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► **To cite this version:**

Bettina Sonntag, Monika Summerer, Ruben Sommaruga. Factors involved in the distribution pattern of ciliates in the water column of a transparent alpine lake. *Journal of Plankton Research*, 2010, 10.1093/plankt/FBQ117 . hal-00626239

HAL Id: hal-00626239

<https://hal.science/hal-00626239>

Submitted on 24 Sep 2011

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Journal:	<i>Journal of Plankton Research</i>
Manuscript ID:	JPR-2010-078.R2
Manuscript Type:	Short Communication
Date Submitted by the Author:	07-Aug-2010
Complete List of Authors:	Sonntag, Bettina; University of Innsbruck, Ecology Summerer, Monika; University of Innsbruck, Ecology Sommaruga, Ruben; University of Innsbruck, Institute of Ecology, lab. of Plankton Ecology and Aquatic Photobiology
Keywords:	Balanion planctonicum, UV radiation, Askenasia chlorelligera, Urotricha, Cyclops

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Manuscripts

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Abstract:

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 UVR levels and zooplankton predation, as well as competition for food resources.

Key Words: *Askenasia chlorelligera*, *Balanion planctonicum*, *Cyclops*, *Urotricha*, UV radiation

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 (CDOM) 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. Such photoprotective compounds like mycosporine-like amino acids (MAAs) have been reported for several *Chlorella*-bearing ciliates (Tartarotti *et al.*, 2004; Sommaruga *et al.*, 2006; 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 August 30, 2005 from the oligotrophic Gossenköllesee (maximum depth = 9.9 m) situated at 2,417 m above sea level in the Austrian Central Alps (47°13'N, 11°00'E) by vertical net tows (10- μ m mesh size) and placed them

1
2 in a 10-L carboy after removal of zooplankton (100- μ m mesh size net). After mixing the carboy
3 several times, the water was distributed into 1-L-quartz-tubes and exposed in situ at 0.30 m depth
4 under sunny conditions for 7 h centred at solar noon. Three experimental conditions (each with
5 three replicates) were tested: full sunlight (PAR + UVR, hereafter FULL), PAR only by excluding
6 most of the UVR with a vinyl chloride foil (sharp cut-off: 0% transmittance at 390 nm, 50% at 405
7 nm), and darkness (DARK = control) by excluding radiation with aluminium paper and a black
8 plastic foil. At T_0 (from the carboy) and after 7 h of exposure, 250 mL samples were fixed with
9 Bouin's solution (5% f. c.) and quantitatively protargol stained (Skibbe, 1994; Pfister *et al.*, 1999).
10 The ciliates were identified following the taxonomic key of Foissner *et al.* (1999) and quantified
11 using an Olympus BX50 microscope with bright field. As the normality test for this data set failed,
12 statistical differences in the species-specific mortality were analyzed by using a Kruskal-Wallis
13 one-way ANOVA on ranks with Dunnett's post-hoc comparisons against the DARK - control
14 (SigmaStat 3.5).
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17
18 To further understand the depth preference of the ciliates, we assessed their vertical
19 distribution during day and night, as well as their possible co-occurrence with predators and
20 phytoplankton. Triplicate water samples were collected with a 5-L-Schindler-Patalas sampler
21 (Uwitec) at 0, 2, 4, 6, 8, and 9 m depth on August 10, 2005 at 0100 h (T_1), 0700 h (T_2), and 1300 h
22 (T_3). Subsamples of 250 mL each were fixed, prepared and analyzed as described. To statistically
23 determine whether the species remained in certain depths through day and night, we first tested the
24 precision of the data by re-sampling (10,000 bootstraps per replicate; Excel Add-In: Bootstrap),
25 then calculated the weighted mean depth abundances and finally, applied a Friedman repeated
26 measures ANOVA on ranks (SigmaStat 3.5). Additionally, the water temperature and chlorophyll-*a*
27 (Chl-*a*) were measured at each sampling depth (Fig. 1a). Spearman rank order correlations were
28 performed between the vertical profiles of ciliate abundance and depth, temperature and Chl-*a*
29 (Table 1). Further, the downwelling irradiance was measured under sunny conditions within 2 h of
30 solar noon with a profiling radiometer (PUV-501B, Biospherical Instruments) at 305, 320, 340, 380
31 nm and between 400 and 700 nm (PAR; Fig. 1b and 1c). The diffuse attenuation coefficients (K_d)
32 were calculated after Laurion *et al.* (2000). The K_d and the respective 1% attenuation depth ($Z_{1\%}$)
33 for PAR and UVR were: $K_{d \text{ PAR}} = 0.17 \text{ m}^{-1}$ ($Z_{1\%} = 27.7 \text{ m}$), $K_{d \text{ 380 nm}} = 0.18 \text{ m}^{-1}$ ($Z_{1\%} = 26.1 \text{ m}$), $K_{d \text{ 340 nm}} = 0.26 \text{ m}^{-1}$ ($Z_{1\%} = 17.4 \text{ m}$), $K_{d \text{ 320 nm}} = 0.33 \text{ m}^{-1}$ ($Z_{1\%} = 14.0 \text{ m}$), and $K_{d \text{ 305 nm}} = 0.44 \text{ m}^{-1}$ ($Z_{1\%} =$
34 10.5 m).
35
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38 Irrespective of day or night time the distribution pattern of the ciliates persisted (Fig. 2)
39 suggesting the existence of factors constraining the colonization of specific water layers in this lake.
40 As previously described in Wille *et al.* (1999), *A. chlorelligera*, *B. planctonicum*, and one *Urotricha*
41 were the dominant species. Wille *et al.* (1999) identified the *Urotricha* species as cf. *pelagica*,
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2 however, our re-analysis of their samples using protargol-staining of Lugol-formaldehyde-fixed
3 samples indicated that it was the same *Urotricha* cf. *castalia* species as found in our study.
4
5 Nevertheless, definite species identification was not possible in both cases as one important
6
7 characteristic of *Urotricha castalia*, i.e., the somatic extrusomes, was not visible.
8

