Effect of UV Radiation on the Bacterivory of a Heterotrophic Nanoflagellate

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The effects of UV-B radiation on the heterotrophic nanoflagellate *Bodo saltans* (Kinetoplastida) were examined under controlled conditions with artificial UV sources and also under natural solar radiation in an oligotrophic lake. In both types of experiments, the characteristic elongated cell morphology of this flagellate changed into a spherical one. This effect was due to UV-B but also to UV-A radiation, and after 4 h of exposure at 0.5 m of depth, 99% (UV-B plus UV-A plus photosynthetically active radiation) and 69% of the cells (UV-A plus photosynthetically active radiation) were spherical. At 6 m of depth where only 10% of the UV-B (305 nm) at the surface was measured, no significant effect was observed. The spherical cells were nonmotile, but before the morphological change took place, the swimming speed was ca. 3.5 times lower in the plus-UV-B treatment. The negative relation between the abundance of spherical cells and the average ingestion of fluorescently labeled bacteria per cell indicates that these cells are not able to feed upon bacteria. In bacterivory experiments lasting for 6 h, the total number of grazed bacteria was up to 70% lower in the plus-UV-B treatment than in the control without UV-B. This resulted in a positive feedback between UV-B and bacterial growth. The high sensitivity of *B. saltans* to solar UV-B and UV-A radiation strongly reduces its ability to live near the surface at times of high UV radiation.

Since the recognition of the microbial loop, it has become evident that heterotrophic nanoflagellates (2 to 20 μm in diameter) can function as consumers of picoplankton biomass in different types of aquatic systems (1, 5, 27, 28). Because heterotrophic nanoflagellates (HNF) have a rapid turnover time and high bacterivory rates, they process a significant part of the energy and material in the pelagic region (3). Moreover, HNF are ubiquitously distributed in aquatic systems, although the species composition and their autecology are poorly known (16, 17). Consequently, the knowledge on the factors controlling abundance and distribution of different HNF species is very restricted. Predation and food limitation have been identified, however, as the main factors controlling the abundance of HNF, when considered as a functional group (32).

Solar UV-B radiation (290 to 320 nm) is known to be harmful to different aquatic microorganisms and biological processes (12). For example, negative effects have been observed on the biomass production and extracellular enzymatic activity of marine bacteria (10). A significant amount of knowledge is available on the effects of UV-B radiation on phototrophic (chloroplast-bearing) flagellates (4, 6, 7, 9). Studies on the flagellate *Euglena gracilis* have shown that cell morphology, motility, and photosynthesis are negatively affected by UV-B (6). Although much less is known about the UV sensitivity of HNF species, phototrophic and heterotrophic flagellates are only functional categories, and for example within euglenoids, both types of organisms occur (14). Therefore, some effects may be similar or identical in obligate heterotrophic flagellates.

To our knowledge, no study has examined the effects of UV-B on the trophic interaction between HNF and bacteria. The bacterivory rate of HNF has been measured with different methodologies (see reference 13 and references therein), but

as a general rule, experiments have been made under dark conditions. Therefore, there is no information available on how UV-B radiation may affect bacterivory rates of protists.

This study presents results from experiments designed to investigate the effect of solar and artificial UV radiation on *Bodo saltans* (Kinetoplastida). This HNF species isolated from freshwater has been extensively used as a model organism in bacterivory experiments (11, 20, 31). Short- and long-term feeding experiments with fluorescently labeled bacteria were used to evaluate the effect of UV on bacterivory.

