

Behavioral responses of zooplankton to solar radiation changes: in situ evidence

Zengling Ma · Wei Li · Anglv Shen ·
Kunshan Gao

Received: 3 October 2012 / Revised: 5 February 2013 / Accepted: 16 February 2013 / Published online: 28 February 2013
© Springer Science+Business Media Dordrecht 2013

Abstract It is known that copepods can sense solar UV and avoid it vertically or horizontally, but no in situ studies have been documented to monitor their responses to diurnal solar radiation changes. Here, we provided in situ evidence that zooplankton sense changes in solar radiation during a diurnal solar cycle. By comparing the abundance of the zooplankton in a shaded water column with that in the non-shaded adjacent area, we found that, on a cloudy day with low solar radiation levels, the ratios of zooplankton biomass in the shaded areas to those in nearby non-shaded water ranged from 0.90 to 1.49. However, on sunny days with high solar radiation levels, the ratios ranged from 0.83 to 2.88, with the amount of zooplankton in the shaded water being higher than

that in the non-shaded area and higher during the periods of higher irradiance levels. These results indicated that the horizontal migration of zooplankton may be a protective strategy against stressful solar radiation.

Keywords Zooplankton · Copepod · Rotifer · Migration · Solar radiation · UV

Introduction

Solar UV-B radiation (280–315 nm), which increases with ozone depletion, is known to harm aquatic organisms (Häder et al., 2011). Although enforcement of the Montreal Protocol has slowed down ozone depletion, increasing UV radiation (UVR, 280–400 nm) at different latitudes is observed, probably due to cloud cover changes and continuous ozone reduction influenced by climate change (Mackenzie et al., 2011; Manney et al., 2011). Effects of solar UVR on the metabolic activities (Hansson & Hylander, 2009; Häder et al., 2011; Ma et al., 2012, 2013) and behavioral response of zooplankton (Rocco et al., 2001; Rhode et al., 2001; Wold & Norrbin, 2004; Hansson et al., 2007; Ma et al., 2010) are well documented, and UVR suppresses the metabolic activities of zooplankton (Yu et al., 2009; Ma et al., 2013), and destroys both nauplii and adults (Kouwenberg et al., 1999; Dattilo et al., 2005; Ma et al., 2012), or indirectly decreases their survival and fecundity by altering the nutritional value of their food (Scott

Handling editor: Sigrún Huld Jónasdóttir

Z. Ma
Zhejiang Provincial Key Laboratory for Subtropical
Water Environment and Marine Biological Resources
Protection, Wenzhou University, Wenzhou 325035, China

W. Li · K. Gao (✉)
State Key Laboratory of Marine Environmental Science,
Xiamen University, Xiamen 361005, China
e-mail: ksgao@xmu.edu.cn

A. Shen
Key and Open Laboratory of Marine and Estuary
Fisheries (Ministry of Agriculture), Chinese Academy of
Fisheries Science, East China Sea Fisheries Research
Institute, Shanghai 200090, China

et al., 1999; De Lange & Van Reeuwijk, 2003). UV-related harm is usually caused by UV-B (280–315 nm), although its proportion is only about 3.0% that of UV-A or 0.6% PAR in tropical surface waters (Li et al., 2011).

Zooplankton have developed a variety of protective strategies against solar UV stress during their long-term evolution, such as effective photo-enzymatic repair systems (Hansson & Hylander, 2009; Häder et al., 2011), the accumulation of photo-protective substances (Hairton, 1976; Sommaruga & Garcia-Pichel, 1999; Hansson, 2000; Moeller et al., 2005), and behavioral avoidance (Rocco et al., 2001; Rhode et al., 2001; Wold & Norrbin, 2004; Hansson et al., 2007).

Traditionally, the diurnal vertical migration of aquatic organisms had been thought of as a behavior to escape from predators or to search for food organisms (Gliwicz, 1986; Pearre, 2003). Experimental tests indicate that zooplankton can sense UV and migrate so as to avoid it either vertically (Rocco et al., 2001; Rhode et al., 2001; Wold & Norrbin, 2004; Hansson et al., 2007) or horizontally (Ma et al., 2010), and the pattern which occurs probably depends on the tolerance of the species involved to solar UVR and the water environment. However, diurnal vertical migration is suggested to most shape the structure of natural phytoplankton communities (Petzold et al., 2009). Various authors suggest that the horizontal migration of zooplankton is linked to sensing environmental changes (Burks et al., 2002; Romare & Hansson, 2003; Boeing et al., 2004; Iglesias et al., 2007; Li & Gao, 2012). However, little evidence has been documented on their in situ behavior.

To avoid harmful solar radiation, individual members of the zooplankton sometimes need to cross pressure and temperature gradients in the water column, and this requires additional energy expenditure (Loose & Dawidowicz, 1994; Reichwaldt et al., 2005; Cooke et al., 2008). In contrast, horizontal migration takes less energy for them to move to the nearest shade provided by reefs, macrophytes, or other agents (Ma et al., 2010). In our study, we presented the results obtained from in situ experiments carried out in a subtropical reservoir, and which demonstrated the diurnal behavior of the zooplankton in accordance with solar radiation changes.

