

Multifactorial nature of rotifer water layer preferences in an oligotrophic lake

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Rotifer preference for the upper (0–2 m) or deeper layer (5–35 m) of the water column was assessed at midday and midnight in an oligotrophic mountain lake during summer, and related to temperature, food availability, presence of predators and exposure to solar ultraviolet radiation (UVR). Whereas Keratella cochlearis and Synchaeta pectinata showed a population maximum in the deeper layer during midday and in the upper layer during midnight, Asplanchna priodonta, Synchaeta kitina and Filinia terminalis always remained in the deeper layer. In contrast, Polyarthra dolichoptera and S. grandis were the only rotifer species that remained in the upper layer. Possession of mycosporine-like amino acids, a family of photoprotective compounds seemed to be an important strategy for occupying the upper layer. For other species, midday positioning in the deeper layer seemed to be related to UVR avoidance rather than to predation pressure, whereas the upward shift at night was species-dependent. Migrating species seemed favoured by higher temperatures in the upper layer, whereas non-migrating species seemed restricted by factors such as food supply. Our study indicates that rotifers exhibit different species-specific strategies for dealing with factors such as UVR exposure, temperature and food availability.

INTRODUCTION

Zooplankton position themselves in the water column to maximize production, which depends on several factors such as oxygen, temperature, light, food supply, competition, and predation (Hutchinson, 1967; Mikschi, 1989; Ringelberg, 1995; Kessler and Lampert, 2004; Winder *et al.*, 2004 and references therein). It is widely accepted that both freshwater and marine zooplankton generally stay in deeper layers during the day to avoid predators and rise to the upper layers at night to exploit food resources (Worthington, 1931; Lampert, 1989; Gliwicz, 2003; Pearre, 2003; Van Gool and Ringelberg, 2003). However, other authors do not support this hypothesis and argue that a nocturnal ascent to warmer superficial layers can instead constitute a demographic advantage (Williamson *et al.*, 1996; Lampert *et al.*, 2003; Winder *et al.*, 2003).

Temperature is an important factor for zooplankton growth, and low temperatures reduce embryonic and

post-embryonic development rates (Gillooly *et al.*, 2002). According to McLaren (McLaren, 1974), however, cold temperatures could instead constitute a demographic advantage for zooplankton, when size and fecundity are a negative function of temperature. Therefore, depending on varying habitat characteristics, zooplankton may be subject to different trade-offs, and accordingly not all observed patterns of surface avoidance can be explained by predation pressure (Williamson *et al.*, 2001).

Rhode *et al.* (Rhode *et al.*, 2001) suggested that benefits from avoiding both predators and solar ultraviolet radiation (UVR, 290–400 nm) determine the evolution of daytime avoidance of the upper layer. In fact, solar radiation and especially UVR may have detrimental effects on freshwater zooplankton (Sommaruga, 2001; Williamson *et al.*, 2001; Leech *et al.*, 2005a, 2005b; Hansson *et al.*, 2007), including a general decrease in zooplankton biodiversity (Marinone *et al.*, 2006). One strategy to minimize the damage caused by

UVR is to avoid the sunlit upper layers. For example, in Patagonian lakes, Alonso *et al.* (Alonso *et al.*, 2004) showed that copepods stay in deeper layers during the day to avoid exposure to UVR.

Photoprotective compounds such as carotenoids, melanin, and mycosporine-like amino acids (MAAs) known to minimize UV damage are found in many zooplanktons (Hairston, 1979; Sommaruga, 2001; Moeller *et al.*, 2005; Sommaruga *et al.*, 2006). In particular, MAAs appear to be widespread among different taxa of freshwater planktonic organisms except for Cladocera (Tartarotti *et al.*, 2001; Persaud *et al.*, 2007). One of the main sources of MAAs for zooplankton is phytoplankton and distinct lake assemblages contain different concentrations of MAAs depending on UV exposure conditions and other poorly understood factors (Laurion *et al.*, 2002). Contrary to primary producers, zooplankton can not synthesize MAAs but accumulate them through their diet (Moeller *et al.*, 2005), whereas the degree of accumulation (percentage of dry weight) is related to the lake UV-refuge (Tartarotti *et al.*, 2001). MAA research in freshwater plankton has mainly focused on copepods (Tartarotti *et al.*, 2001; Alonso *et al.*, 2004; Moeller *et al.*, 2005; Tartarotti and Sommaruga, 2006; Hansson *et al.*, 2007); however, little is known about these compounds in rotifers.

The objective of this study was to compare the summer water column preferences of rotifers at midday and midnight considering different interacting factors in a whole-lake context. Water layer preference (WLP) of single rotifer species was assessed for two layers of the water column having clear differences in mean temperature, UVR, and predator abundance. We focused on summer for assessing the importance of UVR for WLP of rotifers as it is the period of major incident solar radiation. Midday and midnight WLP of rotifers was compared with the long-term pattern in four consecutive summer periods. We hypothesized that (i) UV-sensitive rotifers avoid the upper layer at midday to minimize UV stress, (ii) possession of MAAs could influence WLP given the photoprotective function of these compounds and (iii) rotifer WLP at midnight would be a species-specific response dependent on factors such as food supply and water temperature.

