J. Limnol., 2014; 73(2): 1-
DOI: 10.4081/jlimnol.2014.684

ORIGINAL ARTICLE

Effects of the proximal factors on the diel vertical migration of zooplankton in a plateau meso-eutrophic lake Erhai, China

Cuilin HU,[1,2] Shengrui WANG,[3] Longgen GUO,[2] Ping XIE[1,2*]

[1]Fisheries College, Huazhong Agricultural University, Wuhan 430072, China; [2]Donghu Experimental Station of Lake Ecosystems, State Key Laboratory of Freshwater Ecology and Biotechnology of China, Institute of Hydrobiology, Chinese Academy of Sciences, Donghu South Road 7, Wuhan 430072, China; [3]Research Center of Lake Environment, Chinese Research Academy of Environment Sciences, Chaoyang District, Beijing 100012, China

---

ABSTRACT

To study the proximal factors inducing diel vertical migration (DVM) in large and small zooplankton species in a plateau Lake in China, we investigated the DVM of crustacean zooplankton in Lake Erhai bimonthly from November 2009 to September 2010. We hypothesized that the factors affecting DVM behaviour in different-sized zooplankton were different. A linear regression was used to assess the relationships between environmental variables and the vertical distribution of zooplankton. All crustacean zooplankton exhibited normal DVM patterns (down during the day, up at night) across sampling months. The weighted mean depth (WMD) of all zooplankton did not show a significant correlation with the WMD of the dominant phytoplankton and chlorophyll-a. However, a negative relationship was observed between the distribution of zooplankton and water temperature in January, March, and July 2010, but the relationship was relatively weak (R^2 between 0.1 and 0.4). The vertical distribution of zooplankton was primarily affected by water transparency (P0.05), whereas the factors inducing DVM behaviour differed between large and small zooplankton. Predation avoidance and phototactic behaviour may be the dominant factors influencing DVM of large species, whereas only phototaxis contributed to the migratory behaviour of small species

Key words: Weighted mean depth, zooplankton, Lake Erhai, diel vertical migration, water transparency.

Received: February 2013. Accepted: February 2014.

INTRODUCTION

Diel vertical migration (DVM) is a common behaviour of zooplankton. It has been investigated extensively in marine and freshwater habitats (see review in Pearre, 2003). This phenomenon should be investigated in terms of both proximate and ultimate factors (Ringelberg and Van Gool, 2003). The development and expression of DVM are affected by several proximate factors, such as solar ultraviolet (UV) radiation (Kikuchi, 1930; Leech *et al*., 2005a; Fischer *et al*., 2006), light changes, temperature and food (Ringelberg and Van Gool, 2003; Doulka and Kehayias, 2011). Predator avoidance was considered to be an ultimate factor for DVM to diminish mortality (Hays, 2003). Zooplankton can move downward during the day to minimise the damage caused by short-wavelength solar UV radiation. Studies have demonstrated pronounced differences in the behavioural responses of zooplankton to UV radiation. Copepods and rotifers exhibit a greater UV tolerance than cladocerans, which often show strong UV avoidance of surface waters (Leech and Williamson, 2000; Leech *et al*., 2005b; Kessler *et al*., 2008).

The predator-avoidance hypothesis has been generally considered the most widely recognised mechanism underlying DVM (Zaret and Suffern, 1976; Neill, 1990; Lampert, 1993; Castro *et al*., 2007; Wojtal-Frankiewicz *et al*., 2010). The predatory behaviour of visually feeding planktivorous fish depends on prey size, resulting in the ascent of large-sized zooplankton to the epilimnion at night and their downward migration into colder and deeper layers during the day to avoid predators (Wojtal-Frankiewicz *et al*., 2010). Zooplankton can sense predator presence, as well as abundance, via fish kairomones which are the chemical substances secreted by fish (Kusch, 1993; Van Gool and Ringelberg, 2002). A high fish biomass can increase the kairomone concentration and strongly stimulate DVM by zooplankton under the condition of light changes (Van Gool and Ringelberg, 2002). In oligotrophic or less productive dystrophic systems, the production of kairomones is generally too low to induce DVM because of low fish density (Williamson *et al*., 2011).

Several previous studies have considered light to be the most important factor that induces DVM (Richards *et al*., 1996; Han and Straškraba, 2001; Ringelberg and Van Gool, 2003). Loose (1993) reported that DVM does not occur in the absence of changes in light intensity despite the presence of fish kairomones. A photoresponse occurs if the relative changes in light intensity exceed a certain threshold. In nature, swimming continues as long as changes in the light intensity at sunrise and sunset exceed the threshold (Ringelberg, 1995). The downward and upward displacement velocities of the zooplankton are reported to be significantly correlated with the relative changes in light intensity at dawn and dusk (Richards *et al*., 1996; Van Gool and Ringelberg, 1997). Ringelberg *et al*. (1991) also found that the maximum relative change in light intensity coincides with the vertical movements of zooplankton in the field. The relative changes in light intensity and phototaxis have been considered as the primary causes and physiological underlying mechanisms for DVM (Ringelberg, 1964; Daan and Ringelberg, 1969; Richards *et al*., 1996). Despite the great amount of researches on DVM, investigations of the factors that influence zooplankton DVM in plateau lakes are scarce. Lake Erhai, a freshwater lake located on the Yungui plateau in south-western China, provided an excellent site for our study. The main objective of the present research was to comparatively analyse the proximate factors affecting the migration behaviours of large and small zooplankton species. We hypothesized that the proximal factors inducing different-sized zooplankton were different and that phototactic behaviour may play an important role in governing DVM of zooplankton in Lake Erhai.

METHODS

Study site

Lake Erhai (25°36’ to 25°58’ N, 100°05’ to 100°18’ E, 1966 m altitude) (Fig. 1) is a meso-eutrophic freshwater lake with a volume of 25.5×10^9 m^3. It is the second largest freshwater lake in Yunnan province, with maximum and mean depths of 20.5 and 10.5 m, respectively. Lake Erhai plays important roles in water supply, fishery, aquaculture, and recreation. Various human activities, including a remarkable increase in the population and the development of agriculture and tourism, have caused the water quality of Lake Erhai to deteriorate over the past few decades (Yan *et al*., 2005).

Sampling and analysis

The data used in this study were collected from five different depths (0, -1.5, -3, -6, and -9 m) every 3 hours (8:00; 11:00; 14:00; 17:00; 20:00; 23:00; 2:00; 5:00) bimonthly from November 2009 to September 2010 at a fixed sampling station (Fig. 1). Water samples were collected using a 5 L Schindler sampler. Quantitative samples of crustacean zooplankton were obtained by sieving 20-L water samples through a 64-µm plankton net. The samples were preserved in 5% formalin. Counts were performed with a microscope under 40× magnification. The copepods and cladocerans were identified following Shen (1979).

