bottom each section representing at least 2-m depth). Fish were then immediately preserved in 4% formalin.

Each fish specimen was dissected, the stomach removed and preserved in 4% formalin for further analysis. Before analysis, they were washed thoroughly to remove the formalin and then placed on a

Petri-dish for identification. The gut was then dissected and the contents were removed and suspended in water. The gut content was analysed to the lowest taxonomic level possible. The number of each prey organism found in the gut was enumerated under a dissecting microscope. The prey organisms were transferred to a calibrated microscope and length measurements were performed. Standard formulae (Dumont et al., 1975) were used to convert body size to dry weight.

Statistical analysis

We used Pearson's moment correlation to test for relationships between environmental variables. We utilised a generalised linear model—GLM (using quasi-Poisson distribution and a log-link function due to over-dispersion in the count data) (Crawley, 2007) to test for a relationship between moon phase and mean abundance of zooplankton groups in the different months of study. The resulting model was subjected to an *F* test. We used a two-way ANOVA to test for an effect of moon phase and water transparency on amplitude/range of migration of zooplankton. We also used a Welch two sample *t* test to check for evidence of differences in water transparency (at 12:00) with moon phase. The amplitude of migration for zooplankton was calculated as the difference between the mean population depth at midday (12:00) and the mean population depth at night (00:00). The mean population depth (*Z*) at each sampling time was obtained using the formula:

$$Z = \frac{\sum [N_i(Z_i a_i)]}{\sum N_i a_i}$$

where N_i, abundance at depth Z_i; Z_i, depth at given time and a_i, number of depths represented by sample *i*.

The weight factor for a_i was therefore 1, 2, 3, 3, 3, 3, 2 for the depths sampled; 0.5, 1.5, 4.5, 7.5, 10.5, 13 and 16.5, respectively (the first two and last depth reading represent <3 depths each, maximum depth was at least 18 m). All statistics were performed using R (version 2.8.1) (R Development Core Team, 2008).

Results

Environmental variables

We observed diel variation in the thermal stratification of Murchison Bay during all months of sampling (Fig. 1), especially in the months of the wet seasons (November 2000 and March 2001). Thermal stratification normally built up during the morning hours but was broken down during the afternoon and night hours (Fig. 1). Levels of dissolved oxygen (Fig. 2) were highest in November and lowest in March. Oxygen saturation was >1 mg l^{-1} during all sampling months at all depths except at night (00:00) in March (Fig. 2). Data collected for dissolved oxygen also show that the greatest differences between high and low oxygen levels were in November and the smallest differences in July.

Phytoplankton biomass in Murchison Bay was high (>1,500 mm^3 m^{-3}) both at the surface (0 m) and in mid water column samples (10 m) during March and July 2001, which lie in a wet season and dry season, respectively. We did not find any significant differences in phytoplankton biomass and composition at the depths sampled during the two sampling months ($P > 0.05$, Fig. 3). The phytoplankton composition in March and July 2001 was dominated by cyanobacteria, which made up to 84 and 92% of total biovolume, respectively, both at the surface and at 10-m depth (Fig. 3).

Secchi depth of the inner Murchison Bay ranged from 0.64 m (March 2001) to 1.98 m (July 2001). There was no significant difference in water transparency ($P = 0.35$) in the sampling months. Midday values of water transparency were higher during periods of full moon than during periods of new moon ($t = -3.3541$, df = 5.322, $P < 0.05$).

Zooplankton composition and abundance

The mean of zooplankton density from all sampling occasions at the depths sampled was 202.7 ± 44 (ind. l^{-1}). The zooplankton community was numerically dominated by cyclopoid copepods (84.9%). Among the cyclopoid copepods, 60.5% were nauplii, 25.2% were copepodites (I–V) and 13.1% were adults. *Tropocyclops* spp. was the most abundant among the adult cyclopoid copepods followed by *Thermocyclops neglectus*, *T. oblongutus*, *T. emini* and *Mesocyclops* spp., respectively. Calanoid copepods, cladocera and rotifers represented 6.6, 2.6 and 5.9% of the zooplankton community, respectively. Zooplankton densities in the month of November (244 ± 43.1 ind. l^{-1}) was significantly higher ($F = 15.7$, $P < 0.01$) than either in March (185 ± 6.6 ind. l^{-1}) or July