Materials and methods

Study area and experimental design

Experiments were conducted in situ in Siyuangu reservoir (24°26′25″N, 118°05′59″E) located in the Campus of Xiamen University, which is a mesotrophic, turbid natural lake with an area of approximately 0.5 km² and a mean depth of 2.5 m. The zooplankton community was dominated by copepods and rotifers, and both refuges (macrophytes and reefs) and predators (fishes) occurred in the reservoir. The experiments were performed on a cloudy day (April 22th) and sunny days (April 24th and 25th) in 2011.

To ensure that the experiments were easy to perform, near shore waters of about 2-m depth were selected as experimental sites. To artificially create an area with reduced solar radiation compared with the adjacent water, layers of wire mesh filters (neutral over the wavelengths involved) fixed to a hollow plastic ring 1.0 m in diameter were floated on the water surface, reducing the solar radiation level by 50%, compared to the adjacent area without shade. In the center of the neutral filters, a circular hole 30 cm in diameter was cut, through which a plankton net was sunk to the lake bottom (Fig. 1). The hole was covered with the same neutral filter by pulling a connecting line through it (Fig. 1). For the control, a plankton net was in the adjacent water without any shelter.

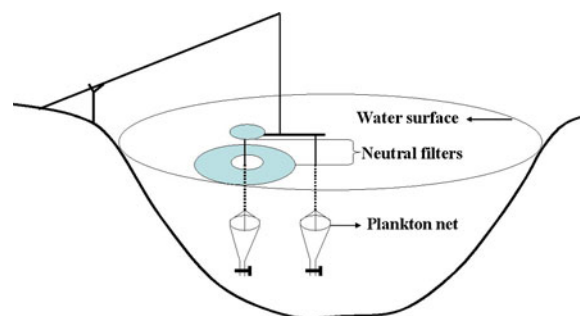


Fig. 1 Schematic diagram of the experimental design for testing the effects of solar radiation on horizontal migration of zooplankton in Siyuangu reservoir. The neutral filters were used to filter out 50% solar irradiance in all wavelengths in the shaded treatment

Plankton sampling, species identification, and wet weight and chl *a* content determination of the total zooplankton

To investigate the changes in total zooplankton biomass in the shaded and adjacent non-shaded waters over time, and with changes in solar radiation, zooplankton samples were collected once per hour by vertically hauling a plankton net (diameter 20 cm, length 60 cm, and mesh diameter 76 μm) from the bottom to the water surface. All samples were removed from the net, immediately preserved in 5% formalin, and stained with Bengal's red before identification under a microscope. The dominant zooplankton members were identified down to genera or species level. Subsequently, the sampled individuals were filtered onto GF/F filters and the wet weight of the zooplankton was determined for the shaded and non-shaded areas.

The phytoplankton was sampled by vertical hauling of the plankton net (diameter 20 cm, length 60 cm, and mesh diameter 64 μm) and was immediately fixed with Lugol's solution after being removed from the net. The dominant species were identified down to genera or species level under a microscope. In order to determine whether the phytoplankton abundance was different in the shaded versus the non-shaded site, chl *a* concentrations in the water columns were determined using the standard method.

Determination of abiotic factors

The pH, dissolved oxygen (DO), and temperature of the shaded and non-shaded waters were measured with a CTD (YSI 600XL, Yellow Spring Instruments, USA) to evaluate the possible effects of environmental differences on zooplankton distribution. The vertical profile of solar radiation in the water column was measured using a broadband ELDONET filter radiometer (Real Time Computer, Möhrendorf, Germany) which had three channels for measuring photosynthetically active radiation (PAR, 400–700 nm), UV-A radiation (UV-A, 315–400 nm), and UV-B radiation (UV-B, 280–315 nm).

Data analysis

To evaluate the effects of solar radiation on vertical zooplankton distribution or horizontal migration, we correlated the zooplankton abundance of sampling

time T_n with the mean solar radiation during the period between T_n and T_{n-1} (previous sampling time). Since the time interval between the two neighboring samplings was about 1 h, there was enough time for zooplankton to move between the two water areas which were within a distance of less than 1 m.

Results

Variation in solar radiation and underwater irradiance profile during the experimental period