MATERIALS AND METHODS

Artificial UV-B sources. Artificial UV-B irradiation was provided by a set of four tubes of UV-A-340 (Q-Panel Co., Cleveland, Ohio). These lamps have a maximum emission at 340 nm and produce no radiation below 280 nm. The integration of irradiance values between 280 and 320 nm was 1.4 W m^{-2} ($84 \text{ J m}^{-2} \text{ min}^{-1}$). The spectrum emitted by the lamps was compared with two outdoor spectra for June and October measured at an altitude of 577 m above sea level and a latitude of $47^{\circ}16'N$ (Fig. 1). The integrated values over the same wavelength range for these two spectra were 2.74 and 0.94 W m^{-2} , respectively. In all experiments, background light for the photorepair process was additionally supplied by two white fluorescent tubes of 36 W. The integration of the irradiance between 350 and 450 nm, i.e., the wavelength range effective for the photoreactivation process (24), was 11.7 W m^{-2} . The UV lamps were preburned for 600 h before the spectrum was measured, and experiments were conducted within the next 80 h. Before each experiment, the lamps were switched on for 2 h to reach a constant emission spectrum.

UV measurements. The spectrum of the lamps as well as the two spectra in Fig. 1 was measured at high resolution (0.5 nm) with a Bentham DM150 double monochromator spectroradiometer by M. Blumthaler (Institute of Medical Physics, University of Innsbruck). During the experiments in the field, underwater UV radiation was measured from a floating platform placed over the deepest part of the lake with a PUV-500A radiometer from Biospherical Instruments, Inc. (San Diego, Calif.). This instrument measured the downwelling UV radiation at four nominal wavelengths (305, 320, 340, and 380 nm) with a moderate full-width half-maximum band of $\leq 10 \text{ nm}$ and the photosynthetically active radiation (PAR) (400 to 700 nm).

Experimental design. Laboratory experiments were done in a walk-in chamber at $15 \pm 1^{\circ}\text{C}$. Because of the heat produced by the lamps, a water bath was used to keep the temperature inside the containers within $\pm 1^{\circ}\text{C}$. All treatments were performed in duplicate and consisted of the exposure of *B. saltans* to (i) UV-B plus UV-A plus PAR, (ii) UV-A plus PAR with Mylar D foil (50% transmittance at 320 nm) to cut off the UV-B, and (iii) darkness. In preliminary experiments,

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FIG. 1. Spectrum emitted by the Q-Panel A-340 lamps and two spectra measured at 577 m above sea level and 47°16'N in June and October. Measurements were made with a double monochromator spectroradiometer (Bentham DM150). SZA, solar zenith angle.

the sensitivity of the HNF cultures, grown in the dark, to artificial and natural solar PAR was tested by removing all UV radiation (UV-A and UV-B) with a vinyl chloride foil (CI Kasei Co., Tokyo, Japan; 50% transmittance at 405 nm). Changes in the transmittance of the different foils were tested repeatedly in a spectrophotometer, and foils were replaced if necessary.

Culture conditions. *B. saltans* was originally isolated from Lake Constance (Germany). Cultures were maintained at 15°C in a barley seed infusion (two seeds autoclaved in 100 ml of tap water) inoculated with natural bacteria. In all cases, before inoculation, the medium was filtered through a 0.2-μm-pore-size filter (polycarbonate; Poretics) to remove suspended particles.

Bacterial prey. After removing the flagellates by filtration through a 1-μm-pore-size filter (Poretics), bacteria from the *B. saltans* culture were grown at 25°C in a medium consisting of 10 mg of Bacto Peptone and 5 mg of yeast extract liter⁻¹. After reaching the exponential phase, the bacteria were harvested by centrifugation (22,000 × *g* for 10 min) and stained with 0.2 mg of 5-[(4,6-dichlorotriazin-2-yl)amino] fluorescein (DTAF), ml⁻¹ according to the procedure of Sherr and Sherr (26) to produce fluorescently labeled bacteria (FLB). Finally, 1-ml concentrated aliquots were placed in Eppendorf tubes and frozen at -20°C for later use.