METHOD

Study site

Lake Tovel (46°15'N, 10°57'E; area=38 ha, volume=7.4 10⁶ m³, z_{\max} = 39 m, z_{mean} = 19 m) is an oligotrophic mountain lake in the Adamello Brenta Natural Park (Trentino, Italy) located at 1178 m above sea level. The lake is ice-covered from December to

April. The fish fauna of Lake Tovel consists of two littoral species, minnow (*Phoxinus phoxinus* L.) and stone loach (*Othrias barbatula* L.) and one pelagic species, arctic charr (*Salvelinus alpinus* L.). Limnological characteristics of the lake are detailed in Obertegger *et al.* (Obertegger *et al.*, 2007).

Sampling

We assessed rotifer WLP in August 2003 and July 2005. In 2005, we focused on the depth preferences of single species at midday and midnight after the first WLP study which indicated maximal diel zooplankton displacements at those time points (data not shown). Care was taken to choose a sampling date following at least 1 week of sunny weather. Midday distribution in the WLP study was compared with midday layer preference in summer during a 4-year period to contrast the temporal and spatial stability of the observed pattern. Summer sampling was limited to the period with >10 h daylight (May–August, 2002–2005) and was carried out on a biweekly schedule in 2002 and 2003 and a monthly schedule in 2004 and 2005.

Zooplankton samples were taken in three replicates with a 3 L Kemmerer-like sampler at the surface, 1, 2, 5, 10, 15, 20, 25, 30, and 35 m depth over the deepest part of the lake, filtered through a 10 µm plankton net and fixed with formalin (1% v/v final concentration). Species composition and biomass were determined as described in Obertegger *et al.* (Obertegger *et al.*, 2005). Briefly, the whole sample was counted with a stereo microscope (model Wild Macroscope M420) due to low zooplankton abundance (<250 specimens per sample). Species identification was according to Braioni and Gelmini (Braioni and Gelmini, 1983), Obertegger *et al.* (Obertegger *et al.*, 2006) and Einsle (Einsle, 1996).

In the WLP 2003 study, phytoplankton samples were collected at midday from the same depths as for zooplankton using the same water sampler. In the WLP 2005 study, integrated phytoplankton and chlorophyll *a* (Chl *a*) samples were taken with a weighted tube for the upper layer and the 0–20 m depth (euphotic zone) both at midday and midnight. During the summers 2002–2005, single phytoplankton samples were collected at the identical depths as for zooplankton using the same 3 L water sampler. Subsamples were fixed with acid Lugol's solution, and algae were counted with an inverted microscope. Algal biovolume was estimated from cell dimensions and was separated by the greatest axial linear dimension into a potentially edible (≤ 20 µm) and non-edible fraction (> 20 µm) according to the range of food particles fed on by most phytophagous rotifers (Miracle, 1974; Wallace *et al.*, 2006).

Vertical profiles of water temperature, dissolved oxygen (Hydrolab DS4a multiprobe), and Secchi disk readings were taken on each sampling occasion.

Hourly solar radiation values were obtained from the lake meteorological station. Photosynthetically active radiation (PAR) was measured with an LI-193 Spherical Quantum Sensor (LI-COR, Inc., Lincoln, NE, USA). Underwater UVR was measured with a PUV 501B multichannel radiometer (Biospherical Instruments, Inc., San Diego, USA).

MAA and Chl *a* measurements

In conjunction with zooplankton samples, several vertical net hauls (70 μm) were taken from the upper layer at midday in summer 2005. Depending on species seasonal abundance, approximately 100 individuals of rotifer species were concentrated with a micropipette on a wet Whatman GF/F filter. Whereas *P. dolichoptera* could be found in sufficient abundance for MAA analyses on every sampling occasion, specimens of *S. kitina*, *S. pectinata*, *S. grandis* and *K. cochlearis* were rare and required screening of the whole upper layer water sample to obtain an adequate number of individuals for MAA analysis. All filters were frozen at -80°C until extraction within 3 months. MAAs were extracted and analysed according to the protocol recommended for zooplankton in Tartarotti and Sommaruga (Tartarotti and Sommaruga, 2002).

For Chl *a* analysis, 1 L of lake water was filtered through a membrane filter (0.45 μm), and the pigments were extracted with alkaline acetone in the dark at 4°C . The concentration of Chl *a* was estimated according to the trichromatic method (APHA, 1998).

Data analysis

On the basis of PAR and UVR attenuation profiles ($Z_{1\%}^{320\text{nm}} = 3.2\text{--}3.8\text{ m}$, $Z_{1\%}^{340\text{nm}} = 4.1\text{--}5.4\text{ m}$, and $Z_{50\%}^{\text{PAR}} = 3.2\text{--}4.6\text{ m}$; Fig. 1), two water layers were considered for data analysis, i.e. from surface to 4 m depth (upper layer) and from $>4\text{ m}$ to 35 m depth (lower layer). Therefore, the surface and 1 and 2 m samples belonged to the upper layer and the 5 m and deeper samples to the lower layer.