9
10 Among the three ciliate species, *B. planctonicum* was the only one that showed a moderate
11 UV sensitivity in the full sunlight treatment ($p = 0.029$) which is consistent with its avoidance of
12 surface waters (Fig. 2a and 3). Though, comparing the abundance at T_0 (*A. chlorelligera*: 2.9 ± 0.3
13 mL^{-1} , *B. planctonicum*: $2.7 \pm 0.2 \text{ mL}^{-1}$, *U. cf. castalia*: $0.3 \pm 0.0 \text{ mL}^{-1}$) and after 7 h incubation in
14 the dark control, values for *A. chlorelligera* and *U. cf. castalia* were unchanged, but in *B.*
15
16 *planctonicum* there was a decrease of 19%. Food depletion during exposure does not seem to
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18 explain the mortality of *B. planctonicum* because many cryptomonads were found at the end of the
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20 experiment (recognizable in the QPS-preparations). However, reduced cell numbers of *B.*
21
22 *planctonicum* in the control suggest that there was probably an effect caused by the experimental
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24 manipulation or sampling.
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28 The significant positive correlation of *B. planctonicum* with phytoplankton biomass (i.e.,
29 Chl-*a*) suggests a strong dependence of this species on its main food source (Table 1) as indicated
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31 by Wille *et al.* (1999). *Balanion planctonicum* is known as an efficient algal feeder not able to
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33 survive longer starvation periods and to be dependent on a minimum density of 1500 algal cells mL^{-1}
34
35 preferably cryptomonads (Müller, 1991; Weisse *et al.*, 2001). In Gossenköllesee, cryptomonads
36
37 are almost absent during day in the upper meters of the water column, whereas near the lake bottom
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39 up to 2000 cells mL^{-1} can be found (unpublished data).
40

41
42 Weisse *et al.* (2001) observed in experiments that *B. planctonicum* was a superior
43
44 competitor when cryptomonad numbers were $< 3 \times 10^4 \text{ mL}^{-1}$. The same authors argued that with
45
46 respect to the use of food resources, *B. planctonicum* probably had an advantage over other small
47
48 algivorous prostomatids such as *Urotricha farcta* and *Urotricha furcata* in oligo- to mesotrophic
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50 lowland lakes, when food was not abundant (Weisse *et al.*, 2001). The superior competitive ability
51
52 of *B. planctonicum* for food resources could be an explanation for the distribution of prostomatids
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54 observed in Gossenköllesee. In this hypothesis, *B. planctonicum* outcompetes *U. cf. castalia* and
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56 displaces it to the upper water layers where for most time of the day less phytoplankton is available.
57
58 This in turn results in a reduced population size of the latter species, despite living at higher water
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60 temperatures than *B. planctonicum* (Fig. 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 less suitable algal food items compared to the zone of the deep chlorophyll maximum.
In fact, there is evidence that prostomatid ciliates cannot survive on a diatom diet (Müller and

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2 Schlegel, 1999). Moreover, when a mixture of diatoms and cryptomonads has been offered to
3
4 prostomatid ciliates such as *B. planctonicum*, they clearly selected for the latter (Müller and
5
6 Schlegel, 1999).