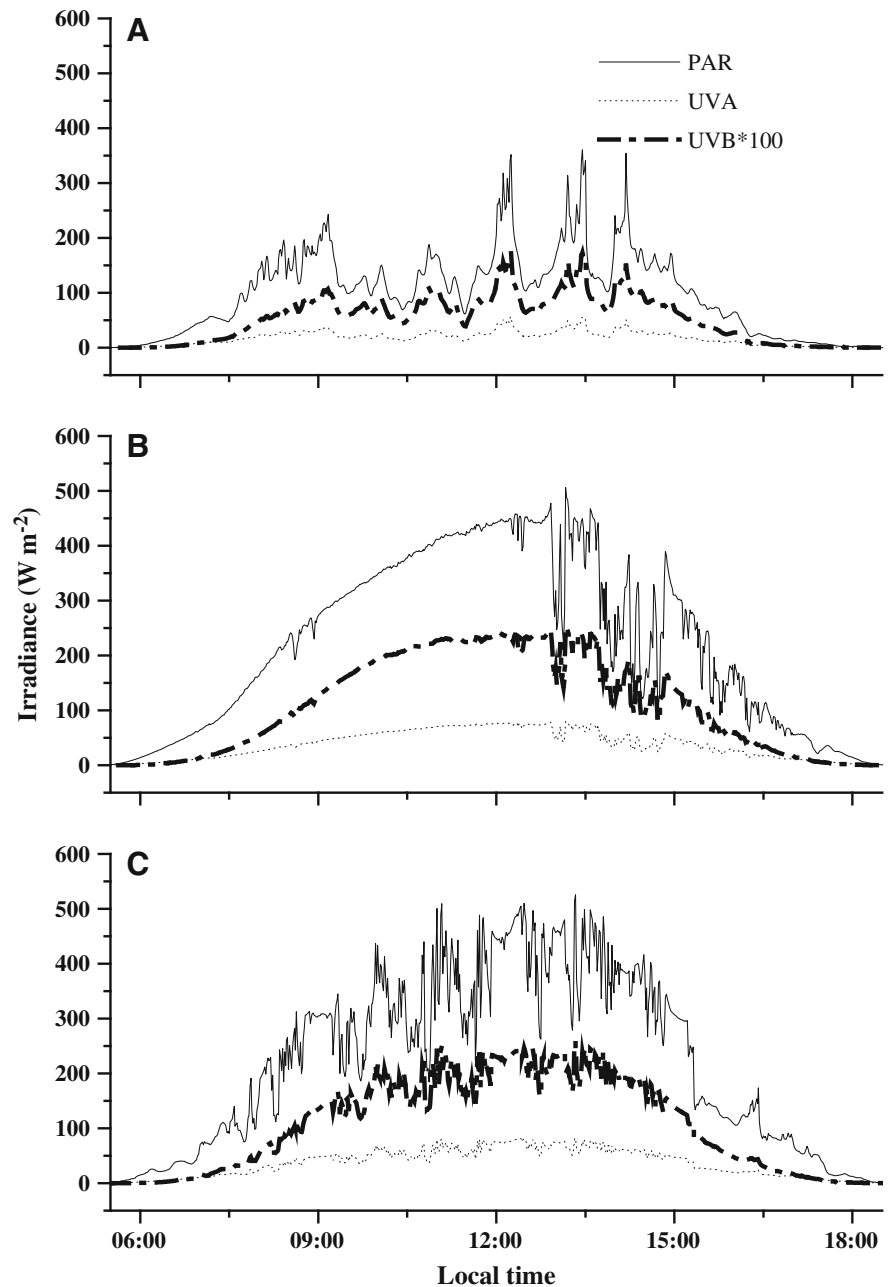
When the experiments were carried out on cloudy and sunny days (Fig. 2), the highest surface PAR levels were 360 on April 22th (cloudy), and 506 and 525 W m^{-2} , on 24th and 25th (sunny), 2011. The highest UV-A irradiance was 55.4, 80.8, and 82.6 W m^{-2} , and that of UV-B was 1.74, 2.51, and 2.56 W m^{-2} , on these days (Figs. 2A–C). The transparency of the shaded and non-shaded areas was the same and was consistent throughout the study period, with a PAR attenuation coefficient ($K_{\text{d-PAR}}$) of 0.42 m^{-1} , a $K_{\text{d-UV-A}}$ of 1.10, and $K_{\text{d-UV-B}}$ of 1.94 m^{-1} (Fig. 3). The daily doses of PAR at the surface water were 4.6 (April 22th, 2011), 10.4 (April 24th, 2011), and 10.3 (April 25th, 2011) MJ m^{-2} ; those of UV-A were 0.79, 1.74, and 1.70 MJ m^{-2} ; and those of UV-B were 0.024, 0.051, and 0.050 MJ m^{-2} .

Dominant planktonic species and predators in the reservoir during the experimental period

Taxonomic analyses revealed the cyanobacterial dominance of the phytoplankton communities throughout the study period. The dominant species were *Pediastrum simplex*, *Microcystis flos-aquae*, *Anabeana oscillarioides*, *Oscillatoria* sp., *Ceratium hirundinella*, and *Melosira granulata*. The phytoplankton abundance was 18.35 (± 2.44) and 18.66 (± 2.67) $\mu\text{g chl } a \text{ L}^{-1}$ in the shaded and non-shaded water columns during the experimental period.

The zooplankton community was composed mainly of rotifers and copepods, with *Keratella valga*, *Brachionus forficula*, *Asplanchna priodonta*, *Filinia longiesta*, and *Thermocyclops taihokuensis* being the dominant species. The predators collected by repeatedly vertical hauling with a plankton net (mesh diameter 505 μm) were juvenile fishes, such as crucian carp *Carassius auratus* and *Pseudorasbora parva*.