The effects of depth and time and their interaction on square-root-transformed species abundance were tested by a two-way ANOVA followed by a Bonferroni *post hoc* multiple comparison test. STATISTICA 6.0 (Stat Soft, Inc., Tulsa, OK, USA) was used for this analysis.

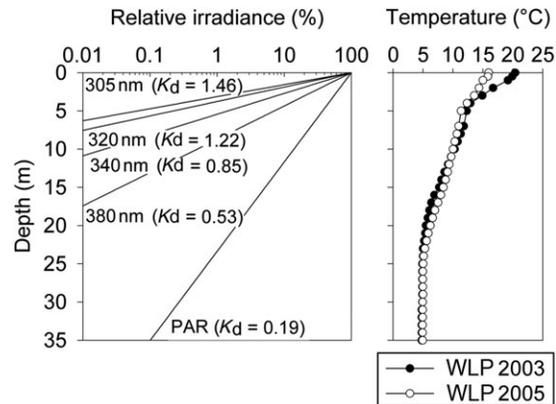


Fig. 1. Left panel: percentage of surface irradiance for four wavelengths in the UV and PAR. Values for the vertical attenuation coefficients (K_d) are per meter. Right panel: temperature profile in WLP 2003 and 2005 study.

RESULTS

Zooplankton WLP

During the WLP study in 2003 and 2005, both sampling days showed comparable incident global solar radiation (3.1 and 3.4 MJ m^{-2} at midday, respectively).

Temperature profiles showed little variation between day and night (temperature differences at the surface $<1^{\circ}\text{C}$) and were essentially similar for the 2 sampling days. However, there was a temperature gradient of ca. 5°C between the upper and lower water layers in the WLP studies of 2003 and 2005 (Fig. 1).

Zooplankton abundance in 2003 was low and the WLP could be properly assessed for only four rotifer species. *Keratella cochlearis* Gosse showed a statistically significant change in its WLP (Table I) with its highest abundance found at midday in the lower layer and at midnight in the upper layer (Fig. 2). *Filinia terminalis* Plate, *S. kitina* Rousselet, and *A. priodonta* showed an upward displacement of their population maximum from midday to midnight, but remained in the deeper layer (Fig. 2). However, *F. terminalis* and *S. kitina* showed a statistically significant midday to midnight change in their WLP, whereas *A. priodonta* did not (Table I).

In 2005, zooplankton abundance was higher, and the WLP of additional species could be assessed. *Keratella cochlearis* showed the same WLP as in 2003 (Fig. 3, Table I). On the contrary, *S. kitina* exhibited a statistically significant reverse shift to deeper depths at midnight in contrast to 2003, but still remained in the lower layer (Fig. 3, Table I). The abundance of *S. pectinata* Ehrenberg was low (<5 individuals L^{-1}) for all depths at midday, but was higher (ca. 18 individuals L^{-1}) in the upper layer at midnight (Fig. 3) showing a statistically

Table I: Two-way ANOVA for the effects of time, depth and their interaction (time × depth) on square-root-transformed abundance of species in WLP

Taxon	df	2003		2005	
		F	P-value	F	P-value
<i>K. cochlearis</i>					
Time	1	28.4	0.014	546.6	0.000
Depth	9	11.4	0.000	92.6	0.000
Time × depth	9	16.7	0.000	98.9	0.000
Error	40				
<i>S. kitina</i>					
Time	1	2.2	0.149	813.3	0.000
Depth	9	48.7	0.000	270.9	0.000
Time × depth	9	6.4	0.000	70.5	0.000
Error	40				
<i>F. terminalis</i>					
Time	1	6.6	0.000		
Depth	9	82.0	0.000		
Time × depth	9	39.1	0.000		
Error	40				
<i>A. priodonta</i>					
Time	1	14.1	0.000		
Depth	9	18.1	0.000		
Time × depth	9	1.6	0.161		
Error	40				
<i>P. dolichoptera</i>					
Time	1			37.6	0.000
Depth	9			65.0	0.000
Time × depth	9			1.2	0.321
Error	40				
<i>S. pectinata</i>					
Time	1			65.1	0.000
Depth	9			17.2	0.000
Time × depth	9			12.3	0.000
Error	40				

significant population displacement (Table I). *Polyarthra dolichoptera* Idelson had its maximum abundance in the upper layer both at midday and midnight, and did not show any change in its WLP.

