SHORT COMMUNICATION

Factors involved in the distribution pattern of ciliates in the water column of a transparent alpine lake

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The recurrent depth preference of three ciliate species (two prostomatids and one haptorid) in a transparent alpine lake indicates the existence of niche partitioning among them involving potential factors such as avoidance of high ultraviolet radiation levels and zooplankton predation, as well as competition for food resources.

Ciliate assemblages in lowland lakes are characteristically composed of many species that change throughout the year in relation to food-availability, predation and abiotic environmental parameters (e.g. Müller *et al.*, 1991; Sonntag *et al.*, 2002, 2006). In contrast, high-altitude lakes are colonized by only few ciliate species (Wille *et al.*, 1999). As in alpine lakes (i.e. located above the treeline), the concentration of chromophoric dissolved organic material is low, consequently transparency to photosynthetically active (PAR, 400–700 nm) and ultraviolet radiation (UVR, 280–400 nm) is high (Sommaruga and Psenner, 1997; Laurion *et al.*, 2000; Sommaruga and Augustin, 2006). Up to now, the few studies available on the effect of UVR on ciliates indicate that sensitivity is species-specific (Giese *et al.*, 1965; Wickham and Carstens, 1998; Mostajir *et al.*, 1999; Sommaruga *et al.*, 1999; Sanders *et al.*, 2005). How ciliates cope with UVR in transparent alpine lakes is unknown; however, possible strategies include distribution in deep water layers during the day where most of the UV-B is attenuated, possession of efficient DNA repair mechanisms and accumulation of photoprotective compounds. Among photoprotective compounds mycosporine-like amino acids (MAAs) have been reported for several *Chlorella*-bearing ciliates (Tartarotti *et al.*, 2004; Sonntag *et al.*, 2007) including one species from an alpine lake (Summerer *et al.*, 2008).

A previous study in the alpine Gossenköllesee reported that the ciliate community was dominated by

three species, namely the dominant *Balanion planctonicum* found in deep water layers, the *Chlorella*-bearing *Askenasia chlorelligera* distributed in the whole water column and one *Urotricha* species present in the upper meters (Wille *et al.*, 1999). Based on the observation that the distribution pattern of *B. planctonicum* in this alpine lake is different from that found in lowland less-transparent lakes, we hypothesized that not only food had a considerable influence on the depth preference of this algivorous species, but also UV sensitivity.

To test this hypothesis, we collected planktonic ciliates on 30 August 2005 from the oligotrophic Gossenköllesee (maximum depth = 9.9 m) situated at 2417 m above the sea level in the Austrian Central Alps (47°13′N, 11°00′E) by vertical net tows (10-μm mesh size) and placed them in a 10-L carboy after removal of zooplankton (100-μm mesh size net). After mixing the carboy several times, the water was distributed into 1-L-quartz tubes and exposed *in situ* at 0.30 m depth under sunny conditions for 7 h centred at solar noon. Three experimental conditions (each with three replicates) were tested: full sunlight (PAR + UVR, hereafter FULL), PAR only by excluding most of the UVR with a vinyl chloride foil (sharp cut-off: 0% transmittance at 390 nm, 50% at 405 nm) and darkness (DARK = control) by excluding radiation with aluminium paper and a black plastic foil. At T_0 (from the carboy) and after 7 h of exposure, 250 mL samples were fixed with Bouin's solution (5% final concentration) and quantitatively protargol stained (Skibbe, 1994; Pfister *et al.*, 1999). The ciliates were identified following the taxonomic key of Foissner *et al.* (Foissner *et al.*, 1999) and quantified using an Olympus BX50 microscope with bright field. As the normality test for this data set failed, statistical differences in the species-specific mortality were analysed by using a Kruskal–Wallis one-way ANOVA on ranks with Dunnett's *post hoc* comparisons against the DARK—control (SigmaStat 3.5).