Fig. 2 Incident solar radiation (W m^{-2}) of PAR (400–700 nm), UV-A (315–400 nm), and UV-B (280–315 nm) measured from dawn to dusk on April 22th (A), 24th (B), and 25th (C), 2011



Variation in temperature, DO, and pH of surface water in shaded and non-shaded areas

Little difference in temperature ($<1.5^{\circ}\text{C}$), DO ($<0.47 \text{ mg O}_2 \text{ L}^{-1}$) concentration, or pH (<0.05) of the surface waters was found between the shaded and non-shaded areas, although their diurnal variation was relatively high (Table 1). The surface water temperature ranged from 21.9 to 24.5°C during the

experimental period, and DO and pH of the shaded and non-shaded surface waters ranged from 9.65 to 11.51 $\text{mg O}_2 \text{ L}^{-1}$ and from 8.00 to 8.88 (Table 1).

Effects of solar radiation on horizontal migration of zooplankton

On the cloudy day (April 22th, 2011), the ratios of total zooplankton biomass in the shaded areas to those in

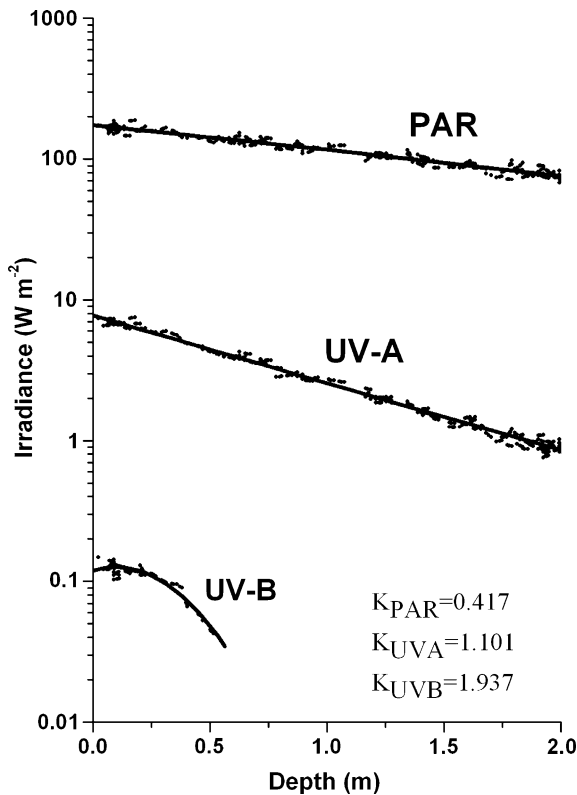


Fig. 3 Representative profile showing the underwater radiation of solar PAR (400–700 nm), UV-A (315–400 nm), and UV-B (280–315 nm) in $W m^{-2}$ for the unshaded treatment, with $K (m^{-1})$ showing the attenuation coefficients. The profile was measured at 12:00 on April 24, 2011

the nearby non-shaded water ranged from 0.90 to 1.49. Most of the values were close to 1.00 during the daytime except for the twilight periods which showed

the lowest value (0.90) (Fig. 4A). On sunny days, the ratio showed a similar pattern to the variation in diurnal solar radiation: increasing in the morning with sunrise, reaching peak values at noon, and then decreasing with declining solar radiation (Figs. 4B, C). The values from 09:30 to 15:30 on the 24th (Fig. 4B) and those from 10:30 to 17:30 on April 25th (Fig. 4C) were all above 1.5 and with the highest values close to 3.0. This indicated that the zooplankton was about 50–200% more abundant in the shaded areas. When plotted against solar radiation levels, the ratios linearly correlated ($R^2 = 0.71, p < 0.01$) with the mean solar radiation between the sampling points (Fig. 5).

Discussion

Since water temperature, DO, and pH and phytoplankton abundance did not differ between the shaded and non-shaded area, the zooplankton horizontal migration to shaded water was the evidence that they used the shade as a shelter from strong solar radiation.

Both biotic factors, such as predators, macrophytes, and food resources (Romare & Hansson, 2003; Iglesias et al., 2007), and abiotic factors, such as light, DO, pH, and water temperature (Sell, 1998; Boeing et al., 2004; Li & Gao, 2012), influence the migration of zooplankton. Water flow driven by wind might play a role in narrowing the differences in water temperature, DO, and pH between shaded and non-shaded areas. Zooplankton can tolerate DO as low as $0.5 mg O_2 L^{-1}$ by producing sufficient hemoglobin (Weider & Lampert, 1985; Sell, 1998). The DO of the shaded and non-

Table 1 Variations in surface temperature (ST), pH, and dissolved oxygen (DO) concentration of shaded and adjacent non-shaded (control) waters measured during the experimental period

Parameter		ST ($^{\circ}C$)		DO ($mg L^{-1}$)		pH	
Date	Time	Control	Shaded	Control	Shaded	Control	Shaded
22th April, 2011	8:00	22.9	22.8	10.02	9.65	8.10	8.09
	13:00	23.8	22.3	10.66	10.77	8.65	8.65
	18:00	23.1	22.2	11.45	10.84	8.84	8.81
24th April, 2011	8:00	22.2	21.9	10.48	10.48	8.12	8.10
	13:00	24.5	23.6	10.99	11.12	8.79	8.83
	18:00	23.2	22.5	11.51	11.30	8.88	8.86
25th April, 2011	8:00	22.3	22.2	10.48	10.02	7.95	8.00
	13:00	24.3	22.9	10.99	11.11	8.85	8.86
	18:00	23.8	22.5	11.51	11.30	8.86	8.83