According to the distance between the depth of maximum abundance at midday and midnight, rotifer displacement was divided into three categories: (i) *K. cochlearis* showed a population displacement up to 8 m (WLP 2003 and 2005 study; Figs 2 and 3), *S. kitina* (WLP 2003 and 2005 study; Figs 2 and 3) and *F. terminalis* (WLP 2003 study; Fig. 2) up to 5 m, (ii) for *S. pectinata* (WLP 2005 study; Fig. 3) a displacement distance was not possible to determine, (iii) while *A. priodonta* (WLP 2003 study; Fig. 2) and *P. dolichoptera* (WLP 2005 study; Fig. 3) did not show any statistically significant displacement in their population maxima. The estimated swimming speed over the 12 h interval (i.e. midday–midnight, distance 8 m) was 0.185 mm s⁻¹ or 1.046 body lengths s⁻¹ for *K. cochlearis*. The species *S. kitina* and *F. terminalis* had a lower swimming speed (0.116 mm s⁻¹ for a distance of 5 m), but *S. kitina* was faster (1.146 and 0.809 body length s⁻¹, respectively) when calculated in relation to its body length.

Seasonal midday WLP of zooplankton

During the summers 2002–2005, the predatory copepod *C. strenuus* was present in low abundance (mean abundance <1 individual L⁻¹ over the whole water column). Among rotifers, *P. dolichoptera* had the highest abundance (14 individuals L⁻¹), whereas *K. cochlearis*, *F. terminalis*, *A. priodonta*, and *S. pectinata* had lower abundances (7, 11, 8, and 3 individuals L⁻¹, respectively). *Cyclops strenuus*, *K. cochlearis*, *F. terminalis*, *A. priodonta*, and *S. pectinata* always showed a higher abundance in the lower than in the upper layer (Fig. 4). Also *S. kitina* generally stayed in the lower layer; however, in July 2005, this species had its highest abundance in the upper layer coinciding with an unusual bloom of *Cyclotella* sp. on a rainy day (Fig. 4). *Synchaeta*

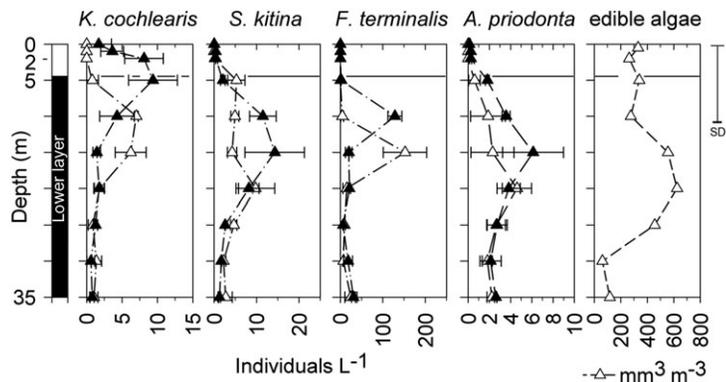


Fig. 2. Mean abundance of different rotifer species at midday and at midnight in WLP 2003 study. Open triangles indicate midday sampling, filled triangles indicate midnight sampling. SD indicates Secchi disk depth; error bars indicate standard deviation. Note the different scaling of the x-axis. The horizontal line indicates the boundary between the upper and lower layers.

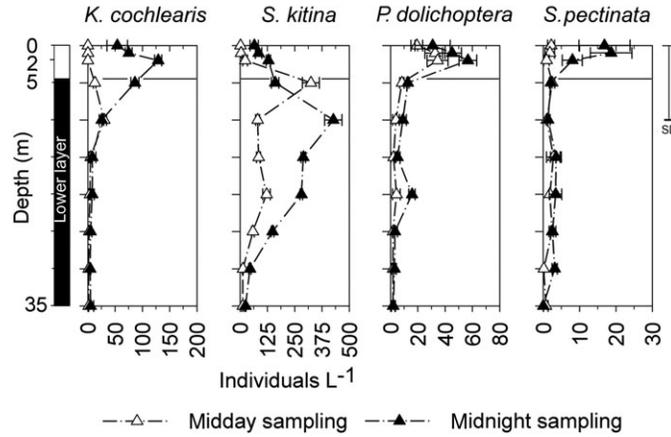


Fig. 3. Mean abundance of different rotifer species at midday and at midnight in WLP 2005 study. Open triangles indicate the midday sampling, and filled triangles indicate the midnight sampling. SD indicates Secchi disk depth; error bars indicate standard deviation. Note the different scaling of the x-axis. The horizontal line indicates the boundary between the upper and lower layers.

grandis Zacharias, the other species of the *stylata-pectinata* group in Lake Tovel, was abundant only during three sampling occasions (i.e. August 2002, 2004, and 2005) with its maximum abundance found in the upper layer (Fig. 4). *Polyarthra dolichoptera* also showed its maximum abundance in the upper layer apart from occasional exceptions (Fig. 4); nevertheless, even then specimens

were found in the upper layer (range: 1–13 individuals L^{-1}).

Summer temperature differences between the upper and lower layers were *ca.* 5°C. Secchi disk readings for the period May–August showed little variation (Table II) with no significant difference between means (ANOVA, $P > 0.05$).