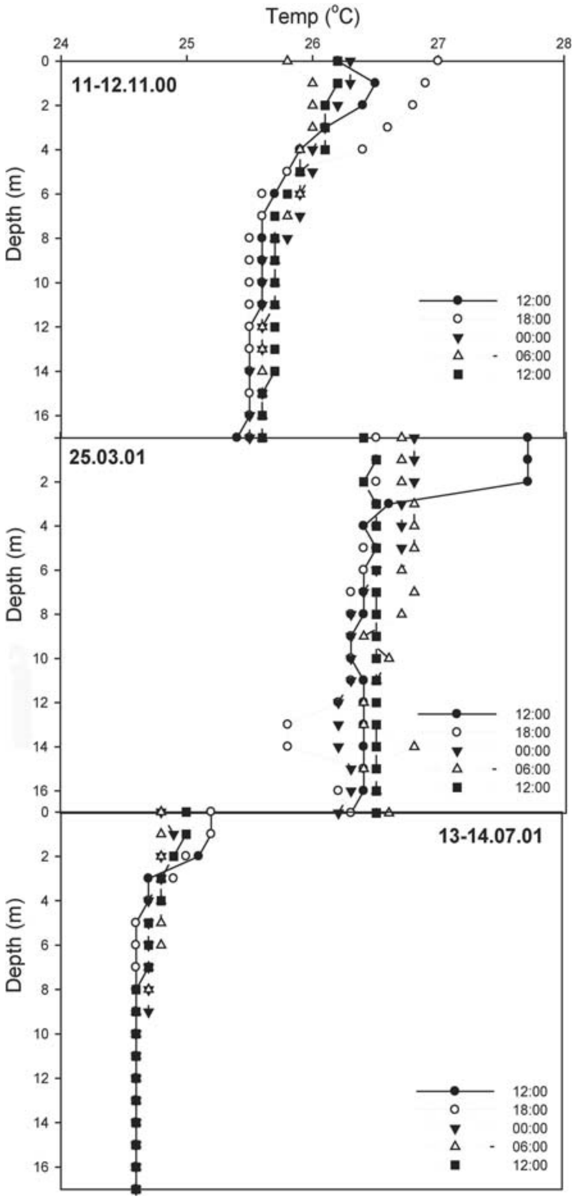


Fig. 1 Water temperature (°C) profiles in Murchison Bay during November 2000, March 2001, and July 2001 showing diel variation in the thermal stratification between the sampling occasions

(163 ± 25.3 ind. l^{-1}). However, zooplankton density was not significantly different ($P > 0.05$) between the wet season month of March and the dry season month of July.

Zooplankton density for the most abundant zooplankton groups (cyclopoid nauplii and copepodites) did not differ significantly between new moon and full moon ($P > 0.05$) in any sampling month. In November 2000, we observed a higher mean abundance of *Thermocyclops* spp. at new moon than at full moon ($P < 0.05$, Table 1). In contrast, in March 2001, mean abundances of *Thermocyclops* spp., *Tropocyclops* spp., *T. galeboides* and *D. excisum* were higher at full moon than at new moon