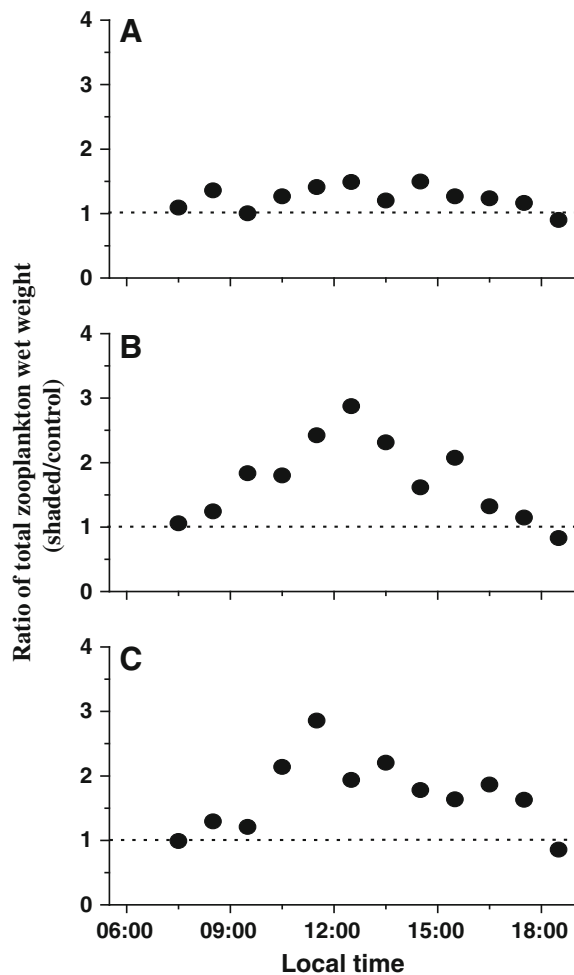


Fig. 4 Ratio of total zooplankton wet weight collected from the shaded area to those from adjacent non-shaded waters (control) on a cloudy day (A April 22th, 2011) and two sunny days (B and C April 24th and 25th, 2011)

shaded surface waters in our study was close to $10.0 \text{ mg O}_2 \text{ L}^{-1}$, which should be suitable for zooplankton, and unlikely to cause the different distribution. The copepod *Centropages tenuiremis* shows no selectivity for seawater with pH values ranging from 7.80 to 8.15 (Li & Gao, 2012). The biggest temperature difference between shaded and adjacent non-shaded waters was less than 1.5°C , within the temperature gradient ($>4^\circ\text{C}$) that inspires a behavioral response (Boscarino et al., 2007). In addition, zooplankton individuals can easily counteract the temperature difference by vertical migration. Therefore, the very small differences in DO, pH, and temperature between the shaded and non-shaded areas in our study were unlikely to cause such differences in

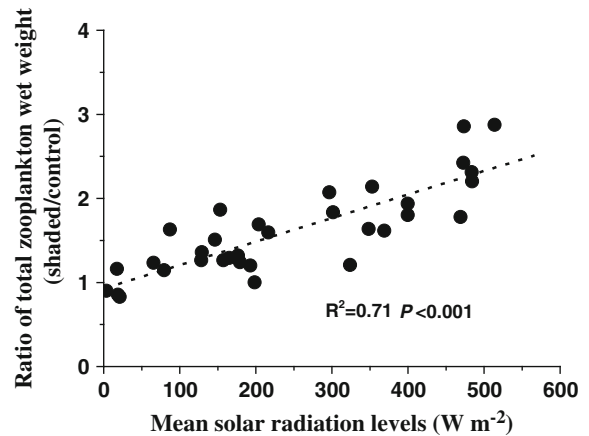


Fig. 5 Ratios of total zooplankton wet weights sampled (T_n) from shaded waters to those from an adjacent non-shaded area (control) as a function of the mean full solar radiation (PAR + UV-A + UV-B) levels between every two neighboring sampling intervals (T_{n-1} to T_n). The time interval between two neighboring samplings was about 1 h. T_n and T_{n-1} represent the time point of one random sampling and its neighboring previous sampling

zooplankton biomass. According to the generally accepted hypothesis, migrations of zooplankton are the consequence of a trade off between feeding and predation risk (Desmarias & Tessier, 1999). Since there was no difference in phytoplankton abundance between the shaded water and non-shaded area, migration of the zooplankton to prey on phytoplankton could be ruled out. Zooplankton often seeks refuge from planktivorous fish against macrophytes (Burks et al., 2002; Wojtal et al., 2003). However, aquatic plants in subtropical shallow lakes offer refuges for zooplankton only at intermediate predator densities (Castro et al., 2007; Iglesias et al., 2007). Predation by fishes on zooplankton is shown to be size-dependent: the pressure being less on smaller copepods and rotifers than on larger sized daphnia (Lynch, 1979; Vanni, 1987; Zimmer et al., 2001; Jakobsen et al., 2003; Badosa et al., 2007), suggesting that the predation pressure is not the key role in regulating the distribution of all zooplankton between shaded and non-shaded water columns. The predator pressure on the distribution of zooplankton between treatments was not measured in our study since the zooplankton community was mainly composed by rotifers and copepods. On the other hand, the shade provided by the neutral net differed from that provided by macrophytes, which also provide refuge so that the zooplankton would be less visible to the predators.