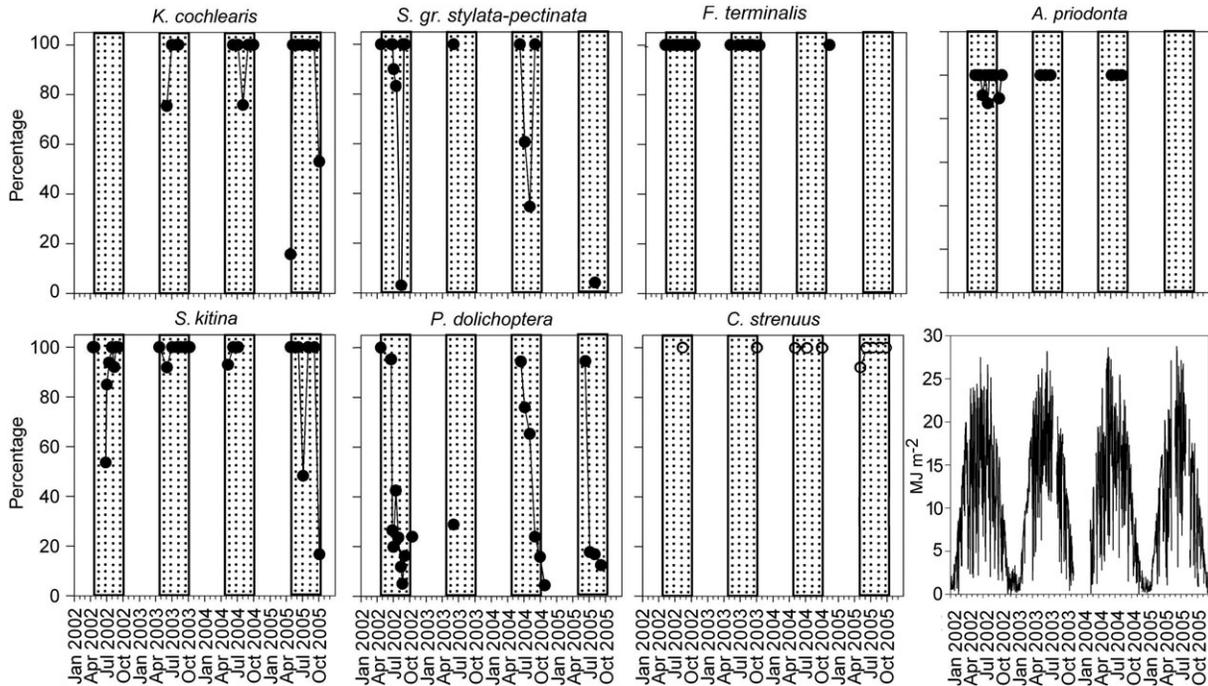


Fig. 4. Mean abundance (%) of zooplankton in the lower layer in summer (May–August; dotted area); % abundance in the lower layer = abundance in the lower layer * 100 / abundance in the lower and upper layers. Open circles for *C. strenuus* indicate mean abundance < 1 individual L^{-1} . Summer abundance of *S. gr. stylata-pectinata* refers to *S. pectinata* and *S. grandis*, whereas the latter only occurred in August 2002, 2004 and 2005. The lower right panel shows the daily incident solar radiation values.

Table II: Mean Secchi disk depth readings for the period May–August for 2002–2005

Year	n	Mean Secchi depth (m)	SD	CV (%)
2002	10	11.0	1.8	16.6
2003	9	9.7	1.2	12.8
2004	5	11.2	2.4	21.6
2005	9	12.2	3.4	27.7

Number of observations (n), standard deviation (SD) and coefficient of variation (CV).

MAAs

The highest concentrations of MAAs were found in *P. dolichopectera*, followed by *S. pectinata*, *S. grandis*, and *K. cochlearis* (Table III). MAAs were not detected in *S. kitina*. In the WLP study 2005, *P. dolichopectera* was the only species in the upper layer at midday with 0.33% MAAs of dry weight. Among MAAs, porphyra-334 was the dominant compound, followed by palythine and mycosporine-glycine. Asterina-330 and shinorine were found in trace amounts (Table III).

Distribution of potentially edible algae

In the WLP 2003 study, the biovolume of edible algae was higher in the deeper than in the upper layer at midday. Midnight data for edible algae were only assessed in the WLP 2005 study, when biovolume of algae and Chl *a* was at least 3-fold higher in the lower than in the upper layer (Fig. 5). The upper and lower layers had similar values of edible algal biovolume and of Chl *a* at midday and midnight (Fig. 5). At midday and midnight, diatoms, chrysophytes, and dinoflagellates constituted the major groups of algae. The biovolume of total and edible algae in summer at midday showed a large variability between years; usually, the lower layer had higher values than the upper layer (Fig. 5).