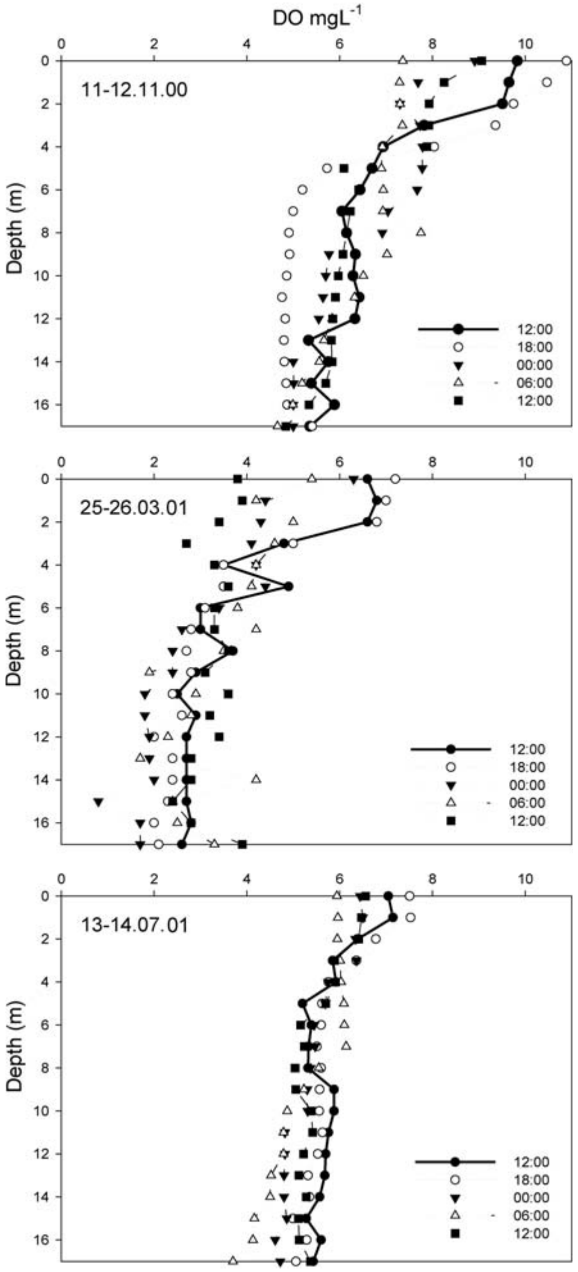


Fig. 2 Dissolved oxygen (mg l^{-1}) profiles in Murchison Bay during November 2000, March 2001, and July 2001 showing diel variation

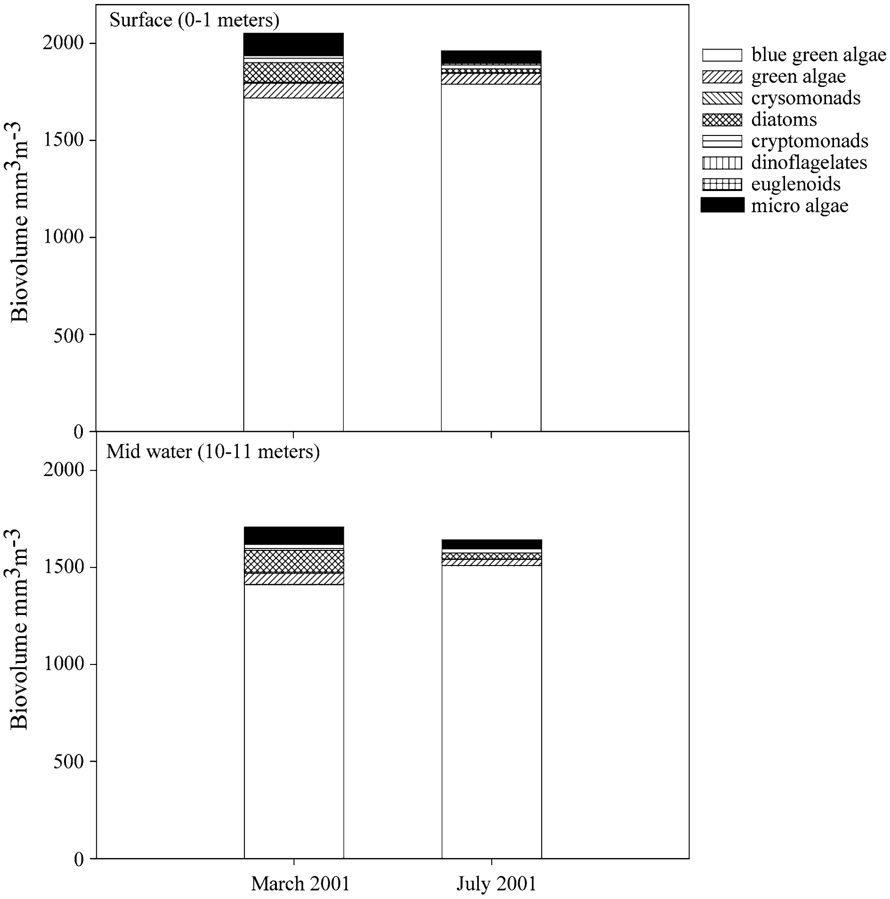


Fig. 3 Composition of phytoplankton at the surface and mid water (10 m) during March and July 2001

($P < 0.05$, Table 1) and in July 2001, there were higher mean abundances for *Thermocyclops* spp. and *D. excisum* at full moon than at new moon ($P < 0.05$, Table 1).