The fact that the accumulation of zooplankton in the shaded water linearly increased with enhanced solar radiation supplied sustainable evidence that the horizontal zooplankton migration was caused by solar radiation, especially harmful UVR, which causes horizontal migration of copepods in laboratory studies (Ma et al., 2010). On the other hand, we did not firmly believe that zooplankton could “see” the shaded area: they might have reached the shaded area just by randomly moving around, and the comfortable feeling encouraged them to stay in the shaded water for a longer period. Solar UVR is recognized as the main cue for vertical avoidance of high solar radiation by zooplankton, in recent years (Rocco et al., 2001; Rhode et al., 2001; Wold & Norrbin, 2004; Hansson et al., 2007). The zooplankton could also have escaped high solar radiation by vertical migration in our study (Fig. 3). However, using horizontal avoidance, individuals can easily move to the nearest shelter for protection with less energy cost compared to vertical migration (Loose & Dawidowicz, 1994; Cooke et al., 2008; Ma et al., 2010). Ma et al. (2010) also show that the zooplankton gathers in areas with moderate PAR levels in the absence of UV-B. However, in natural waters, little evidence is available to support the horizontal migration of zooplankton (Lauridsen et al., 1999; Burks et al., 2002; Balayla & Moss, 2003; Romare & Hansson, 2003; Wojtal et al., 2003; Iglesias et al., 2007). However, in our study, rotifers and copepods showed much higher abundance in the shaded area under higher levels of solar radiation compared to the adjacent non-shaded area (Figs. 4, 5).

Besides behavioral avoidance, protective strategies which the zooplankton might use to cope with UVR are photo-repair and accumulation of photo-protective compounds (Hansson & Hylander, 2009; Ma et al., 2010; Häder et al., 2011). The mycosporine-like amino acids (MAAs) with maximum absorption between 310 and 360 nm (Sinha et al., 2007) are detected in rotifers and copepods, and are known to function as sunscreens against UVR (Sommaruga & Garcia-Pichel, 1999; Hansson et al., 2007; Ma et al., 2010, 2013). Both rotifers and copepods can accumulate more colorless (such as MAAs) or less colored (such as carotenoids) photo-protective compounds in order to increase their defenses against UVR but not to raise the risk of predation (Hansson & Hylander, 2009; Hylander et al., 2009). Nevertheless, the metabolic activities of copepods are suppressed by solar

UVR at similar levels as during the noon period in this study (Ma et al., 2013). From an ecological point of view, levels of solar radiation and shade levels in aquatic environments can play an important role in controlling zooplankton distribution.

Acknowledgments We thank the two anonymous reviewers and the associate editor Sigrún Jónasdóttir for the comments and suggestions that helped to improve this manuscript. This study was funded by the Shanghai Municipal Natural Science Foundation (No. 11ZR1449900), National Natural Science Foundation (No. 40930846, No. 41120164007), Program for Changjiang Scholars and Innovative Research Team (IRT0941), and China-Japan collaboration project from MOST (S2012GR0290). We thank Professor John Hodgkiss and Professor Bill Eaton for their help with the English in this manuscript.

References

- Badosa, A., D. Boix, S. Brucet, R. López-Flores, S. Gascón & X. D. Quintana, 2007. Zooplankton taxonomic and size diversity in Mediterranean coastal lagoons (NE Iberian Peninsula): Influence of hydrology, nutrient composition, food resource availability and predation. *Estuarine, Coastal and Shelf Science* 71: 335–346.
- Balayla, D. J. & B. Moss, 2003. Spatial patterns and population dynamics of plant-associated microcrustacea (Cladocera) in an English shallow lake (Little Mere, Cheshire). *Aquatic Ecology* 37: 417–435.
- Boeing, W. J., D. M. Leech, C. E. Williamson, S. Cooke & L. Torres, 2004. Damaging UV radiation and invertebrate predation: conflicting selective pressures for zooplankton vertical distribution in the water column of low DOC lakes. *Oecologia* 138: 603–612.
- Boscarino, B. T., L. G. Rudstam, S. Mata, G. Gal, O. E. Johannson & E. L. Mills, 2007. The effects of temperature and Predator-prey interactions on the migration behavior and vertical distribution of *Mysis relicta*. *Limnology and Oceanography* 52: 1599–1613.
- Burks, R. L., D. M. Lodge, E. Jeppesen & T. L. Lauridsen, 2002. Diel horizontal migration of zooplankton: cost and benefits of inhabiting the littoral. *Freshwater Biology* 47: 343–365.
- Castro, B. B., S. M. Marques & F. Gonçalves, 2007. Habitat selection and diel distribution of the crustacean zooplankton from a shallow Mediterranean lake during the turbid and clear water phases. *Freshwater Biology* 52: 421–433.
- Cooke, S. L., C. E. Williamson, D. M. Leech, W. J. Boeing & L. Torres, 2008. Effects of temperature and ultraviolet radiation on diel vertical migration of freshwater crustacean zooplankton. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 1144–1152.
- Dattilo, A. M., L. Bracchini, L. Carlini, S. Loïselle & C. Rossi, 2005. Estimate of the effects of ultraviolet radiation on the mortality of *Artemia franciscana* in naupliar and adult stages. *International Journal of Biometeorology* 49: 388–395.