One litre of lake water at each depth was preserved in acetic Lugol’s solution and concentrated to approximately 50 mL after sedimentation for 48 h to quantify the dominant phytoplankton species during the sampling months. After complete mixing, 0.1 mL of the concentrated sample was observed directly in a 0.1-mL counting chamber under 400× magnification. The colonial *Microcystis* cells were separated into single cells with an ultrasonic crusher. The phytoplanktonic organisms were identified following Hu and Wei (2006). Chlorophyll-a (Chl *a*) was determined using spectrophotometry (Lorenzen, 1967) after filtration on Whatman GF-C glass filters and 24-h extraction in 90% acetone. For each sampling occasion, the temperature was measured *in situ* with a probe (the instrument malfunctioned during the sampling in May 2010; for this reason, no temperature data were obtained during that month). The water-transparency data were obtained with a Secchi disk from 8:00 to 17:00 on each sampling date.

Statistical analysis

The weighted mean depth (WMD) is often employed for quantifying the average depth of the vertical distribution of plankton (Frost and Bollens, 1992; Bezerra-Neto and Pinto-Coelho, 2007). The WMD value can be calculated as follows: $WMD=\Sigma N_i D_i \, \Sigma N_i^{-1}$, where N_i is the number of individuals in a given sampling unit (i) and D_i is the depth of the sampling units. To determine the presence of DVM behaviour, the day-night vertical WMD was compared using a two-sample Kolmogorov-Smirnov nonparametric test, which tested the null hypothesis of equal depth distributions. The determination of DVM behaviour was based on the occurrence of significant differences between the daytime and night-time vertical distributions. The WMD at 14:00 minus the WMD at 2:00 was calculated as the migration amplitude of the zooplankton in the present study because the difference between these two hours was most marked.

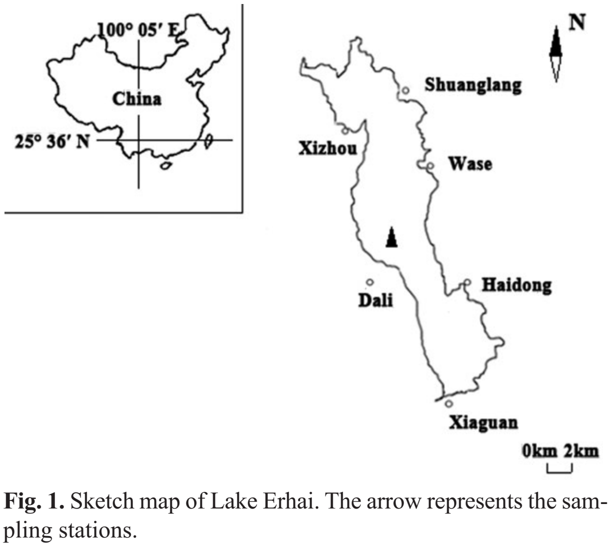

Fig. 1. Sketch map of Lake Erhai. The arrow represents the sampling stations.

A linear regression was used to assess the effects of specific environmental variables (food, temperature, and water transparency) on the vertical distribution of the zooplankton. An ANOVA was used to assess the changes in Secchi depth, zooplankton density, and Chl *a* during the sampling period. A *t*-test was performed to test for differences in the DVM amplitude of different species. The analysed data were log(x+1) transformed prior to analysis to obtain homogeneous data. All statistical analyses were conducted with SPSS version 16.0 for Windows.

RESULTS

Abiotic variables

During the study period, the mean Secchi depth at the sampling station varied between 1.44 m (July 2010) and 2.93 m (May 2010). The water transparency differed significantly (F=55.33, df=5, P=0.000) across the sampling months (Tab. 1). The surface water temperature ranged from 22.18°C to 24.74°C during the warm period (July and September 2010; no data for May 2010) and from 10.10°C to 16.95°C during the cold period (November 2009, January 2010 and March 2010). The differences in temperature between day and night were minimal, and no thermal stratification occurred during the study period (Fig. 2).

Biological variables

The dominant species in the phytoplankton changed in different months. *Psephonema*, *Microcystis,* and *Phormidium* were predominant in November 2009, January and September 2010; *Psephonema*, *Asterionella*, *Microcystis*, *Synedra*, and *Melosira* prevailed in March and May 2010; and *Microcystis* (in colonies) was the dominant species during July 2010 (Fig. 3). *Microcystis* exhibited pronounced DVM from March to September 2010. The species accumulated in the lower strata at daytime and in the upper strata at night, except in March 2010, when a reverse migration pattern was observed. Bacillariophyta (*Synedra*, *Asterionella*, *Melosira,* and *Cyclotella*) and *Psephonema* did not exhibit DVM throughout the sampling period, except for *Synedra* in January 2010. The Chl *a* concentration differed significantly (F=103.92, df=5, P<0.001) among the sampling months. The highest Chl *a* concentration value (18.52 µg L^{-1}) was observed in September 2010, whereas the lowest value (3.28 µg L^{-1}) was observed in March 2010 (Fig. 3).

Zooplankton composition and abundance

The monthly changes in the crustacean zooplankton density were significant (F=29.64, df=5, P<0.001) throughout the study period. The average density of the zooplankton was 75.08±51.66 individuals L^{-1}, with the highest density in July 2010 (159.64±43.73 individuals L^{-1}) and the lowest density in March 2010 (22.31±5.31 individuals L^{-1}). The zooplankton community was numerically dominated by cladocerans (51.63% in density), which consisted primarily of *Daphnia hyalina*, *Bosmina longirostris*, *Ceriodaphnia quadrangularis*, *Diaphanosoma brachyurum,* and *Chydorus sphaericus*. Adult copepods (*Mesocyclops leuckarti* and *Phyllodiaptomus tunguidus*) and nauplii represented 25.52% and 22.85% of the crustacean zooplankton community, respectively (Fig. 4).

Zooplankton diel vertical distribution

In this study, all crustacean zooplankton exhibited DVM, as indicated by the significant differences in WMD between the daytime (11:00 to 14:00) and night-time (23:00 to 2:00) (Tab. 2). The species exhibited similar migration patterns, staying near the surface waters (3 m to 4 m) at night (23:00 to 2:00) and migrating to deeper waters (6 m to 8 m) during the day (11:00 to 14:00) (Fig. 5). To test the effect of food on the DVM amplitude of zooplankton, the different amplitudes were compared between high food availability (November 2009, July and September 2010) and low food availability (January, March and May 2010). No significant differences were found between the two conditions (Tab. 3).

A linear regression analysis (P<0.05) was conducted to test the environmental variables that influenced the distribution patterns of the zooplankton. The regression analysis revealed that the Secchi depth transparency was significantly correlated with the WMD of the zooplankton

Tab. 1. Changes in Secchi depth (m) during sampling period.