Zooplankton migration

The various zooplankton groups and species showed varying DVM behaviour. Groups including the copepod nauplii and copepodites, cladocera *Bosmina* and *Moina*, and all rotifer species did not show DVM. These were mostly uniformly distributed throughout the water column at all hours of the day.

For the groups that showed significant differences in mean abundances at different moon phase (Table 1), we analysed the amplitude of migration at new moon, but found no significant difference except for *D. excisum*, which had a higher migration amplitude in July than March or November ($F = 4.52$, $P < 0.05$) and for *T. galeboides* during March 2001 ($F = 7.8$, $P < 0.05$). Overall the amplitudes at new moon were not higher than at full moon ($P > 0.05$). We also observed an effect of water transparency on the amplitude of migration of *T. galeboides* ($F = 15.93$, $P < 0.01$).

Migrations of all groups presented in Table 1 were typified by a general movement from bottom waters at noon to near surface waters (3–4 m) at dusk, and a noticeable return to the deeper waters (10–12 m) at noon the following day (Fig 4).

Fish

Highest *Rastrineobola argentea* abundance was found at lower depths (5–9 m) during the day (Fig. 5). At dusk they were homogeneously distributed throughout the whole water column. During the night, the highest abundance occurred between 2 and 4 m, returning to a homogeneous distribution over the whole water column at dawn.

Table 1 Mean abundance (ind. l^{-1}, ±SD) at full moon and new moon with statistic of difference (*F*) and significance level (*P*), and amplitude of migration at new moon for zooplankton groups in Murchison Bay in November 2000, March 2001 and July 2001

Taxa	Mean abundance (ind. l^{-1}, ±SD)				Amplitude at new moon (m, ±SD)
	Full moon	New moon	*F*	*P*	
November 2000					
Thermocyclops sp.	6.9 (6.0)	10.5 (5.6)	6.21	0.015	3.39
March 2001					
Tropocyclops sp.	12.4 (8.2)	7.5 (3.4)	11.69	0.001	2.5 (0.8)
Thermocyclops sp.	17.8 (11.8)	10.3 (5.9)	12.49	<0.001	2.7 (0.7)
Thermodiaptomus galeboides	5.2 (3.1)	3.5 (2.6)	5.60	0.021	6.0 (0.3)
Diaphanosoma excisum	6.2 (4.5)	3.0 (2.1)	17.04	<0.001	1.9 (0.5)
July 2001					
Thermocyclops sp.	9.2 (7.1)	4.3 (3.7)	12.92	<0.001	3.2 (1.2)
D. excisum	2.7 (2.0)	1.4 (1.0)	13.51	<0.001	3.4 (3.9)

The diet of *R. argentea* consisted of a variety of food components including nauplii, copepodites, calanoids and cladocera. *Chaoborus* sp. larvae, pupae and insects were found in the guts of *R. argentea* during the night. Cyclopoid copepods were the most important prey to *R. argentea* contributing up to 80% (by number) of the diet (Fig. 6). The percentage of nauplii in the diet was highest in the afternoon (16:00, >30%) and lowest at night (00:00, <1%). The percentages for cladocera in the diet were higher at dusk, night and dawn, than during the day. Adult calanoid copepods (*T. galeboides*) were observed in the diets at dawn and midday only. *Chaoborus* sp. was present in gut contents only at night (00:00).

Highest gut content values were observed after dawn and at dusk (Fig. 7). Peak feeding times of *R. argentea* were from late afternoon till dusk and from dawn to morning.