7
8 *Urotricha* cf. *castalia* was tolerant to short-term exposure to UVR (Fig. 3), however, in a
9
10 mesocosm (1 m deep) experiment done in the same lake and lasting for 16 days, the net growth rate
11
12 of urotrichs was slightly affected by UV-B radiation (Sommaruga *et al.*, 1999). This suggests that,
13
14 though tolerant, it may not be able to cope with UV-B in the upper 2 m of the water column for
15
16 prolonged periods.

17
18 In lowland lakes, many mixotrophic ciliate species, that either bear algal symbionts or
19
20 sequester algal plastids, prevail during the summer months in surface waters where they can
21
22 account for more than 50% of the total ciliate abundance (e.g., Pace, 1982; Müller *et al.*, 1991;
23
24 Dolan, 1992; Carrias *et al.*, 1998; Sonntag *et al.*, 2006). Living in the epilimnion allows
25
26 mixotrophic ciliates to optimally utilize nutrients and light to enable growth of host and symbionts
27
28 (Wöfl and Geller, 2002; Modenutti *et al.*, 2005). This nutritional advantage is an adaptation to
29
30 living in oligotrophic environments when or where food is not abundant or not suitable (Dolan and
31
32 Pérez, 2000). However, colonization of the upper part of the water column also means being
33
34 exposed to potentially damaging levels of incident UVR. Summerer *et al.* (2008) recently reported
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36 the occurrence of MAAs in *A. chlorelligera* in Gossenköllesee that most likely allow this ciliate to
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38 exploit the upper layers, too (Fig. 2c and 4). Interestingly, in a population of *A. chlorelligera* in a
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40 less UV transparent lake, no MAAs were detected (Summerer *et al.*, 2008). Another advantage of
41
42 hosting algal symbionts is the screening of UVR by several *Chlorella* layers that may reduce
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44 damaging effects on UV-sensitive cell compartments like DNA-containing material (Sommaruga
45
46 and Sonntag, 2009; Summerer *et al.*, 2009).

47
48 Finally, another aspect that can influence the distribution of planktonic protists is predation
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50 by zooplankton (e.g., Wickham, 1995; Dobberfuhl *et al.*, 1997). In Gossenköllesee, the only
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52 copepod species present is the cyclopoid *Cyclops abyssorum taticus* that concentrates in deep
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54 water layers during daytime and migrates upwards at night (Tartarotti *et al.*, 1999). In the presence
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56 of cyclopoid copepods, ciliate abundance can be significantly reduced and oligotrich and haptoid
57
58 species (including *Askenasia*) in the size-range of 20-40 µm are known to be heavily grazed
59
60 (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.*

1
2 *chlorelligera* at the greatest depths (Fig. 2c and 4) and suggests avoidance of predation by *C.*
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4 *abyssorum taticus* by jumping only when a predator approaches (Wickham, 1995).

5
6 Colonization by ciliates of extreme environments such as alpine lakes, where food is scarce
7 and UVR levels are high, demands effective adaptation strategies. The present results indicate the
8
9 existence of niche partitioning among the dominant ciliate species in this oligotrophic lake caused
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11 by several factors including adaptation to high UVR levels, competition for food resources, and
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13 avoidance of zooplankton predation (Fig. 4).

14 15 16 ACKNOWLEDGEMENTS

17
18 We thank L. Alfreider, P. Hörtnagl, H. Peter, and M. Tilg for help during field and laboratory work
19
20 and A. Kloss-Brandstätter for statistical advice. Two anonymous reviewers are acknowledged for
21
22 critical comments on an earlier version of the manuscript. This study was supported by the Austrian
23
24 Science Fund (FWF), grants P16559-B06 to RS and P21013-B03 to BS.

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TABLE AND FIGURE LEGENDS

Table 1: 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 August 10, 2005 at T₁ (0100 h), T₂ (0700 h) and T₃ (1300 h). 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.

Fig. 1: Depth profiles of chlorophyll *a* ($\mu\text{g L}^{-1}$) and temperature ($^{\circ}\text{C}$) (a) and of UVR at 305, 320, 340 and 380 nm ($\mu\text{W cm}^{-2} \text{nm}^{-1}$) (b), and PAR ($\mu\text{mol cm}^{-2} \text{nm}^{-1}$) (c) in Gossenköllesee on August 10, 2005.