Month	Time (h)				Mean±S.D.
	8:00	11:00	14:00	17:00	
November	1.70	2.00	2.10	1.80	1.90±0.18
January	2.00	2.30	2.40	2.10	2.20±0.18
March	2.60	2.80	2.90	2.70	2.75±0.13
May	2.75	3.10	3.00	2.85	2.93±0.16
July	1.42	1.40	1.50	1.45	1.44±0.43
September	1.ù70	2.05	1.90	1.65	1.83±0.18

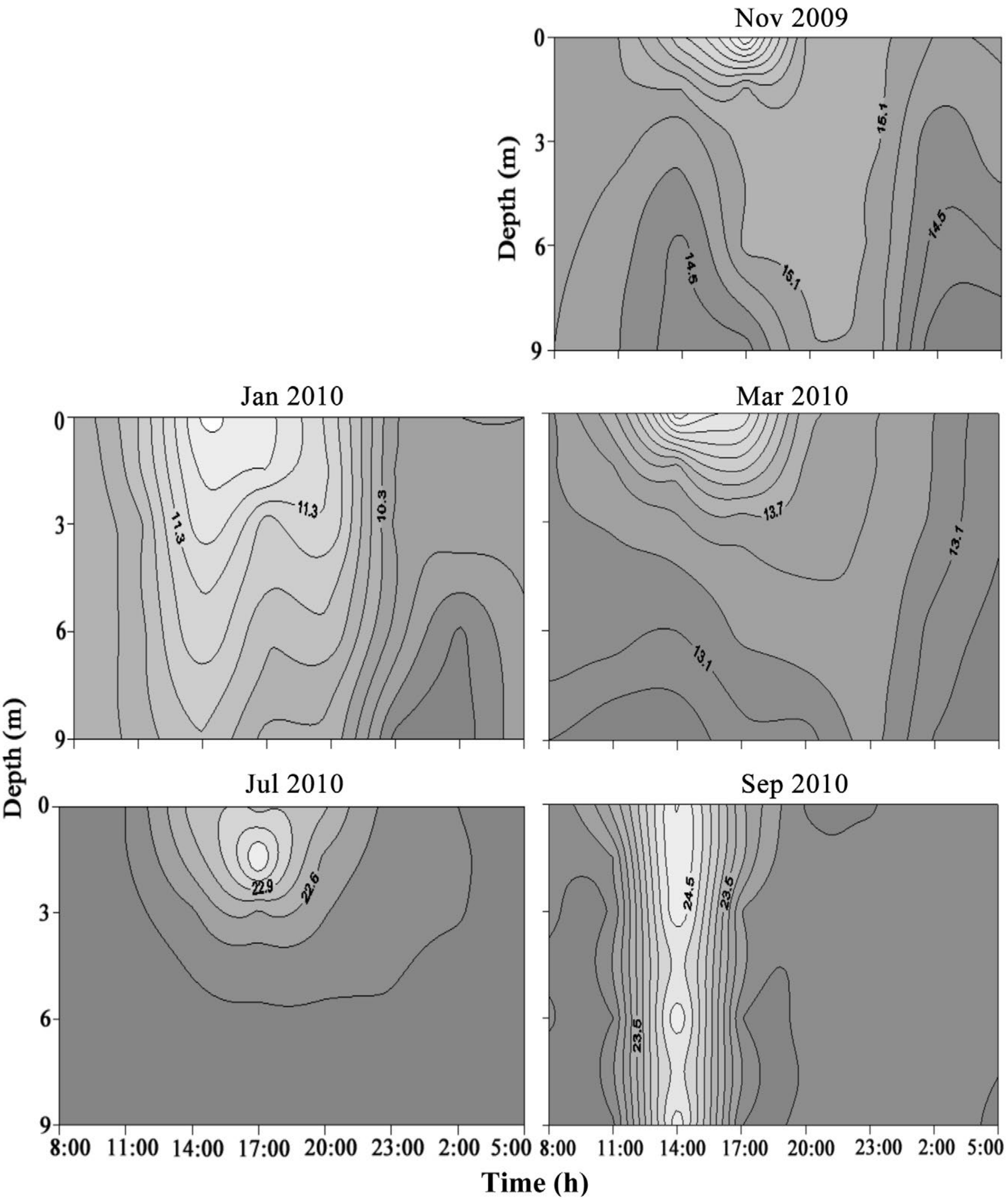

Fig. 2. Diurnal isopleths plot of water temperature in °C during sampling period.

(Tab. 4). The depth of *D. hyalina* during the day increased with increasing transparency in November 2009 and March 2010 (R^2 values between 0.977 and 0.988). The WMD of *B. longirostris* was significantly related to the transparency in November 2009, as well as those in May and July 2010 (R^2 values between 0.991 and 0.995). A similar phenomenon was also observed in *P. tunguidus* and *M. leuckarti* copepods in July and September 2010, with R^2 values of 0.863 and 0.930, respectively. In addition, *C. sphaericus* and *C. quadrangularis* stayed further down in the water column with increasing Secchi depth in November 2009, March and September 2010 (R^2 values from 0.925 to 0.973). However, the WMD of the dominant phytoplankton and the Chl *a* were not able to satisfy

Tab. 2. Summary of results from Kolmogorov-Smirnov's tests on differences in weighted mean depth of different species between day and night.

Species	K-S	P
Daphnia	1.750	0.004
Bosmina	1.633	0.010
Chydorus	2.041	0.000
Ceriodaphnia	1.732	0.005
Diaphanosoma	1.414	0.037
*Phyllodiaptomus**	1.500	0.022
Mesocyclops	2.245	0.000
Nauplii	1.837	0.002

*K-S, Kolmogorov-Smirnov. *The data analyzed with the exception of May 2010.*

Tab. 3. Summary of *t*-test results, comparing the amplitude of diel vertical migration between high (November 2009, July and September 2010) and low food availability (January, March and May 2010).

Species	DVM amplitude	
	t-value	P value
Bosmina	-0.28	0.79
Chydorus	1.04	0.36
Mesocyclops	-0.17	0.87
Nauplii	0.77	0.48

DVM, diel vertical migration.