To further understand the depth preference of the ciliates, we assessed their vertical distribution during day and night, as well as their possible co-occurrence with predators and phytoplankton. Triplicate water samples were collected with a 5-L-Schindler-Patalas sampler (Uwitec) at 0, 2, 4, 6, 8 and 9 m depth on 10 August 2005 at 0100 h (T_1), 0700 h (T_2) and 1300 h (T_3). Subsamples of 250 mL each were fixed, prepared and analysed as described. To statistically determine whether the species remained in certain depths through day and night, we first tested the precision of the data by re-sampling (10 000 bootstraps per replicate; Excel Add-In: Bootstrap), then calculated the weighted mean depth abundances and finally, applied a Friedman repeated measures ANOVA on ranks (SigmaStat 3.5). Additionally, the water temperature and chlorophyll *a* (Chl *a*) were measured at each sampling depth (Fig. 1a). Spearman rank order correlations were performed between the vertical profiles of ciliate abundance and depth, temperature and Chl *a* (Table I). Further, the downwelling irradiance was measured under sunny conditions within 2 h of solar noon with a profiling radiometer (PUV-501B, Biospherical Instruments) at 305, 320, 340 and 380 nm and between 400 and 700 nm (PAR; Figs 1b and c). The diffuse attenuation coefficients (K_d) were calculated after Laurion *et al.* (Laurion *et al.*, 2000). The K_d and the respective 1% attenuation depth ($Z_{1\%}$) for PAR and UVR were: $K_{d\ PAR} = 0.17\ \mathrm{m}^{-1}$ ($Z_{1\%} = 27.7\ \mathrm{m}$), $K_{d\ 380nm} = 0.18\ \mathrm{m}^{-1}$ ($Z_{1\%} = 26.1\ \mathrm{m}$), $K_{d\ 340nm} = 0.26\ \mathrm{m}^{-1}$ ($Z_{1\%} = 17.4\ \mathrm{m}$), $K_{d\ 320nm} = 0.33\ \mathrm{m}^{-1}$ ($Z_{1\%} = 14.0\ \mathrm{m}$) and $K_{d\ 305nm} = 0.44\ \mathrm{m}^{-1}$ ($Z_{1\%} = 10.5\ \mathrm{m}$).

Irrespective of day or night time, the distribution pattern of the ciliates persisted (Fig. 2) suggesting the existence of factors constraining the colonization of
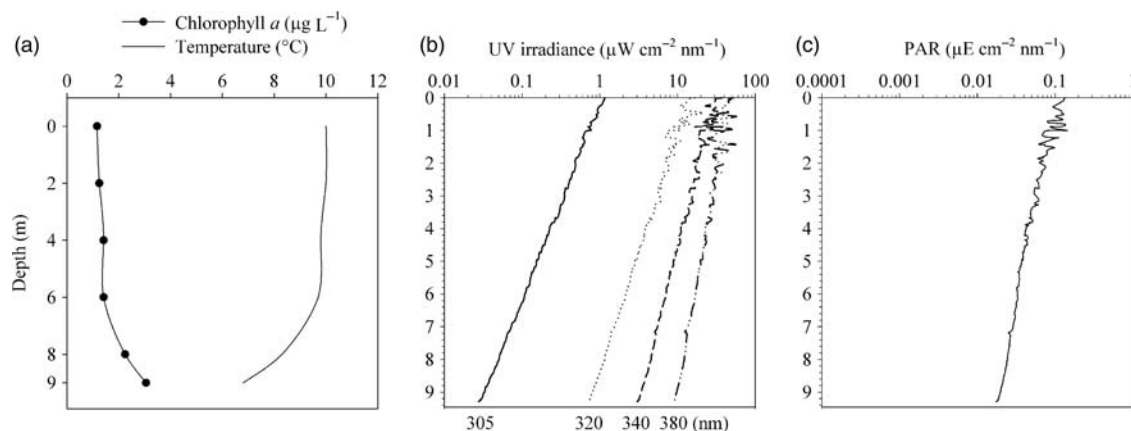

Fig. 1. Depth profiles of chlorophyll *a* (μg L^{-1}) and temperature (°C) (**a**) and of UVR at 305, 320, 340 and 380 nm (μW cm^{-2} nm^{-1}) (**b**), and PAR (μE cm^{-2} nm^{-1}) (**c**) in Gossenköllesee on 10 August 2005.