Fig. 2: Abundance (mean number of cells $\text{mL}^{-1} \pm \text{SD}$) 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 X where several ingested centric diatoms are visible, (b) and *Askenasia chlorelligera* (c) in Gossenköllesee on August 10, 2005 at T₁ (0100), T₂ (0700) and T₃ (1300) local summer time. Note different bar scales.

Fig. 3: Abundance (cells mL^{-1}) of *Askenasia chlorelligera*, *Balanion planctonicum*, and *Urotricha cf. castalia* (mean \pm 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).

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.

TABLES

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3 Table 1: Spearman rank correlations between total ciliate abundance (Tot), *Askenasia chlorelligera* (*Ask*), *Balanion planctonicum* (*Bal*),
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5 2 *Urotricha cf. castalia* (*Uro*), depth (D), temperature (T) and chlorophyll *a* (Chl-*a*) in Gossenköllesee on August 10, 2005 at T₁ (0100 h), T₂
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7 3 (0700 h) and T₃ (1300 h). Correlation coefficients (rs, upper value) and p (lower value) are given (n = 6). Bold values indicate significant
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9 4 correlations (p < 0.05). n.d. . . not determined.

	T ₁						T ₂						T ₃					
	<i>Ask</i>	<i>Bal</i>	<i>Uro</i>	D	T	Chl <i>a</i>	<i>Ask</i>	<i>Bal</i>	<i>Uro</i>	D	T	Chl <i>a</i>	<i>Ask</i>	<i>Bal</i>	<i>Uro</i>	D	T	Chl <i>a</i>
Tot	0.143	1.000	-0.886	0.886	-0.794	0.870	-0.143	0.943	-0.600	0.771	-0.516		-0.429	0.943	-0.886	0.886	-0.928	0.870
	0.803	0.003	0.033	0.033	0.058	0.033	0.803	0.017	0.242	0.103	0.297	n.d.	0.419	0.017	0.033	0.033	0.017	0.033
Ask		0.143	0.086	-0.086	0.324	-0.116		-0.086	0.429	-0.257	0.698		-0.486	0.543	-0.543	0.522	-0.522	
		0.803	0.919	0.919	0.497	0.803		0.919	0.419	0.658	0.136	n.d.	0.356	0.297	0.297	0.297	0.297	0.297
Bal			-0.886	0.886	-0.794	0.870			-0.771	0.886	-0.638			-0.943	0.943	-0.928	0.928	
			0.033	0.033	0.058	0.033			0.103	0.033	0.175	n.d.		0.017	0.017	0.017	0.017	0.017
Uro				-1.000	0.736	-0.986				-0.943	0.941					-1.000	0.986	-0.986
				0.003	0.103	0.003				0.017	0.017	n.d.				0.003	0.003	0.003
D					-0.736	0.986					-0.820						-0.986	0.986
					0.103	0.003					0.058	n.d.					0.003	0.003
T						-0.687												-0.971
						0.136						n.d.						0.003

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1 FIGURES

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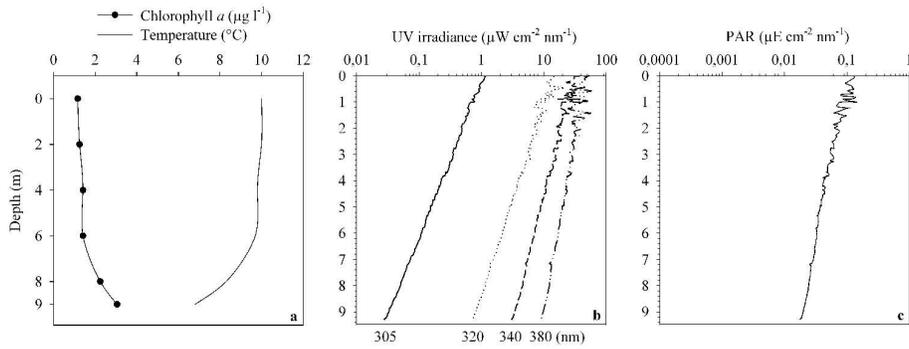


Fig. 1 Sonntag et al.