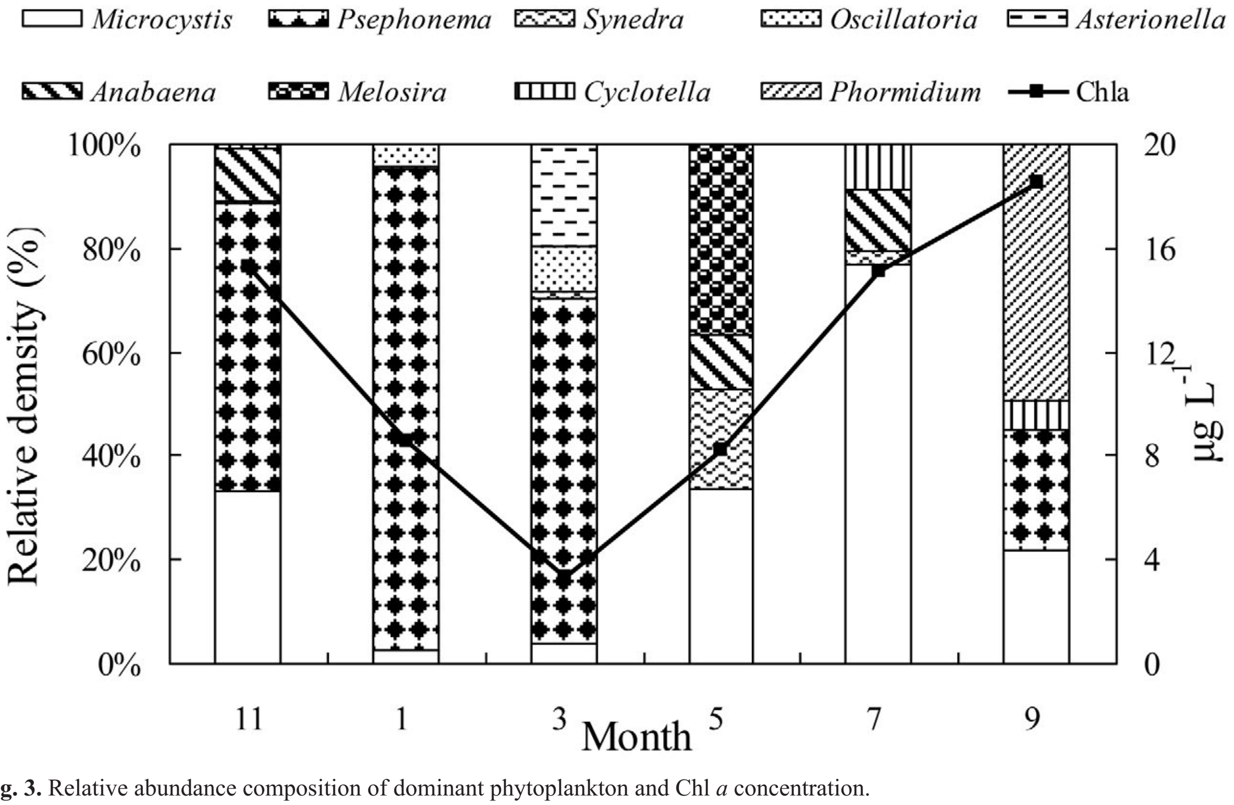

Fig. 3. Relative abundance composition of dominant phytoplankton and Chl *a* concentration.

the significance requirement for modelling inclusion (R^2 values below 0.2), with the exception of *Bosmina* and *Cyclotella* in July (R^2=0.648, P=0.01), and *Bosmina* and Chl *a* in September (R^2=0.517, P=0.027). A significant negative relationship was found between the water temperature and the diurnal distribution of the zooplankton in January, March and July 2010, but the relationship was relatively weak (R^2 between 0.1 and 0.4) (Tab. 5). No relationships were observed for any of the species in November 2009 and September 2010 (P>0.05).

DISCUSSION

The data on the diurnal vertical distribution of the crustacean zooplankton in Lake Erhai show that these populations perform DVM as a specific type of depth-selection behaviour. This observation is based on the significant differences between the day and night vertical distributions. It is reasonable to believe that the crustacean zooplankton performed an upward migration at or near dusk to stay near the surface at night, and a

Tab. 4. Linear regressions model details for crustacean zooplankton weighted mean depth and water transparency in different months.

Date	Species	Model	R^2
11/2009	*Daphnia*	Log WMD=3.242 Log Trans - 0.767 (P=0.008)	0.977
	Bosmina	Log WMD=2.945 Log Trans - 0.572 (P=0.002)	0.995
	Chydorus	Log WMD=3.495 Log Trans - 0.851 (P=0.009)	0.973
03/2010	*Daphnia*	Log WMD=2.700 Log Trans - 0.815 (P=0.004)	0.988
	Ceriodaphnia	Log WMD=5.900 Log Trans - 2.590 (P=0.019)	0.944
05/2010	*Bosmina*	Log WMD=2.286 Log Trans - 0.564 (P=0.003)	0.991
07/2010	*Bosmina*	Log WMD=6.965 Log Trans - 1.981 (P=0.005)	0.985
	Phyllodiaptomus	Log WMD=5.987 Log Trans - 1.544 (P=0.047)	0.863
09/2010	*Ceriodaphnia*	Log WMD=2.228 Log Trans - 0.228 (P=0.025)	0.925
	Chydorus	Log WMD=0.924 Log Trans + 0.369 (P=0.014)	0.959
	Mesocyclops	Log WMD=3.225 Log Trans - 0.637 (P=0.024)	0.930

WMD, weighted mean depth.

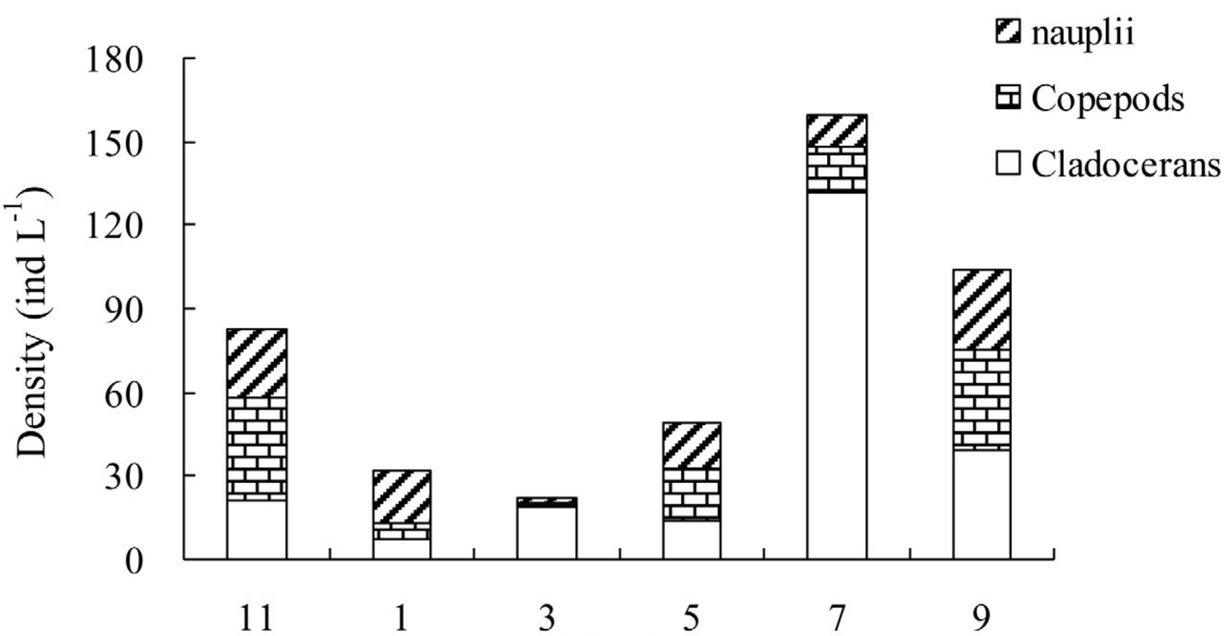

Fig. 4. Monthly variations in density of crustacean zooplankton in Lake Erhai.

downward migration in or near the early morning to spend the daytime in deeper strata. In general, the migratory behaviours of all zooplankton, including both large and small species, were characterised as normal DVM, with individuals ascending at dusk and descending at dawn. Our results indicate that the diurnal distribution of zooplankton is related to water temperature but that the relationship is fairly weak. The weighted mean depth (WMD) of zooplankton is highly correlated with water transparency, suggesting that light availability may be an important factor influencing DVM of large and small zooplankton species.