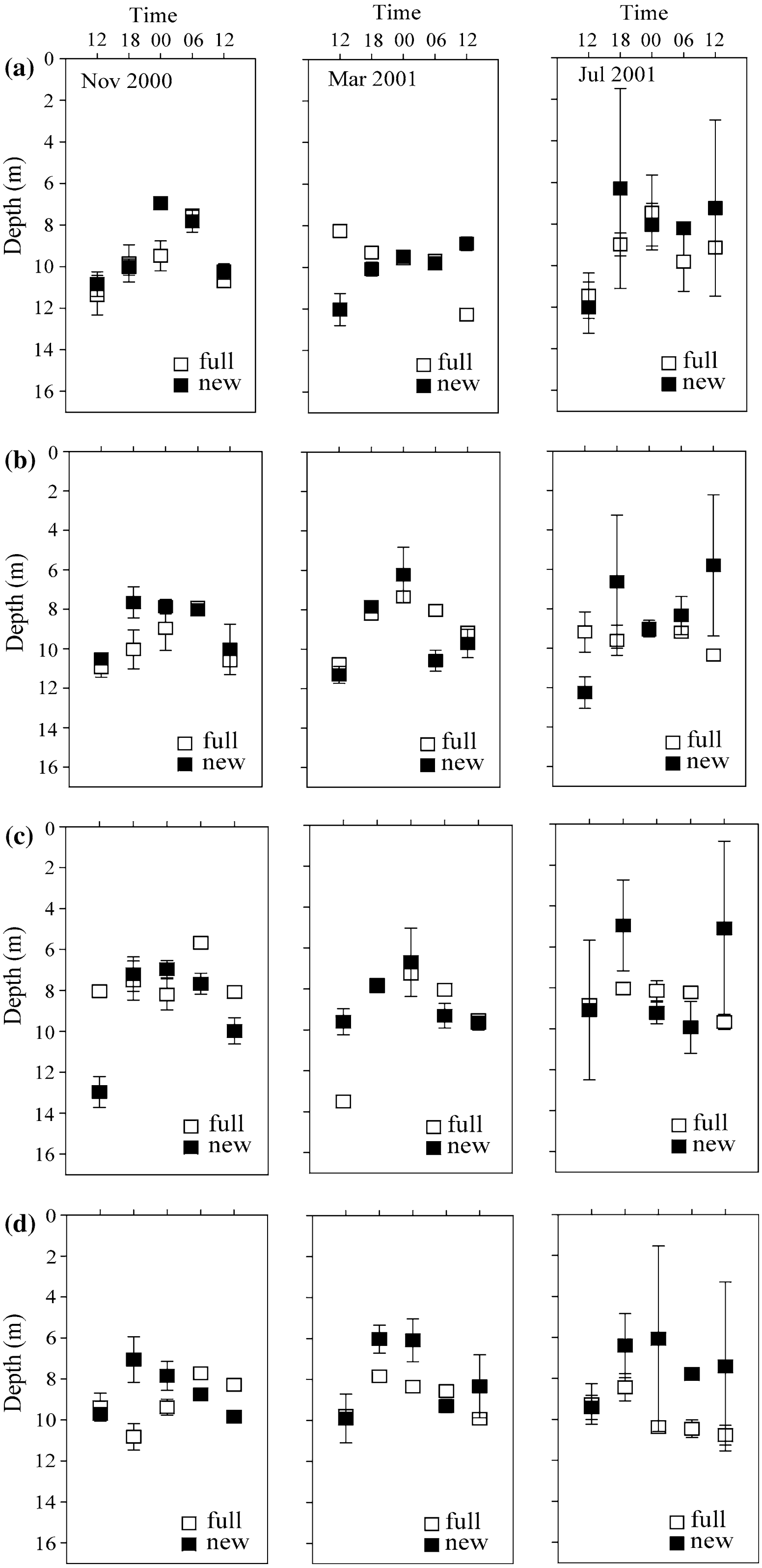
Discussion

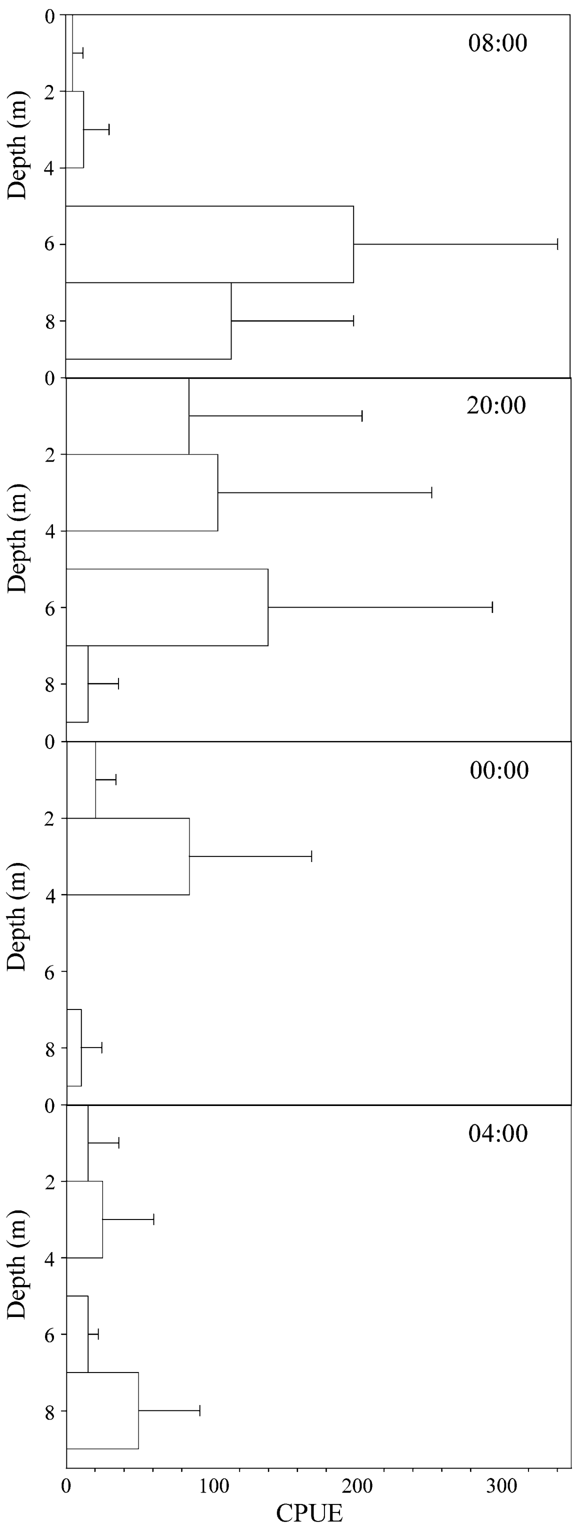
The zooplankton groups and species observed show varying degrees of DVM in Murchison Bay. For the small-sized groups (copepod nauplii and copepodites, rotifers, and *Bosmina* sp. and *Moina* sp.) DVM appears to be absent, yet for the larger-sized zooplankton, DVM patterns were observed especially at new moon. Previous studies on DVM in Lake Victoria (Worthington, 1931; Goldschmidt et al., 1990), which focused on the large copepod and cladocera groups, revealed similar DVM patterns. As predicted by the 'lunar trap' hypothesis (Gliwicz, 1986), mean zooplankton densities were higher at full moon than at new moon for the migrating groups (Table 1) especially in March 2001. The amplitudes of migration were, however, not significantly different at the different moon phases.

The physico-chemical conditions of Murchison Bay were quite typical of shallow eutrophic lakes with high phytoplankton abundance and absence of thermal stratification (Fernando, 1994) due to constant mixing during all the seasons sampled. The phytoplankton community is dominated by bloom-forming cyanobacteria which may contribute to the low levels of water transparency observed, particularly during the wet seasons (November 2000 and March 2001). The amplitude of zooplankton migration can be related to changes in water transparency (Gliwicz & Pijanowska, 1988), and in this study we observed a significant ($P < 0.01$) relationship between amplitudes of migration and water transparency for the copepod calanoid *T. galeboides*. Although water transparency was significantly higher at full moon than at new moon ($t = -3.3541$, df $= 5.322$, $P < 0.05$), we did not observe an interaction effect of water transparency and moon phase on the amplitude of migration for any of the groups analysed.