Bacterivory experiments in the laboratory. Before the experiments started, several controls were run to ensure that the FLB were stable over the UV experiment time and that no photobleaching of the cells occurred. This procedure was done by comparing the abundance of FLB in 0.2-μm-pore-size-filtered tap water before and after exposure during 24 h at ca. two times higher radiation than that to be used in the experiments. Open crystallization dishes (diameter, 9.5 cm) were used as containers for all suspensions and were filled with 200 ml of suspension of *B. saltans* plus bacteria from the same culture flask and allowed to adapt to the experimental conditions for 15 to 20 min. The abundance of *B. saltans* used in the experiments was 10³ to 10⁴ ml⁻¹. Before use, FLB were thawed to experimental temperature and sonicated briefly to disrupt possible cell clumping. Then, FLB were added at about 25% of the total abundance of bacteria present in the culture. After careful mixing, subsamples of 10 ml were taken at time zero (background value) and at 5- to 10-min intervals for 30 min. In experiments lasting for 6 h, samples were taken at the beginning and at the end of the exposure. The samples were fixed with alkaline Lugol (0.5% final concentration), borate-buffered formalin (3% final concentration [26]) was immediately added, and samples were kept refrigerated (4°C) in the dark until analyses within 24 h.

Bacterivory experiments in the field. Bacterivory experiments in the field were done under sunny conditions (around noon) in oligotrophic Lake Redó (42°38'N, 0°46'E) during October. Two different depths, 0.5 and 6 m, were selected, corresponding to ca. 71 and 10% of the UV-B irradiance at the surface, respectively (Fig. 2). Quartz tubes of 1-liter capacity, filled with a suspension of *B. saltans*, bacteria, and FLB, were exposed on a platform made of UV-transparent acrylic (GS 2458; Röhm, Darmstadt, Germany) and suspended at the two depths. Treatments were done in duplicate, and as a control, the quartz tubes were covered with Mylar D. The experiments were done as described above except that subsamples were taken at 0, 1, 2, 4, and 6 h because lower ingestion rates of *B. saltans* were anticipated at the in situ temperature of 8.5°C. The tubes were protected from the sun when retrieved to the surface for subsampling.

Enumeration and microscopical observations. For the direct uptake experiments, samples were stained with 4',6-diamidino-2-phenylindole (DAPI) by the method of Porter and Feig (22), filtered onto 1-μm-pore-size black Poretics filters, and washed three times with cold particle-free tap water. DAPI-stained *Bodo* cells were located at ×1,250 magnification in a Zeiss epifluorescence microscope with a BP 365 excitation filter, FT 395 chromatic beam splitter, and LP 397 barrier filter. FLB inside vacuoles were counted with the BP 450, FT 490,

and LP 510/520 filter set. Ingested FLB from at least 100 flagellates were counted in each replicate. In those experiments in which the disappearance of FLB and bacteria was monitored, samples were filtered onto 0.2-μm-pore-size black Poretics filters. The distribution of bacteria and FLB on the filter was first checked at ×800 magnification, and at least 600 cells were counted at ×1,250 magnification.

In similar experiments, but without adding FLB, small subsamples of 3 ml were taken at 0.5- to 1-h intervals from the three treatments and placed in a sedimentation chamber. The morphology of the cells was observed under an inverted microscope (×400), and the number of motile cells was recorded. At least 50 cells were observed at each time. The speed of *B. saltans* was estimated by measuring the time elapsed to cross distinct grids on the ocular micrometer.

Calculation of bacterivory rates. The instantaneous uptake rate was estimated from the slope of a least-square linear regression between time and the average number of FLB per cell. Flagellates without FLB ingested were included in the calculation. In the 6-h experiments, the equations developed by Marrasé et al. (18) were used to calculate the specific bacterivory rate (*g*) from the decrease of FLB over time as

$$g = -\frac{1}{t} \times \left(\ln \frac{F_t}{F_0} \right) \quad (1)$$

where F_t and F_0 are the concentrations of FLB at times t and zero, respectively. The growth or mortality rate of natural bacteria (a) was calculated as