- De Lange, H. J. & P. L. Van Reeuwijk, 2003. Negative effects of UVB-irradiated phytoplankton on life history traits and fitness of *Daphnia magna*. *Freshwater Biology* 48: 678–686.
- Desmarias, K. H. & A. J. Tessier, 1999. Performance trade-off across a natural resource gradient. *Oecologia* 120: 137–146.
- Gliwicz, M. Z., 1986. Predation and the evolution of vertical migration in zooplankton. *Nature* 320: 746–748.
- Häder, D.-P., E. W. Helbling, C. E. Williamson & R. C. Worrest, 2011. Effects of UV radiation on aquatic ecosystems and interaction with climate change. *Photochemical & Photobiological Science* 10: 242–260.
- Hairton, N. G., 1976. Photoprotection by carotenoid pigments in the copepod *Diaptomus nevadensis*. *Proceedings of the National Academy of Sciences* 73: 971–974.
- Hansson, L.-A., 2000. Induced pigmentation in zooplankton: a trade-off between threats from predation and UV-damage. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 267: 2327–2331.
- Hansson, L.-A. & S. Hylander, 2009. Effects of ultraviolet radiation on pigmentation, photoenzymatic repair, behavior, and community ecology of zooplankton. *Photochemical & Photobiological Science* 8: 1266–1275.
- Hansson, L.-A., S. Hylander & R. Sommaruga, 2007. Escape from UV threats in zooplankton: a cocktail of behavior and protective pigmentation. *Ecology* 88: 1932–1939.
- Hylander, S., N. Larsson & L. A. Hansson, 2009. Zooplankton vertical migration and plasticity of pigmentation arising from simultaneous UV and predation threats. *Limnology and Oceanography* 54: 483–491.
- Iglesias, C., G. Goyenola, N. Mazzeo, M. Meerhoff, E. Rodóand & E. Jeppesen, 2007. Horizontal dynamics of zooplankton in subtropical Lake Blanca (Uruguay) hosting multiple zooplankton predators and aquatic plant refuges. *Hydrobiologia* 584: 179–189.
- Jakobsen, T. S., P. B. Hansen, E. Jeppesen, P. Grønkjær & M. Søndergaard, 2003. Impact of three-spined stickleback *Gasterosteus aculeatus* on zooplankton and chl *a* in shallow, eutrophic, brackish lakes. *Marine Ecology Progress Series* 262: 277–284.
- Kouwenberg, J. H. M., H. Browman, J. J. Cullen, R. F. Davis, J. F. St. Pierre & J. A. Runge, 1999. Biological weighting of ultraviolet (280–400 nm) induced mortality in marine zooplankton and fish. I Atlantic cod (*Gadus morhua*) eggs. *Marine Biology* 134: 269–284.
- Lauridsen, T. L., E. Jeppesen, S. F. Mitchell, D. M. Lodge & R. L. Burks, 1999. Diel variation in horizontal distribution of *Daphnia* and *Ceriodaphnia* in oligotrophic and mesotrophic lakes with contrasting fish densities. *Hydrobiologia* 408(409): 241–250.
- Li, W. & K. Gao, 2012. A marine secondary producer respire and feeds more in a high CO₂ ocean. *Marine Pollution Bulletin* 64: 699–703.
- Li, G., K. Gao, D. Yuan, Y. Zheng & G. Yang, 2011. Relationship of photosynthetic carbon fixation with environmental changes in the Jiulong River estuary of the south China Sea, with special reference to the effects of solar UV radiation. *Marine Pollution Bulletin* 62: 1852–1858.
- Loose, C. J. & P. Dawidowicz, 1994. Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. *Ecology* 75: 2255–2263.
- Lynch, M., 1979. Predation, competition, and zooplankton community structure: an experimental study. *Limnology and Oceanography* 24: 253–272.
- Ma, Z., W. Li & K. Gao, 2010. Horizontal migration of *Acartia pacifica* Steuer (copepoda) in response to UV-radiation. *Journal of Photochemistry and Photobiology B: Biology* 101: 233–237.
- Ma, Z., W. Li & K. Gao, 2012. Impacts of solar UV radiation on grazing and lipids oxidation of *Acartia pacifica* Steuer (Copepod). *Acta Oceanologica Sinica* 31: 126–134.
- Ma, Z., W. Li & K. Gao, 2013. Impacts of UV radiation on respiration, ammonia excretion and survival of copepods with different feeding habits. *Hydrobiologia* 701: 209–218.
- Mackenzie, R. L., P. J. Aucamp, A. F. Bais, L. O. Björn, M. Ilyas & S. Madronich, 2011. Ozone depletion and climate change: impacts on UV radiation. *Photochemical & Photobiological Sciences* 10: 182–198.
- Manney, G. L., M. L. Santee, M. Rex, N. J. Livesey, M. C. Pitts, P. Veefkind, E. R. Nash, I. Wohltmann, R. Lehmann, L. Froidevaux, L. R. Poole, M. R. Schoeberl, D. P. Haffner, J. Davies, V. Dorokhov, H. Gernandt, B. Johnson, R. Kivi, E. Kyrö, N. Larsen, P. F. Levelt, A. Makshtas, C. T. McElroy, H. Nakajima, M. C. Parrondo, D. W. Tarasick, P. von der Gathen, K. A. Walker & N. S. Zinoviev, 2011. Unprecedented Arctic Ozone loss in 2011. *Nature* 478: 469–475.
- Moeller, R. E., S. Gilroy, C. E. Williamson, G. Grad & R. Sommaruga, 2005. Dietary acquisition of photoprotective compounds (mycosporine-like amino acids, carotenoids) and acclimation to ultraviolet radiation in a freshwater copepod. *Limnology and Oceanography* 50: 427–439.
- Pearre, S., 2003. Eat and run? The hunger/satiation hypothesis in vertical migration: history, evidence and consequences. *Biological Reviews* 78: 1–79.
- Petzold, T., L. Rudolf, K. Rinke & J. Benndorf, 2009. Effects of zooplankton diel vertical migration on a phytoplankton community: a scenario analysis of the underlying mechanisms. *Ecological Modelling* 220: 1358–1368.
- Reichwaldt, E. S., I. D. Wolf & H. Stibor, 2005. Effects of a fluctuating temperature regime experienced by *Daphnia* during diel vertical migration on *Daphnia* life history parameters. *Hydrobiologia* 543: 199–205.
- Rhode, S. C., M. Pawlowski & R. Tollrian, 2001. The impact of ultraviolet radiation on the vertical distribution of zooplankton of the genus *Daphnia*. *Nature* 412: 69–72.
- Rocco, C., O. Oppezzo, R. Pizarro, R. Sommaruga, M. Ferraro & H. Zagarese, 2001. Ultraviolet damage and counteracting mechanisms in the freshwater copepod *Boeckella poppei* from the Antarctic peninsula. *Limnology and Oceanography* 47: 829–836.
- Romare, P. & L.-A. Hansson, 2003. A behavioral cascade: top-predator induced behavioral shifts in planktivorous fish and zooplankton. *Limnology and Oceanography* 48: 1956–1964.
- Scott, J. D., L. Chalker-Scott, A. E. Foreman & M. D'Angelo, 1999. *Daphnia pulex* fed UVB-irradiated *Chlamydomonas reinhardtii* show decreased survival and fecundity. *Photochemistry and Photobiology* 70: 308–313.
- Sell, A. F., 1998. Adaptation to oxygen deficiency: contrasting patterns of haemoglobin synthesis in two coexisting *Daphnia* species. *Comparative Biochemistry and Physiology*, part A 120: 119–125.