The WMDs of all crustacean zooplankton except for *Diaphanosoma* and nauplii were highly and positively correlated with water transparency despite the low density of some species in certain months (*e.g*., *Chydorus* and *Ceriodaphnia*) (Tab. 4; most R^2 values above 0.9). Only a few previous studies have explicitly examined the relationship between vertical distribution and water transparency. Wissel and Ramacharan (2003) observed that the vertical positions of all crustacean zooplankton were strongly affected by the Secchi transparency, suggesting that the water transparency was the best predictive factor, but this effect depended on the time of year. Because significant changes occurred in the temperature and oxygen profiles, and because zooplankton often reacts to different environmental cues, the major determinant governing vertical distribution varies among months (Wissel and Ramacharan, 2003). However, in Lake Erhai, the entire water column is mixed during the sampling months. Given sufficient temperature and DO values (see below), transparency became the dominant variable for the entire year. Dodson (1990) observed a marked increase in the amplitude of *Daphnia* with increasing Secchi transparency, a pattern attributed to visual predation. Semyalo *et al*. (2009) found that the amplitude of *Thermodiaptomus galeboides* was correlated with the midday (12:00) water transparency. This correlation is also interpreted as evidence for the avoidance of visual predation. Large-sized zooplankton species that are vulnerable to planktivorous fish often remain in weak light conditions as a refuge, whereas small species usually do not react or change their migratory behaviour in the same environment (Wissel and Ramacharan, 2003; Bezerra-Neto and Pinto-Coelho, 2007; Semyalo *et al*., 2009; Holliland *et al*., 2012). *Neosalanx taihuensis* is the dominant zooplanktivorous fish in Lake Erhai (Erhai Administration). It is a visual predator and shows strong positive selection for large-sized species (Liu and Zhu, 1994; Yin *et al*., 1997). Therefore, the avoidance of fish predation is considered to be one of the reasons that the vertical distribution of large zooplankton, such as *Daphnia*, *Diaphanosoma,* and *Phyllodiaptomus,* is influenced by water transparency. However, a result of the present study differing significantly from previous findings (Wissel and Ramacharan, 2003; Bezerra-Neto and Pinto-Coelho, 2007; Semyalo *et al*., 2009), is that the small zooplankton that *N. taihuensis* initially avoid, such as *Bosmina*, *Chydorus,* and *Ceriodaphnia* (Liu and Zhu, 1994) exhibited DVM patterns similar to those of the large species in our study (Fig. 5). We deduced that there was another factor, apart from predation pressure, that affected the migratory behaviour (normal DVM) of zooplankton in Lake Erhai.

Feeding conditions, in terms of the availability of phytoplankton (*sensu* Ricklefs, 2007), have been reported to be one of the proximate factors that influence the vertical distribution of zooplankton (Ringelberg and Van Gool, 2003; Guglielmo *et al*., 2011). However, in the present study, the expected correlation between the distributions of herbivorous grazers and their food (phytoplankton and Chl *a*) was not evident. For the most part, phytoplankton was distributed fairly evenly in the water, with the exception of *Microcystis*, whereas all zooplankton showed distribution patterns that differed between day and night. Since Lake Erhai is a meso-eutrophic lake, phytoplankton

Tab. 5. Regression coefficients (R^2) for associations between zooplankton density and water temperature in different months.

Date	Species	R^2	P
01/2010	*Daphnia*	0.079	0.044
	Phyllodiaptomus	0.190	0.003
	Mesocyclops	0.409	0.000
03/2010	*Daphnia*	0.192	0.003
	Bosmina	0.267	0.000
	Ceriodaphnia	0.351	0.000
	Chydorus	0.365	0.000
	Mesocyclops	0.274	0.000
	nauplii	0.123	0.015
07/2010	*Diaphanosoma*	0.423	0.000
	Phyllodiaptomus	0.243	0.001
	Mesocyclops	0.421	0.000