279x215mm (600 x 600 DPI)

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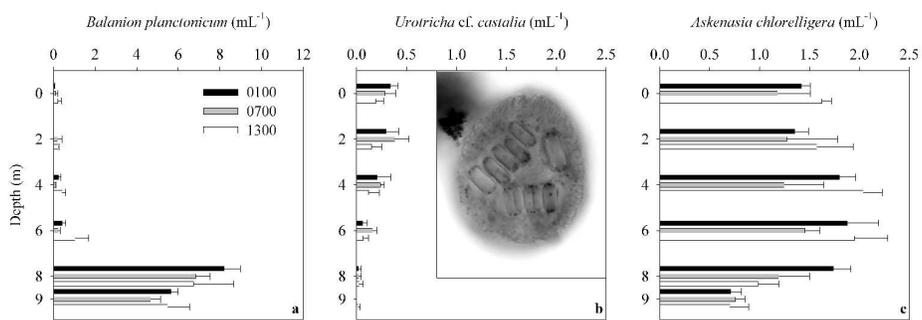


Fig. 2 Sonntag et al.

279x215mm (600 x 600 DPI)

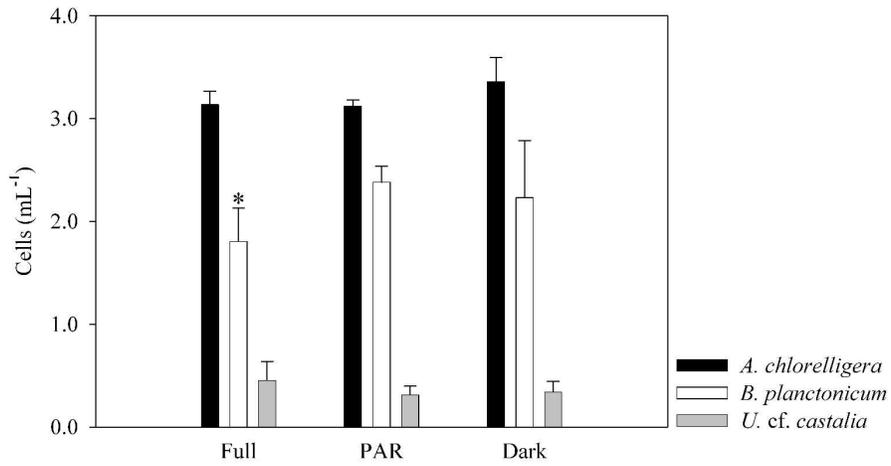
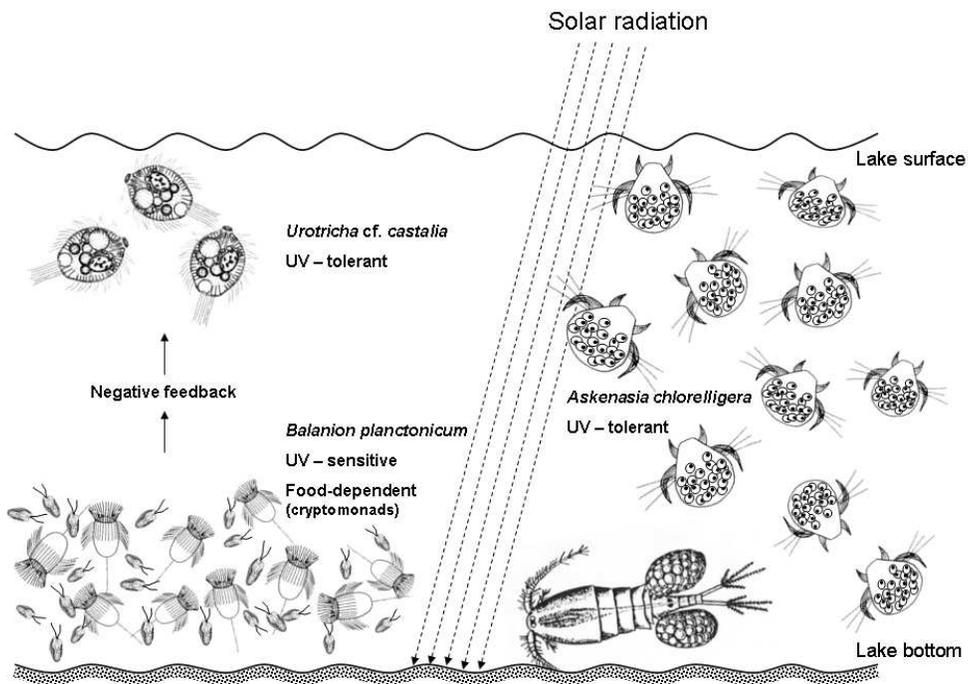


Fig. 3 Sonntag et al.

200x260mm (600 x 600 DPI)



254x190mm (96 x 96 DPI)

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