Table I: *Spearman rank correlations between total ciliate abundance (Tot), Askenasia chlorelligera (Ask), Balanion planctonicum (Bal), Urotricha cf. castalia (Uro), depth (D), temperature (T) and chlorophyll a (Chl a) in Gossenköllesee on 10 August 2005 at T_1 (0100 h), T_2 (0700 h) and T_3 (1300 h)*

T_1

	Ask	Bal	Uro	D	T	Chl a
Tot	0.143 (0.803)	**1.000** (0.003)	**−0.886** (0.033)	**0.886** (0.033)	−0.794 (0.058)	**0.870** (0.033)
Ask		0.143 (0.803)	0.086 (0.919)	−0.086 (0.919)	0.324 (0.497)	−0.116 (0.803)
Bal			**−0.886** (0.033)	**0.886** (0.033)	−0.794 (0.058)	**0.870** (0.033)
Uro				**−1.000** (0.003)	0.736 (0.103)	**−0.986** (0.003)
D					−0.736 (0.103)	**0.986** (0.003)
T						−0.687 (0.136)

T_2

	Ask	Bal	Uro	D	T	Chl a
Tot	−0.143 (0.803)	**0.943** (0.017)	−0.600 (0.242)	0.771 (0.103)	−0.516 (0.297)	n.d.
Ask		−0.086 (0.919)	0.429 (0.419)	−0.257 (0.658)	0.698 (0.136)	n.d.
Bal			−0.771 (0.103)	**0.886** (0.033)	−0.638 (0.175)	n.d.
Uro				**−0.943** (0.017)	**0.941** (0.017)	n.d.
D					−0.820 (0.058)	n.d.
T						n.d.

T_3

	Ask	Bal	Uro	D	T	Chl a
Tot	−0.429 (0.419)	**0.943** (0.017)	**−0.886** (0.033)	**0.886** (0.033)	**−0.928** (0.017)	**0.870** (0.033)
Ask		−0.486 (0.356)	0.543 (0.297)	−0.543 (0.297)	0.522 (0.297)	−0.522 (0.297)
Bal			**−0.943** (0.017)	**0.943** (0.017)	**−0.928** (0.017)	**0.928** (0.017)
Uro				**−1.000** (0.003)	**0.986** (0.003)	**−0.986** (0.003)
D					**−0.986** (0.003)	**0.986** (0.003)
T						**−0.971** (0.003)

Correlation coefficients (rs, upper value) and P (lower value) are given (n = 6). Bold values indicate significant correlations (P < 0.05). n.d., not determined.

specific water layers in this lake. As previously described in Wille *et al.* (Wille *et al.*, 1999), *A. chlorelligera*, *B. planctonicum* and one *Urotricha* were the dominant species. Wille *et al.* (Wille *et al.*, 1999) identified the *Urotricha* species as cf. *pelagica*; however, our re-analysis of their samples using protargol-staining of Lugol-formaldehyde-fixed samples indicated that it was the same *Urotricha* cf. *castalia* species as found in our study. Nevertheless, definite species identification was not possible in both cases as one important characteristic of *Urotricha castalia*, i.e. the somatic extrusomes, was not visible.

Among the three ciliate species, *B. planctonicum* was the only one that showed a moderate UV sensitivity in the full sunlight treatment ($P = 0.029$) which is consistent with its avoidance of surface waters (Figs 2a and 3). Though, comparing the abundance at T_0 (*A. chlorelligera*: 2.9 ± 0.3 mL^{-1}, *B. planctonicum*: 2.7 ± 0.2 mL^{-1}, *U.* cf. *castalia*: 0.3 ± 0.0 mL^{-1}) and after 7 h incubation in the dark control, values for *A. chlorelligera* and *U.* cf. *castalia* were unchanged, but in *B. planctonicum* there was a decrease of 19%. Food depletion during exposure does not seem to explain the mortality of *B. planctonicum* because many cryptomonads were found at the end of the experiment (recognizable in the QPS preparations). However, reduced cell numbers of *B. planctonicum* in the control suggest that there was probably an effect caused by the experimental manipulation or sampling.