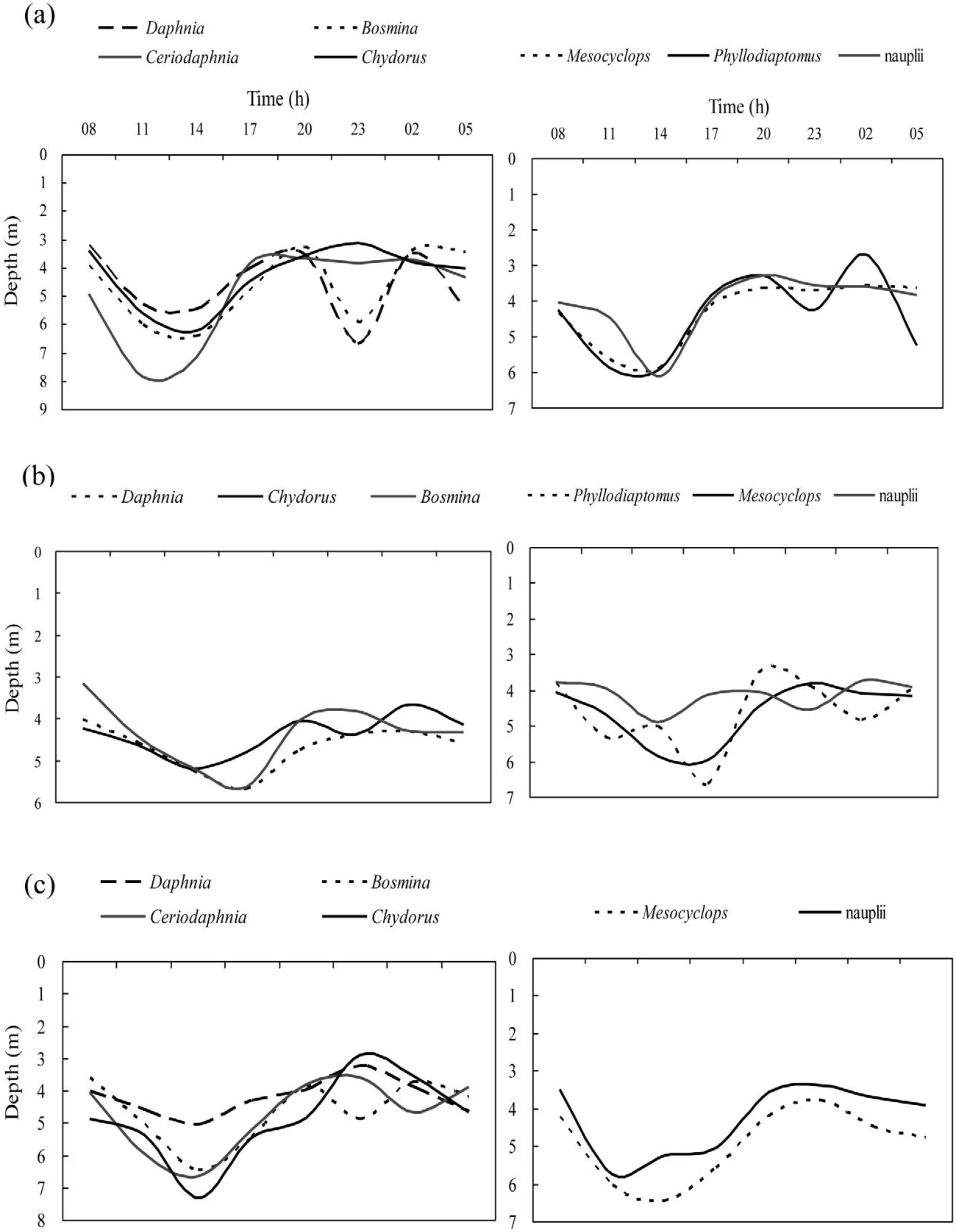

Fig. 5. Diurnal weighted mean depth (WMD) of zooplankton during sampling periods November 2009 (a), January 2010 (b), March 2010 (c), May 2010 (d), July 2010 (e), and September 2010 (f).

To be continued on next page.

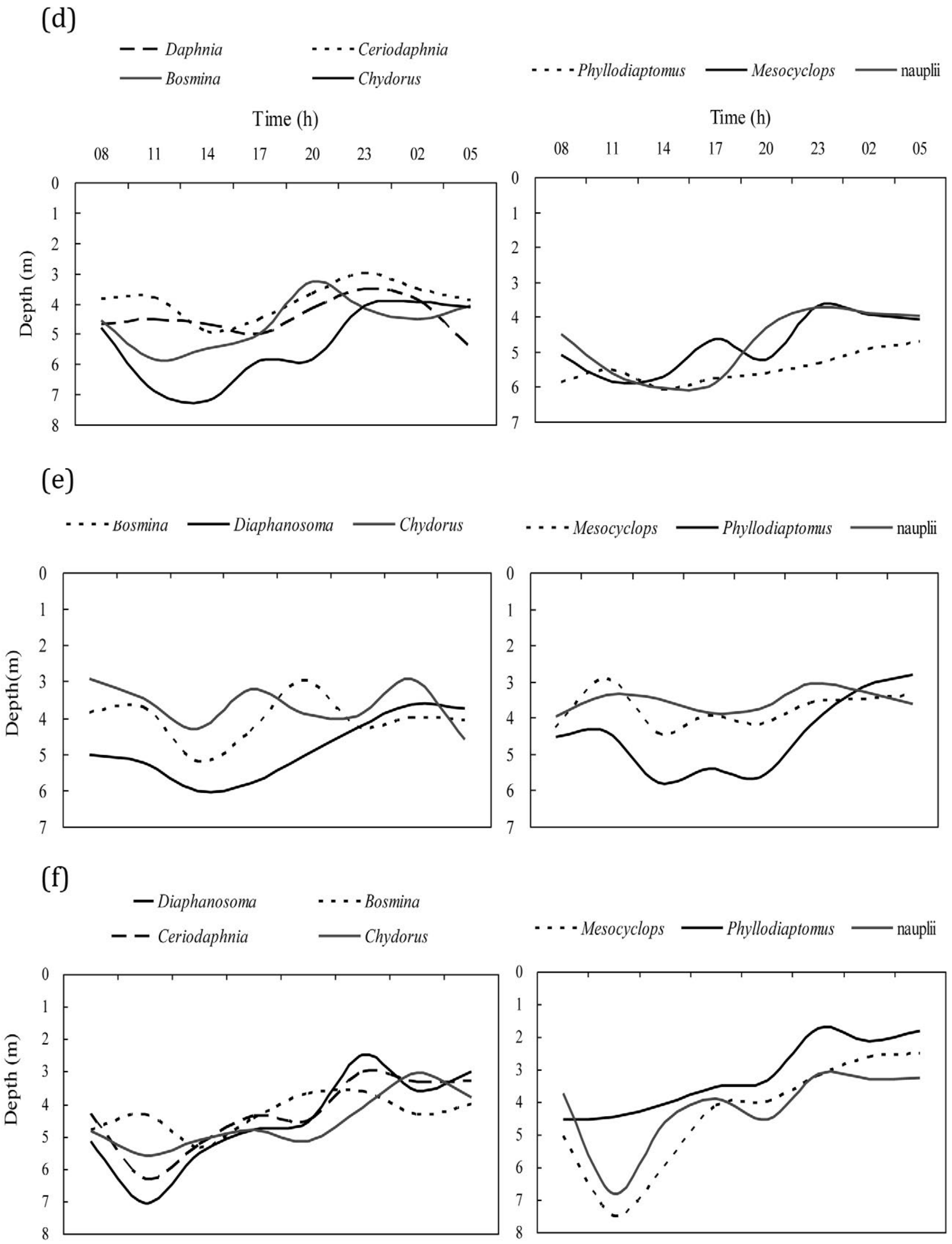

Fig. 5. Continued from previous page.

production may be sufficient to provide most herbivorous zooplankton grazers with adequate food resources to produce a vertical distribution that is unrelated to phytoplankton availability. Similar results have been reported by Easton and Gophen (2003) in Lake Kinneret. Zooplankton performs a high-amplitude migration if phytoplankton is abundant (Semyalo *et al*., 2009). In contrast, if food availability declines and the competition for food increases, the amplitude decreases (Huntley and Brooks, 1982; Dagg, 1985) or migration ceases (Johnson and Jacobson, 1987; Flik and Ringelberg, 1993; Beklioglu *et al*., 2008). The impacts of food availability on the DVM amplitude of zooplankton were not significant between high and low food abundance in Lake Erhai (Tab. 3). These results further support the abovementioned statement that the vertical distributions of zooplankton were not regulated by food in this lake.