Lake Victoria has a high number of zooplankton predators (Mwebaza-Ndawula, 1994) of which the zooplanktivore *R. argentea* is probably the most

Fig. 4 Mean population depth of zooplankton (**a**—*Tropocyclops* spp. **b**—*Thermocyclops* spp. **c**—*Thermodiaptomus galeboides* and **d**—*Diaphanosoma excisum*) at full moon (*open squares*) and new moon (*closed squares*) during November 2000, March 2001 and July 2001 (*error bars* indicate 1 SD)





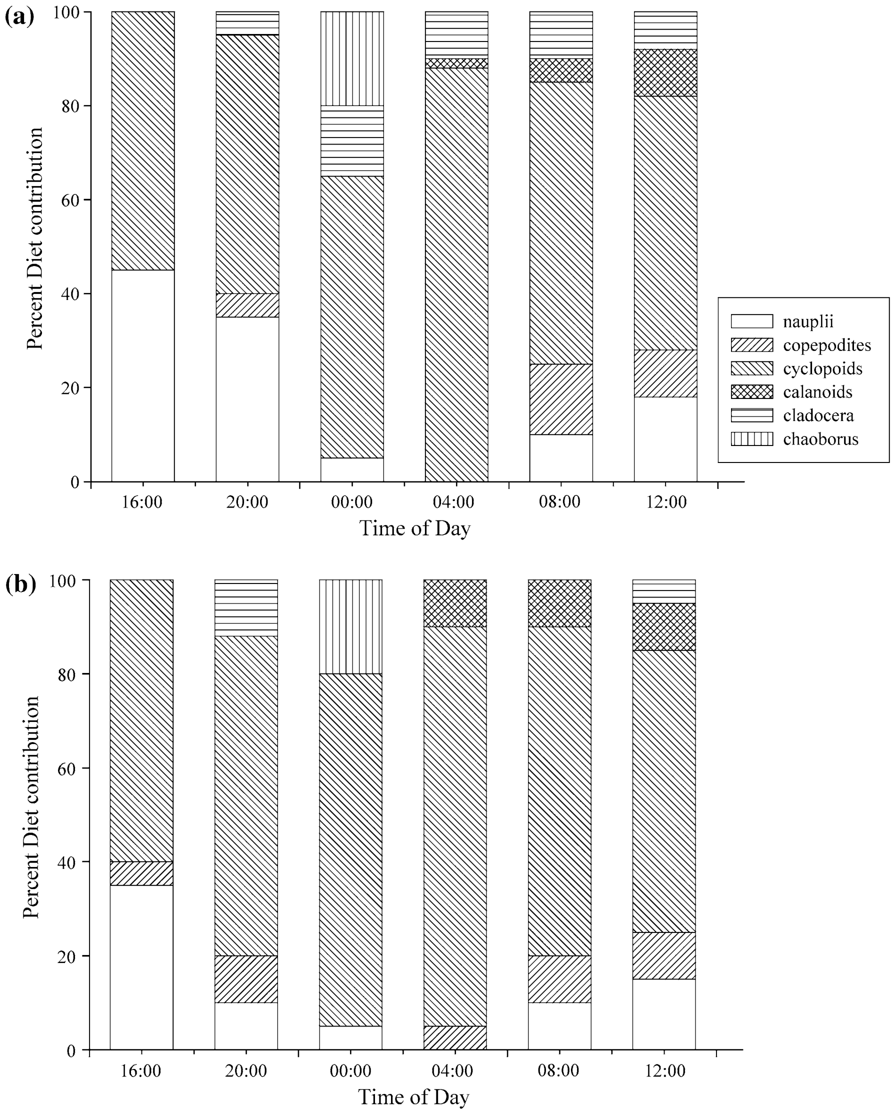
◀ **Fig. 5** Diurnal distribution patterns of *Rastrineobola argentae* averaged for May, June, and July 2001. Data are given in CPUE (catch per unit effort: i.e. number of fish caught per 20 m^2 net area with 30 min deployment time; *error bars* indicate 1 SD)