The significant positive correlation of *B. planctonicum* with phytoplankton biomass (i.e. Chl *a*) suggests a strong dependence of this species on its main food source (Table I) as indicated by Wille *et al.* (Wille *et al.*, 1999). *Balanion planctonicum* is known as an efficient algal feeder not able to survive longer starvation periods and to be dependent on a minimum density of 1500 algal cells mL^{-1} preferably cryptomonads (Müller, 1991; Weisse *et al.*, 2001). In Gossenköllesee, cryptomonads are almost absent during day in the upper meters of the water column, whereas near the lake bottom up to 2000 cells mL^{-1} can be found (unpublished results).

Weisse *et al.* (Weisse *et al.*, 2001) observed in experiments that *B. planctonicum* was a superior competitor when cryptomonad numbers were $<3 \times 10^4$ mL^{-1}. The same authors argued that with respect to the use of food resources, *B. planctonicum* probably had an advantage over other small algivorous prostomatids such as *Urotricha farcta* and *Urotricha furcata* in oligo- to mesotrophic lowland lakes, when food was not abundant (Weisse *et al.*, 2001). The superior competitive ability of *B. planctonicum* for food resources could be an explanation for the distribution of prostomatids observed in Gossenköllesee. In this hypothesis, *B. planctonicum* outcompetes *U.* cf. *castalia* and displaces it to the upper
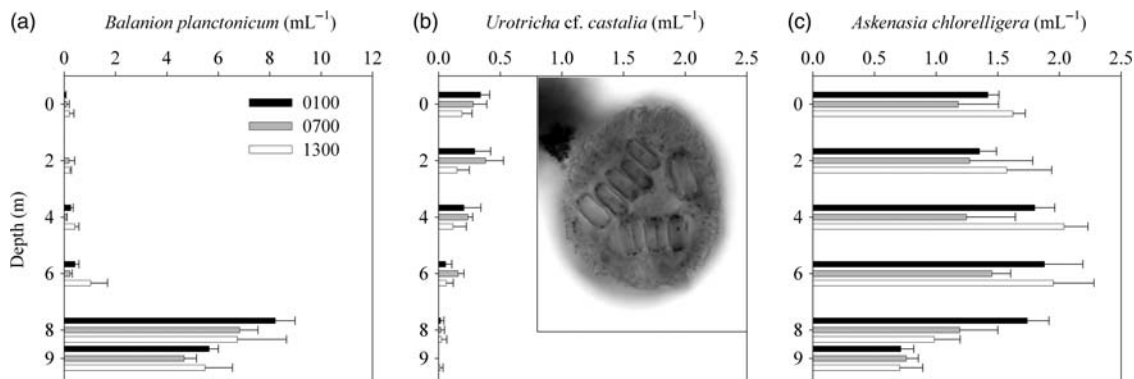
Fig. 2. Abundance (mean number of cells mL^{-1} ± SD) along a depth gradient of *Balanion planctonicum* (**a**), *Urotricha* cf. *castalia* with insert showing a micrograph of a protargol-stained specimen taken at a magnification of ×1000 where several ingested centric diatoms are visible (**b**), and *Askenasia chlorelligera* (**c**) in Gossenköllesee on 10 August 2005 at T$_1$ (0100), T$_2$ (0700) and T$_3$ (1300) local summer time. Note different bar scales.

water layers where for most time of the day less phytoplankton is available. This in turn results in a reduced population size of the latter species, despite living at higher water temperatures than *B. planctonicum* (Figs 1a, 2b and 4). Interestingly, in the QPS preparations, we regularly observed individuals of *U.* cf. *castalia* with ingested centric diatoms (see insert in Fig. 2b). Thus, the water layers this species colonizes not only have lower phytoplankton biomass but probably also have less suitable algal food items compared with the zone of the deep chlorophyll maximum. In fact, there is evidence that prostomatid ciliates cannot survive on a diatom diet (Müller and Schlegel, 1999). Moreover, when a mixture of diatoms and cryptomonads has been offered to prostomatid ciliates such as *B. planctonicum*, they clearly selected for the latter (Müller and Schlegel, 1999).