A vertically mixed water column was observed throughout the year in Lake Erhai (Fig. 2). The dissolved oxygen (DO) concentration in the deep strata is high (5.15-7.28 mg L^{-1}; Zhao *et al*., 2011) in the mixed state. Thus, the zooplankton exhibited a strong DVM pattern under this condition during all months sampled. Bezerra-Neto and Pinto-Coelho (2007), studying the DVM of *Thermocyclops inversus* in Nado reservoir, have reported a similar result. They stated that during the circulation period, the whole water column is oxygenated, and the amplitude of vertical migration is significantly greater than that occurring during the stratification period. Previous studies have suggested that temperature can have a strong impact on the vertical distribution of zooplankton, but those studies were primarily performed in stratified systems (Matsumura-Tundisi *et al*., 1984; Makino *et al*., 2003; Thackeray *et al*., 2006). Although a negative relationship was observed between temperature and the distribution of zooplankton in the present study, temperature was not the determining factor because of the relatively low R^2 values (ranging only from 0.1 to 0.4).

The normal DVM of zooplankton is characterised by ascent during nighttime and descent during the day in a 24-h cycle (Wojtal-Frankiewicz *et al*., 2010). The behavioural mechanisms underlying these distributions have been supported by the predator-avoidance hypothesis (Wojtal-Frankiewicz *et al*., 2010; Holliland *et al*., 2012). However, other researchers have proposed opposing arguments (Loose, 1993; Richards *et al*. 1996; Van Gool and Ringelberg, 1997). Richards *et al*. (1996) reported that the response of zooplankton to a relative change in light intensity can cause DVM behaviour in the absence of predation pressure. The role of phototaxis in DVM has been demonstrated in various species, such as *Daphnia magna* (Clarke, 1932; Daan and Ringelberg, 1969), *Daphnia longispina* (Ringelberg, 1993), the marine calanoid *Acartia tonsa* (Stearns and Forward, 1984), and crab *Rhithropanopeus* larvae (Forward, 1985). Lake Erhai is located on the Yungui plateau, and the altitude is as much as 1966 m. The normal migration of small zooplankton may be induced by the large relative changes in light intensity at dawn and dusk. Furthermore, the migration of small zooplankton may reflect the causes of migration for large zooplankton in addition to predator avoidance. The relationship between water transparency and WMD can also be explained by the changes in light intensity. Downward swimming leads to light intensity decreases, which result in a diminished influence of relative increases in light intensity at dawn. However, in clear water, these decreases in light intensity are smaller than that in turbid water, and phototactic downward swimming is less affected (Ringelberg, 1995). Thus, the daytime distribution depth of the zooplankton is influenced by the water transparency. The results of the present study show that in the case of sufficient food, temperature, and oxygen, the vertical distribution of both large and small zooplankton was primarily affected by water transparency. This result may be due to the effect of predation avoidance and phototactic behaviour in large species and only phototactic behaviour in small species in the Lake.

CONCLUSIONS

In conclusion, strong normal DVM patterns were observed for all crustacean zooplankton in a plateau lake, Lake Erhai. The diurnal vertical distribution of zooplankton was influenced by temperature in certain months, but the relationship was relatively weak. The daytime distribution of all zooplankton was primarily affected by water transparency, but the factors inducing DVM behaviour differed between large and small zooplankton. Predation avoidance and phototactic behaviour were considered to be the dominant factors influencing the DVM of large species, whereas only phototaxis contributed to the migratory behaviour of small species. The comparative studies about the factors influencing zooplankton DVM in different trophic levels of plateau lakes need further research.

ACKNOWLEDGMENTS

This work was supported in part by the National Major Technology Projects of the Water Pollution Control and Management (2012ZX07105-004) and in part by the National Nature Science Foundation (41173118, 40703017 and 40873079). We deeply appreciated the editor and two anonymous reviewers for their helpful comments which have substantially improved the quality of the manuscript. We also would like to thank Dr. Zhixin Ke for his helpful suggestions to this manuscript. In addition, the authors specially thank Dr. Bin Hu, Wenbin Liu, Sai Zhang, and Haiping Hu for their help in the sample collection.

REFERENCES

Beklioglu M, Gozen AG, Yildirim F, Zorlu P, Onde S, 2008. Impact of food concentration on diel vertical migration behaviour of *Daphnia pulex* under fish predation risk. Hydrobiologia 614:321-327.

Bezerra-Neto JF, Pinto-Coelho RM, 2007. Diel vertical migration of the copepod *Thermocyclops inversus* (Kiefer, 1936) in a tropical reservoir: the role of oxygen and the spatial overlap with Chaoborus. Aquat. Ecol. 41:535-545.

Castro BB, Marques SM, Goncalves F, 2007. Habitat selection and diel distribution of the crustacean zooplankton from a shallow Mediterranean lake during the turbid and clear water phases. Freshw. Biol. 52:421-433.

Clarke GL, 1932. Quantitative aspects of the change of photopic sign in *Daphnia*. J. Exp. Biol. 9:180-211.

Daan N, Ringelberg J, 1969. Further studies on the positive and negative phototactic reation of *Daphnia magna* Straus. Neth. J. Zool. 19:525-540.

Dagg MJ, 1985. The effects of food limitation on diel migratory behavior in marine zooplankton. Arch. Hydrobiol. Beih. Ergeb. Limnol. 21:247-255.

Dodson S, 1990. Predicting diel vertical migration of zooplankton. Limnol. Oceanogr. 35:1195-1201.

Doulka K, Kehayias G, 2011. Seasonal vertical distribution and diel migration of zooplankton in a temperate stratified lake. Biologia 66:308-319.

Easton J, Gophen M, 2003. Diel variation in the vertical distribution of fish and plankton in Lake Kinneret: a 24-h study of ecological overlap. Hydrobiologia 491:91-100.

Fischer JM, Nicolai JL, Williamson CE, Persaud AD, Lockwood RS, 2006. Effects of ultraviolet radiation on diel vertical migration of crustacean zooplankton: An in situmesocosm experiment. Hydrobiologia 563:217-224.

Flik BJG, Ringelberg J, 1993. Influence of food availability on the initiation of diel vertical migration in Lake Maarsseveen. Arch. Hydrobiol. Beih. Ergeb. Limnol. 39:57-65.

Forward RB Jr, 1985. Behavioural responses of larvae of the crab *Rhithropanopeus harrisii* (Brachyura: Xanthidae) during diel vertical migration. Mar. Biol. 83:9-18.

Frost BW, Bollens SM, 1992. Variability of diel vertical migration in the marine planktonic copepod *Pseudocalanus newmani* in relation to its predators. Can. J. Fish. Aquat. Sci. 49:1137-1141.

Guglielmo L, Minutoli R, Bergamasco A, Granata A, Zagami G, Antezana T, 2011. Short-term changes in zooplankton community in Paso Ancho basin (Strait of Magellan): functional trophic structure and diel vertical migration. Polar Biol. 34:1301-1317.

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

Hays GC, 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. Hydrobiology 503:163-170.

Holliland PB, Ahlbeck I, Westlund E, Hansson S, 2012. Ontogenetic and seasonal changes in diel vertical migration amplitude of the calanoid copepods *Eurytemora affinis* and *Acartia* spp. in a coastal area of the northern Baltic proper (in press).