Table III: Mean MAAs content in different rotifers ($\mu\text{g MAAs mg}^{-1}$ dry weight \pm standard deviation) and MAA content in % for the different compounds

Taxa	n	$\mu\text{g MAAs mg}^{-1}$					
		DW \pm SD	% MG	% SH	% PR	% PI	% AS
<i>P. dolichopectera</i>	8	6 \pm 4.5	23	1	48	24	4
<i>S. pectinata</i>	5	2 \pm 0.1	—	—	66	20	14
<i>S. grandis</i>	3	2 \pm 0.1	—	—	75	29	8
<i>K. cochlearis</i>	4 ^a	0.2	—	—	—	100	—
<i>S. kitina</i>	2	—	—	—	—	—	—

Number of samples (n), mycosporine-glycine (MG), shinorine (SH), porphyra-334 (PR), palythine (PI), asterina (AS). — indicates under the detection limit.

^aMAAs were found only in one sample.

DISCUSSION

In Lake Tovel, rotifers showed a species-specific WLP in the two WLP studies which was largely coincident with the pattern observed during summer samplings. Therefore, our results were representative for summer when UVR and plankton production are high.

Avoidance of the upper layer

The predation avoidance hypothesis states that zooplankton avoid the upper layer at midday because of predation pressure (Worthington, 1931; Lampert, 1989; Gliwicz, 2003; Pearre, 2003; Van Gool and Ringelberg, 2003). Generally, rotifers are too small to be preyed on by vertebrate predators such as most adult fish (Wallace *et al.*, 2006), and the actual predation seems to be limited to the littoral or benthic zone by juvenile fish (Walz, 1995). The impact of fish on rotifer communities is more often indirect through predation on their crustacean competitors (Brooks and Dodson, 1965; Wallace *et al.*, 2006). However, invertebrate predators such as *Asplanchna* or *Cyclops* efficiently prey on rotifers in the pelagic zone with *Asplanchna* being a more efficient predator than cyclopoids such as *Mesocyclops edax* based on a *per capita* predation rate coefficient (Williamson, 1993). Whereas the impact of *C. strenuus* seemed negligible because of its low abundance (mean abundance during summer 2002–2005: <1 individuals L^{-1}), *A. priodonta* was more common (mean abundance during summer 2002–2005: 8 individuals L^{-1}). Interestingly, only *P. dolichopectera* and *S. grandis* inhabited the upper layer, whereas the herbivorous rotifers *K. cochlearis*, *S. kitina*, *F. terminalis*, and *S. pectinata* and the invertebrate predators *C. strenuus* and *A. priodonta* occupied the lower layer during midday. The co-occurrence of predators and prey in the water layer offering a refuge from UVR has been observed in transparent Patagonian lakes (Alonso *et al.*, 2004).

The underwater attenuation values of UVR (e.g. $K_{d320} = 1.22\text{--}1.42 \text{ m}^{-1}$) and low dissolved organic carbon concentration (DOC $< 1 \text{ mg L}^{-1}$; Tardio *et al.*, 2006) in Lake Tovel indicate that this lake was similarly transparent to UVR as other lakes located at even higher altitude (Tartarotti *et al.*, 2001). The damaging effects of UVR for zooplankton are well known (Williamson *et al.*, 2001; Leech *et al.*, 2005a, 2005b), and the avoidance of the upper layer in relation to UVR has been reported for several species of cladocerans and copepods (e.g. Leech and Williamson, 2000, 2001; Rhode *et al.*, 2001; Alonso *et al.*, 2004; Cooke and Williamson, 2005; Leech *et al.*, 2005a, 2005b). Williamson *et al.* (Williamson *et al.*, 2001) also noted that the rotifer predator *A. priodonta*, a species highly

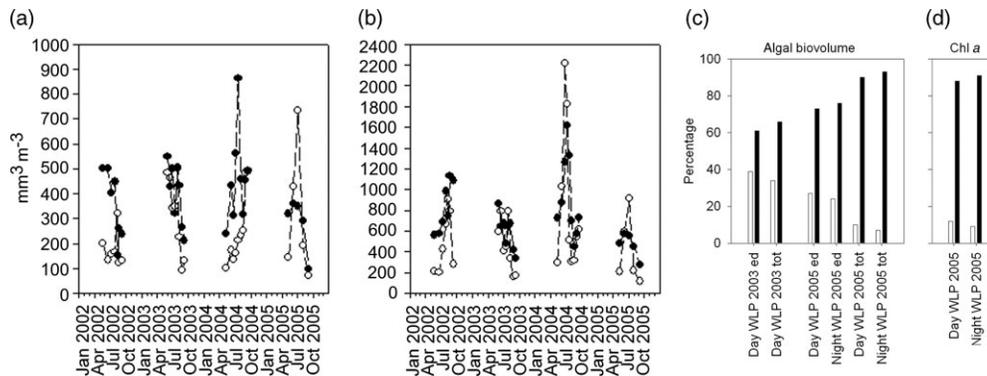


Fig. 5. (a) Biovolume of edible algae in summer for the 4-year study, midday sampling; (b) Total biovolume of algae in summer for the 4-year study, midday sampling. Filled circles indicate biovolume in the lower layer and open circle in the upper layer. In summer 2003, May sampling was missing. (c) Percentage of algal biovolume (edible, ed; total, tot) in WLP sampling. (d) Percentage of Chl *a* for WLP 2005 sampling. Black bars indicate the values in the lower layer, white bars in the upper layer.