Urotricha cf. *castalia* was tolerant to short-term exposure to UVR (Fig. 3); however, in a mesocosm (1 m deep) experiment done in the same lake and lasting for 16 days, the net growth rate of urotrichs was slightly affected by UV-B radiation (Sommaruga *et al.*, 1999). This suggests that, though tolerant, it may not be able to cope with UV-B in the upper 2 m of the water column for prolonged periods.

In lowland lakes, many mixotrophic ciliate species, which either bear algal symbionts or sequester algal plastids, prevail during the summer months in surface waters where they can account for more than 50% of the total ciliate abundance (e.g. Pace, 1982; Müller *et al.*, 1991; Dolan, 1992; Carrias *et al.*, 1998; Sonntag *et al.*, 2006). Living in the epilimnion allows mixotrophic ciliates to optimally utilize nutrients and light to enable growth of host and symbionts (Wölfl and Geller, 2002; Modenutti *et al.*, 2005). This nutritional advantage is an adaptation to living in oligotrophic environments when or where food is not abundant or not suitable (Dolan
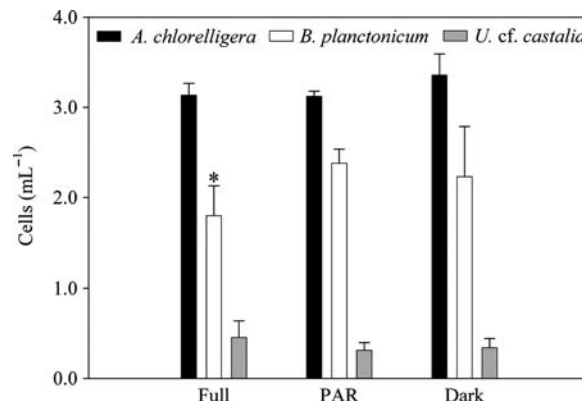

Fig. 3. Abundance (cells mL^{-1}) of *Askenasia chlorelligera*, *Balanion planctonicum* and *Urotricha* cf. *castalia* (mean ± SD) after 7 h of exposure at the lake surface. The ciliates were exposed to the full solar UVR (FULL), photosynthetically active radiation (PAR) or kept in the dark (DARK = control). *Indicates significant difference ($P = 0.029$).

and Pérez, 2000). However, colonization of the upper part of the water column also means being exposed to potentially damaging levels of incident UVR. Summerer *et al.* (Summerer *et al.*, 2008) recently reported the occurrence of MAAs in *A. chlorelligera* from Gossenköllesee that most likely allow this ciliate to exploit the upper layers, too (Figs 2c and 4). Interestingly, in a population of *A. chlorelligera* in a less UV transparent lake, no MAAs were detected (Summerer *et al.*, 2008). Another advantage of hosting algal symbionts is the screening of UVR by several *Chlorella* layers that may reduce damaging effects on UV-sensitive cell compartments such as DNA-containing material (Sommaruga and Sonntag, 2009; Summerer *et al.*, 2009).