- Sinha, R. P., S. P. Sinha & D.-P. Häder, 2007. Database on mycosporines and mycosporine-like amino acids (MAAs) in fungi, cyanobacteria, macroalgae, phytoplankton and animals. *Journal of Photochemistry and Photobiology B: Biology* 89: 29–35.
- Sommaruga, R. & F. Garcia-Pichel, 1999. UV-absorbing mycosporine-like compounds in planktonic and benthic organisms from a high-mountain lake. *Archiv für Hydrobiologie* 144: 255–269.
- Vanni, M. J., 1987. Effects of food availability and fish predation on a zooplankton community. *Ecological Monographs* 57: 61–88.
- Weider, L. J. & W. Lampert, 1985. Differential response of *Daphnia* genotypes to oxygen stress: respiration rates, hemoglobin content and low-oxygen tolerance. *Oecologia* 65: 487–491.
- Wojtal, A., P. Frankiewicz, K. Izydorczyk & M. Zalewski, 2003. Horizontal migration of zooplankton in a littoral zone of the lowland Sulejow Reservoir (Central Poland). *Hydrobiologia* 506–509: 339–346.
- Wold, A. & F. Norrbin, 2004. Vertical migration as a response to UVR stress in *Calanus finmarchicus* female and nauplii. *Polar Research* 23: 27–34.
- Yu, J., G. Yang & J. Tian, 2009. Effects of UV-B radiation on ingestion, fecundity, population dynamics and antioxidant enzyme activities of *Schmackeria inopinus* (Copepoda Calanoida). *Journal of Experimental Marine Biology and Ecology* 381: 74–81.
- Zimmer, K. D., M. A. Hanson, M. G. Butler & W. G. Duffy, 2001. Size distribution of aquatic invertebrates in two prairie wetlands, with and without fish, with implications for community production. *Freshwater Biology* 46: 1373–1386.