vulnerable to UVR, is only present in the upper layer of a lake having high DOC values and low UVR impact. Thus, midday avoidance of the upper layer caused by UVR is a plausible hypothesis for zooplankton in Lake Tovel. During the day, herbivorous zooplankters probably faced a trade-off between damage by UVR in the upper layer and mortality by invertebrate predators in the lower layer. We suggest that this trade-off was in favour of possible predation, which depended on several factors such as predator abundance, escape reactions, and body size, instead of exposure to UVR.

Behavioural avoidance implies the capacity to detect UVR, which has been shown for *Daphnia magna* (Storz and Paul, 1998), but not for rotifers. The genus *Polyarthra* is reported to avoid the surface (Leech *et al.*, 2005a), but in Lake Tovel this was generally not the case; likewise, *S. grandis* was also found in the upper layer. Since invertebrate predators and herbivorous competitors were mainly restricted to the lower layer, these species could take advantage of reduced predation and competition at the surface, but were, on the other hand, exposed to UVR.

MAAs content and significance for UV protection

In transparent lakes, zooplankton have different strategies to minimize UVR damage including behavioural avoidance, efficient DNA repair, morphological adaptations, and possession of photoprotective compounds such as MAAs, melanin, and carotenoids (Hairston, 1976; Sommaruga, 2001; Tartarotti *et al.*, 2004; Cooke *et al.*, 2006; Tartarotti and Sommaruga, 2006; Hansson *et al.*, 2007). Little is known about MAAs in rotifers; thus, one important finding of our study was that *P. dolichoptera*, *S. pectinata*, *S. grandis*, and *K. cochlearis* had

these photoprotective compounds although in very different concentrations. The MAA concentrations for *P. dolichoptera* and *K. cochlearis* were in the same range as previously found for these species in a transparent alpine lake (Tartarotti *et al.*, 2001). However, this is the first report for *S. pectinata* and *S. grandis*. *Polyarthra dolichoptera* accumulated higher concentrations of MAAs (0.33% in WLP 2005 and up to 1% of dry weight during summer) compared with *Synchaeta* spp. and *K. cochlearis*. Although accumulation of MAAs is probably not the only strategy for UVR tolerance, it is certainly an important one that could have allowed this species to thrive in the upper layer.

Keratella cochlearis had lower MAA concentrations than *P. dolichoptera*, and we hypothesize that this species remained in the lower layer at midday and shifted to the upper layer at midnight in agreement with the UVR avoidance hypothesis. However, Leech and Williamson (Leech and Williamson, 2000) reported that *K. cochlearis* is highly tolerant to UVR in laboratory experiments. Leech *et al.* (Leech *et al.*, 2005a) also reported that the genus *Keratella* is found in the epilimnion of both low and high UV lakes. One possible explanation for the contrasting findings is that tolerance to natural UVR in field studies could be different from that observed in laboratory experiments (Persaud and Williamson, 2005) and may be species-specific, too.

In the two *Synchaeta* species, the MAA content was similar and in comparison to *K. cochlearis* higher. Interestingly, *S. pectinata* avoided the upper layer, whereas *S. grandis* did not. This indicates that not only photoprotection, but additional strategies or feeding requirements, possibly species-specific, are important for WLP. Species such as *S. pectinata* and *K. cochlearis* shared the same resources at night as *Polyarthra* but were not able to accumulate MAAs in significant amounts. Interestingly,

Taira *et al.* (Taira *et al.*, 2004) found that MAAs concentration in a marine alga was up to four times less at night than at midday. Laurion *et al.* (Laurion *et al.*, 2002) argued that MAAs in freshwater phytoplankton are only synthesized under conditions of high solar UVR. Thus, it is possible that shifting rotifer species had only limited access to MAA producing phytoplankton in comparison to *P. dolichoptera*. Although experimental evidence is needed, an additional, possible explanation could be the different feeding modalities found among these species. For example, *Polyarthra* spp. is a specialist feeder, whereas *K. cochlearis* is a generalist one (Herzig, 1987). *Synchaeta* species such as *S. kitina* and *S. pectinata* are also specialist feeders (Merriman and Kirk, 2000), but may feed on different algae than *P. dolichoptera*.

Food and temperature effect

Improved feeding conditions in the upper layer seem to be the driving force for an ascent of zooplankton (Pearre, 2003). However in Lake Tovel, species such as *F. terminalis*, *S. kitina*, and *A. priodonta* were persistently located in the lower layer, whereas only *K. cochlearis* and *S. pectinata*, located in the lower layer during midday, showed a preference for the upper layer during midnight.