Hu HJ, Wei YX, 2006. The freshwater algae of China: Systematics, taxonomy and ecology. Beijing, Science Press (in Chinese).

Huntley M, Brooks ER, 1982. Effects of age and food availability on diel vertical migrations in *Calanus pacificus*. Mar. Biol. 71:23-31.

Johnson G, Jacobson P, 1987. The effect of food limitation on vertical migration in *Daphnia longispina*. Limnol. Oceanogr. 32:873-880.

Kessler K, Lockwood RS, Williamson CE, Saros JE, 2008. Vertical distribution of zooplankton in subalpine and alpine lakes: Ultraviolet radiation, fish predation, and the transparency-gradient hypothesis. Limnol. Oceanogr. 53:2374-2382.

Kikuchi K, 1930. Diurnal migration of plankton Crustacea. Q. Rev. Biol. 5:189-206.

Kusch J, 1993. Behavioural and morphological changes in ciliates induced by the predator *Amoeba proteus*. Oecologia 96:354-359.

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

Leech DM, Paeletti A, Williamson CE, 2005a. Zooplankton behavioral responses to solar UV radiation vary within and among lakes. J. Plankton Res. 27:461-471.

Leech DM, Williamson CE, 2000. Is tolerance to UV radiation in zooplankton related to body size, taxon, or lake transparency? Ecol. Appl. 10:1530-1540.

Leech DM, Williamson CE, Moeller RE, Hargreaves BR, 2005b. Effects of ultraviolet radiation on the seasonal vertical distribution of zooplankton: a database analysis. Arch. Hydrobiol. 162:445-464.

Liu ZW, Zhu SQ, 1994. Food and feeding behavior of icefish (*Neosalanx taihuensis* Chen) in Lake Dianchi. Acta Zool. Sinica 40:253-261 (in Chinese with English abstract).

Loose CJ, 1993. Lack of endogenous rhythmicity in Daphnia diel vertical migration. Limnol. Oceanogr. 38:1837-1841.

Lorenzen CJ, 1967. Determination of chlorophyll and pheo-pigments: spectrophoto- metric equations. Limnol. Oceanogr. 12:343-346.

Makino W, Yoshida T, Sakano H, Ban S, 2003. Stay cool: habitat selection of a cyclopoid copepod in a north temperate oligotrophic lake. Freshw. Biol. 48:1551-1562.

Matsumura-Tundisi T, Tundisi, JG, Tavares, LS, 1984. Diel migration and vertical distribution of Cladocera in Lake D. Helvecio (Minas Gerais, Brazil). Hydrobiologia 113:299-306.

Neill WE, 1990. Induced vertical migration in copepods as a defense against invertebrate predation. Nature 345:524-526.

Pearre S, 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. Biol. Rev. 78:1-79.

Richards SA, Possingham HP, Noye J, 1996. Diel vertical migration: modeling light-mediated mechanisms. J. Plankton Res. 18:2199-2222.

Ricklefs RE, 2007. The economy of nature. W.H. Freeman and Company: 172 pp.

Ringelberg J, 1964. The positively phototactic reaction of *Daphnia magna* Straus: A contribution to the understanding of diurnal vertical migration. Neth. J. Sea Rea. 2:841- 847.

Ringelberg J, 1993. Phototaxis as a behavioural component of diel vertical migration in a pelagic *Daphnia*. Arch. Hydrobiol. Ergeb. Limnol. 39:45-55.

Ringelberg J, 1995. An account of a preliminary mechanistic model of swimming behaviour in *Daphnia*: its use in understanding diel vertical migration. Hydrobiologia 307:161-165.

Ringelberg J, Flik BJG, Lindenaar D, Royackers K, 1991. Diel vertical migration of *Daphnia hyalina* (sensu latiori) in Lake Maarsseveen: Part 1. Aspects of seasonal and daily timing. Arch. Hydrobiol. 121:129-145.

Ringelberg J, Van Gool E, 2003. On the combined analysis of proximate and ultimate aspects in diel vertical migration (DVM) research. Hydrobiologia 491:85-90.

Semyalo R, Nattabi JK, Larsson P, 2009. Diel Vertical Migration of zooplankton in a eutrophic bay of Lake Victoria. Hydrobiologia 635:383-394.

Shen JR, 1979. Fauna Sinica, Crustacea, Freshwater Copepoda. Beijing, Science Press: 450pp (in Chinese).

Stearns DE, Forward RB, 1984. Photosensitivity of the calanoid copepod *Acartia tonsa*. Mar. Bioi. 82:85-89.

Thackeray SJ, George DG, Jones RI, Winfield IJ, 2006. Statistical quantification of the effect of thermal stratification on patterns of dispersion in a freshwater zooplankton community. Aquat. Ecol. 40:23-32.

Van Gool E, Ringelberg J, 1997. The effect of accelerations in light increase on the phototactic downward swimming of *Daphnia* and the relevance to diel vertical migration. J. Plankton Res. 19:2041-2050.

Van Gool E, Ringelberg J, 2002. Relationship between fish kairomone concentration in a lake and phototactic swimming by *Daphnia*. J. Plankton Res. 24:713-721.

Williamson CE, Fischer JM, Bollens SM, Overholt EP, Breckenridge JK, 2011. Toward a more comprehensive theory of zooplankton diel vertical migration: Integrating ultraviolet radiation and water transparency into the biotic paradigm. Limnol. Oceanogr. 56:1603-1623.

Wissel B, Ramacharan CW, 2003. Plasticity of vertical distribution of crustacean zooplankton in lakes with varying levels of water colour. J. Plankton Res. 25:1047-1057.

Wojtal-Frankiewicz A, Frankiewicz P, Jurczak T, Grennan J, McCarthy TK, 2010. Comparison of fish and phantom midge influence on cladocerans diel vertical migration in a dual basin lake. Aquat. Ecol. 44:243-254.

Yan CZ, Jin XC, Zhao JZ, Shen B, Li NB, Huang CZ, Xiong ZH, 2005. [Ecological protection and sustainable utilization of Lake Erhai, Yunnan].[Article in Chinese with English Abstract]. Environ. Sci. 26:38-42.

Yin GJ, Cao KJ, Yu ZT, Gong SY, 1997. [The reproduction, feeding habits and growth of Salangid fishes *Neosalanx taihuensis* and *Neosalanx Oligodontis* in Wanghu Lake].[Article in Chinese with English Abstract]. J. Lake Sci. 9:63-70.

Zaret TM, Suffern JS, 1976. Vertical migration in zooplankton as a predator avoidance mechanism. Limnol. Oceanogr. 21:804-813.

Zhao HC, Wang SR, Zhao M, Jiao LX, Liu B, Jin XC, 2011. [Relationship between the DO and the environmental factors of the water body in Lake Erhai]. [Article in Chinese with English abstract]. Environ. Sci. 32:1552-1559.