important (Mwebaza-Ndawula, 1998; Wanink, 1999). Predation in tropical lakes like Lake Victoria plays an important role in structuring zooplankton communities (Fernando, 1994), and as a result the zooplankton community of Murchison Bay is mostly dominated by small zooplankton (e.g. copepod nauplii, rotifers and small cladocera—*Bosmina* sp. and *Moina* sp.), similar results have been observed in other bays of Lake Victoria (Mwebaza-Ndawula, 1994). In a study in the northern parts of Lake Victoria Mwebaza-Ndawula (1998) found that larger copepods were more abundant in offshore areas probably due to lower fish (*R. argentea*) abundance and small copepods and cladocera were more abundant in inshore waters that also had high abundance of fish. Predation is often an ultimate cue for DVM, yet though we are able to show in this study that it is evident, we were unable to adequately study its influence on DVM of zooplankton. It has been suggested that in lakes where food and temperature gradients are absent, the influence of predation on DVM may also depend on the water transparency (Gliwicz & Pijanowska, 1988).

The food resource for herbivorous zooplankton in Murchison Bay is dominated by cyanobacteria which may be harmful (Haande et al., 2007) and are most often neither ingestible nor nutritious to zooplankton (Gliwicz, 1990; Lürling and Van Donk, 1997). Zooplankton grazers observed in our study are probably dependant on algae other than cyanobacteria as a food resource. It is evident from our results (Fig. 1) that, whichever phytoplankton groups, the zooplankton in Murchison Bay feed on, they may be uniformly distributed throughout the water column both by composition and amount, and thus most zooplankton are uniformly distributed throughout the water column (Larsson & Kleiven, 1996; Larsson, 1997).

Towards the end of the day, there may be a higher degree of competition for food especially in the lower, darker depths where zooplankton populations are slightly more abundant (Jakobsen & Johnsen,

Fig. 6 Diurnal changes in diet composition of *Rastrineobola argentae* during the months of (**a**) May 2001 ($n = 60$) and (**b**) July 2001 ($n = 60$)



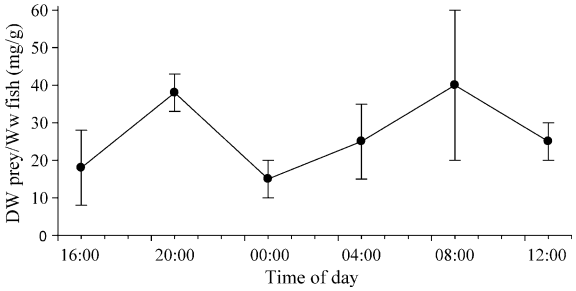


Fig. 7 Diurnal prey uptake of *Rastrineobola argentae* prey organisms in July 2001 ($n = 60$)

1987b). Thus, under cover of darkness after dusk the zooplankton may move towards the surface where the food resource is less depleted (Jakobsen & Johnsen, 1987a). The feeding pattern of the zooplanktivore (*R. argentea*, Fig. 7) indicates their feeding increases just after dusk, which coincides with the beginning of the zooplankton ascent. Analysis of gut contents shows that predation of larger plankton such as copepods, cladocera and *Chaoborus* sp. increases at dawn. The larvae of the zooplankton predator *Chaoborus* sp. were observed as part of fish gut contents during the night although we were unable to successfully trap them in zooplankton samples. *Chaoborus* sp. may also migrate to surface waters during the night when visual predation is least, to exploit the abundant zooplankton resource (Ringelberg, 1999; Rejas et al., 2007; Oda & Hanazato, 2008). The high numbers of

Chaoborus sp. larvae in fish gut contents during the night also suggest that predation pressure on zooplankton from *Chaoborus* sp. may also increase then.

Several studies have shown that there are a sizeable number of zooplankton and fish predators in Lake Victoria (Okedi, 1990; Wanink, 1999; Semyalo, 2003; Goudswaard et al., 2004; Njiru et al., 2004; Manyala & Ojuok, 2007), hence predator avoidance is an important factor influencing any observed DVM patterns. However, the lack of food and temperature gradients (Figs. 1, 3) may particularly affect the ascent of zooplankton and as observed water transparency is low, most zooplankton spend much of the day in the mid part of the water column (Fig. 4). Food, temperature and water transparency conditions may have contributed to lower the amplitudes and strength of DVM patterns in zooplankton in this lake. Further research incorporating zooplankton predators like *Chaoborus* sp. and *Caridina nilotica* which also fall prey to *R. argentea* (Wanink, 1999), would provide additional information on the factors influencing DVM in this eutrophic bay.

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