Finally, another aspect that can influence the distribution of planktonic protists is predation by zooplankton (e.g. Wickham, 1995; Dobberfuhl *et al.*, 1997). In Gossenköllesee, the only copepod species present is the
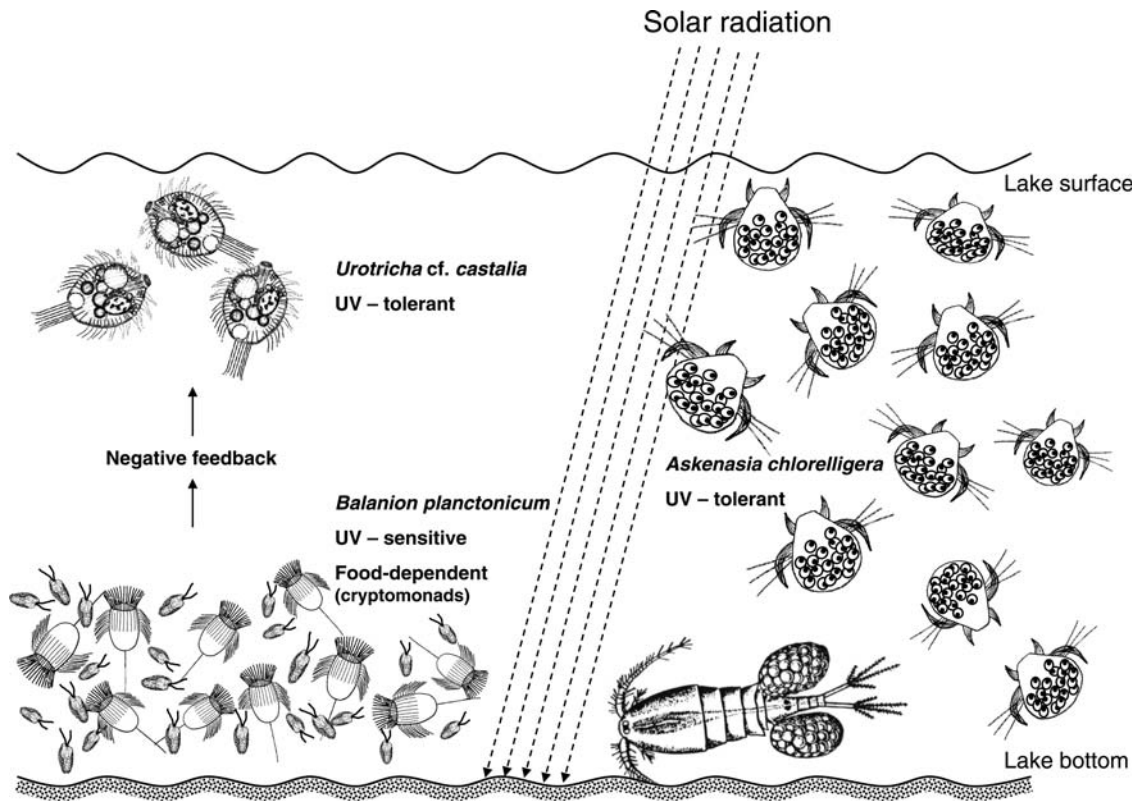
Fig. 4. Scheme of the distribution of *Askenasia chlorelligera*, *Balanion planctonicum* and *Urotricha* cf. *castalia* in the alpine lake Gossenköllesee during the ice-free summer period indicating the main factors involved. Drawings modified from Remane *et al.* (1986), Streble and Krauter (1988) and Foissner *et al.* (1999). For details see text.

cyclopoid *Cyclops abyssorum tatricus* that concentrates in deep water layers during daytime and migrates upwards at night (Tartarotti *et al.*, 1999). In the presence of cyclopoid copepods, ciliate abundance can be significantly reduced and oligotrich and haptorid species (including *Askenasia*) in the size-range of $20-40 \mu$m are known to be heavily grazed (Wiackowski *et al.*, 1994; Dobberfuhl *et al.*, 1997; Zöllner *et al.*, 2003). In contrast, smaller ciliates such as *Urotricha* and *Balanion* species seem to cope well with grazing pressure by copepods because of their small size and their characteristic rapid jumps (Wiackowski *et al.*, 1994; Dobberfuhl *et al.*, 1997; Zöllner *et al.*, 2003). *Askenasia chlorelligera* from Gossenköllesee also performs rapid jumps and responds to the pressure wave of an approaching object (personal observation). This behaviour appears to be in agreement with the lower concentration of *A. chlorelligera* at the greatest depths (Figs 2c and 4) and suggests avoidance of predation by *C. abyssorum tatricus* by jumping only when a predator approaches (Wickham, 1995).

Colonization by ciliates of extreme environments such as alpine lakes, where food is scarce and UVR levels are high, demands effective adaptation strategies.

The present results indicate the existence of niche partitioning among the dominant ciliate species in this oligotrophic lake caused by several factors including adaptation to high UVR levels, competition for food resources and avoidance of zooplankton predation (Fig. 4).

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