Filinia terminalis is reported to be cold stenotherm (Nogrady and Segers, 2002) and to feed on bacteria associated with detritus (Ruttner-Kolisko, 1980). Temperature and food supply may be more suitable for this species in the cold lower layer where most decaying food accumulates. *Synchaeta kitina* is reported to be easily food-limited (May, 1983), to be a specialized feeder (Merriman and Kirk, 2000), and to prefer Chrysophyceae and Cryptophyceae (Puorriot, 1977; Herzig, 1987). Over 80% of Chrysophyceae and 70% of Cryptophyceae were found in the lower layer both during midday and midnight in the WLP study 2005, and also in summer, these algae were more abundant in the lower layer. The predation success of *A. priodonta*, a non-visual predator, depends on high food concentrations (Sarma, 1993). Besides, this species shows an enormous plasticity in its diet, feeding on zooplankton and phytoplankton of varying size (Kappes *et al.*, 2000). Thus, *A. priodonta* may have found better feeding conditions in the lower layer because it contained higher abundance of both algae and rotifers. In general, rotifers also found a better food supply in the lower layer because of the higher biovolume of total and edible algae (that usually characterized this layer). Nevertheless, we cannot be sure what specific species actually fed on because we did not analyse their diet. Based on the above considerations, however, we hypothesize that for *F. terminalis*, *S. kitina*, and *A. priodonta* better

food and environmental conditions in the lower layer determined their persistent location there.

Keratella cochlearis and *S. pectinata* instead showed a population displacement from midday to midnight to the upper layer, where they probably faced a reduced food supply. Reduced food in the upper layer could be an effect of UVR penetration. UVR is known to inhibit algal growth, photosynthetic rates, and nutrient uptake (Hessen *et al.*, 1997; Doyle *et al.*, 2005). Only species that are resistant to starvation by feeding at low resource levels or by accumulating reserve substances can show a population shift to the upper layer. Particularly, *K. cochlearis* is known to be typical for oligotrophic conditions (Ruttner-Kolisko, 1974) and to be adapted to lower food concentrations (Walz, 1995). The importance of satiation for a population shift of rotifers would merit more experimental work to explore this causal relationship. *Polyarthra dolichoptera* also seemed to be influenced by food supply as it had on some exceptional occasions its maximum abundance in the lower layer, even if many individuals (>1 to 35 individuals L^{-1}) were still present in the upper layer. Likewise, the unusual presence of *S. kitina* and *Cyclotella* sp. in the upper layer during a rainy day in summer 2005, suggested that a potential food source can cause a shift to the upper layer under conditions of low solar radiation. This finding indicated that under reduced UVR pressure, species are able to adjust their WLP to better exploit food resources.

Apart from food, however, the adaptive value of an upward displacement can also be higher temperatures which offer a demographic advantage by accelerating development of fish, crustaceans, and rotifers (Neverman and Wurtsbaugh, 1994; Williamson *et al.*, 1996; Armengol and Miracle, 2000; Van Gool and Ringelberg, 2003; Winder *et al.*, 2003; Park *et al.*, 2004). Furthermore, Lampert *et al.* (Lampert *et al.*, 2003) showed that the greater the temperature difference between an upper layer, warm and poor in food, and a lower one, cold and rich in food, the more pronounced the population shift of *D. hyalina* × *galeata*. In Lake Tovel, the temperature difference between the upper ($\geq 15^{\circ}\text{C}$ above a depth of 2 m) and the lower layer ($< 10^{\circ}\text{C}$ below a depth of 10 m) could explain the species shift from the lower to the upper layer. Egg development time in rotifers decreases from 5 days to 1 day by increasing the temperature from 10°C to 15°C (Bottrell *et al.*, 1976). Therefore, the hypothesis of a demographic advantage seems reasonable, even if it needs to be tested for *S. pectinata* and *K. cochlearis*. *Polyarthra dolichoptera*, through its tolerance to UVR, could particularly have had a demographic advantage by constantly exploiting the higher water temperatures in the upper layer.

Field evidence indicated that rotifer WLP in this UVR transparent lake was subject to different trade-offs regarding the effects of UVR, temperature, and food availability. Laboratory experiments, however, are needed to clarify the interaction of these factors. Although we cannot directly conclude that they alone were responsible, we have ample indirect evidence that UVR, temperature, and food availability played a major role in rotifer WLP. Specifically, we suggest that species avoided the upper layer as a response to underwater UVR and exceptions were tied to the possession of MAAs. High concentrations of these photoprotective compounds probably permitted *P. dolichoptera* to occupy the upper layer. Two *Synchaeta* species, however, had different WLPs even with similar MAA concentrations, indicating that additional strategies were involved. Furthermore, at night only some species shifted to the upper layer where the demographic advantage of high temperatures over better feeding conditions in the lower layer may have prevailed. We suggest the costs of migration may not always be offset by a higher development rate because some species always stayed in the lower food-rich layer probably as response to food limitation.

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