$$a = \frac{1}{t} \times \left(\ln \frac{N_t}{N_0} \right) \quad (2)$$

where N_t and N_0 are the concentrations of natural bacteria at times t and zero, respectively. Then, the number of natural bacteria consumed per unit volume during the 6 h (G) is calculated as

$$G = \frac{a}{g} \times (N_t - N_0) \quad (3)$$

and the total number of bacteria consumed (TG) per unit volume in that time is calculated as

$$TG = F_0 - F_t + G \quad (4)$$

Scanning electron microscopy. Treated (exposed to UV-B radiation) and untreated *B. saltans* cells were fixed with glutaraldehyde (final concentration, 2.5%) and filtered onto glass fiber filters (Whatman GF/C) under low pressure. The filters were placed in OsO₄ (1% final concentration) for 1 h and washed with a phosphate buffer, 0.01 M (pH 7.4). Subsequently, the samples were dehydrated in methanol of increasing grade concentrations (50 to 100%) and critical point dried. Photos were taken at ×10,000 magnification in a Zeiss DSM-950 scanning electron microscope with an Ilford FP4 film of 125 ASA.

RESULTS

Laboratory experiments. The results from the exposure of *B. saltans* to only artificial or solar PAR (UV-B and UV-A

FIG. 2. Profile of the relative UV irradiance at 305 and 340 nm (A) and temperature (B) in Lake Redó. Measurements of UV radiation were made with a PUV-500A radiometer (Biospherical Instruments).

FIG. 3. Scanning electron micrographs of *B. saltans*: typical elongated shape of unexposed cells (A) and spherical cell after exposure to UV-B radiation (B). Scale bars, 1 μm . Arrowheads indicate the flagella.

excluded with vinyl chloride foil) showed no effects on morphology or motility. However, if exposed to UV-B radiation, a change in morphology (Fig. 3) and a decrease in the number of motile cells (Fig. 4) were evident. During the first 4.5 h of exposure to UV-B, the percentage of motile cells decreased slightly, but afterwards, a steep decrease by ca. 80% was observed. This change was accompanied by differences in cell morphology and vacuolization. Normal cells were elongated and of about 7 to 10 μm in length, but with increasing exposure time, the cells became spherical with a diameter of about 4 to 6 μm , with the flagella always present. After 5 h, 65% of the flagellates had a spherical shape. These cells moved by rotation but at very low speed. At 6.5 h, cells rotated in the same place without any displacement. After 7 h, all cells were spherical and no movement was detected. This effect was not reversible even after 7 days in the dark or subsequent exposure to only PAR (artificial or natural). In the dark treatment, cells were motile and elongated at all times. In the treatment in which cells received only UV-A and PAR, the appearance of spherical cells was delayed, and after 12 h, 65% of the cells were still motile (Fig. 4). Changes in speed seemed to occur independently from the change in morphology. At 4.5 h of plus-UV-B treatment, the speed of elongated cells was 3.5 times lower than in the dark or without UV-B (average $\pm$ standard deviation, 13 ± 3 and $45 \pm 9 \mu\text{m s}^{-1}$, respectively).

No photobleaching of the FLB was found after exposition to the UV lamps for 24 h. In those experiments in which *B. saltans* was exposed for only 30 min, the slopes of the least-square regressions between the average FLB uptake per cell versus time for the three different treatments were not significantly different (F test, $P > 0.1$) (Fig. 5). When *B. saltans* was exposed for 6 h, the specific grazing rate (g) was strongly reduced under the plus-UV-B treatment (Table 1). Comparing the total number of bacteria consumed (TG) between the treatments with UV-B and without UV-B, the former was about 2.6 to 3.3 times lower than the latter. A small decrease in g was also observed in the treatment without UV-B compared with the dark one. Bacterial growth rates (a) were always negative in the treatment without UV-B and in the dark, while in plus-

UV-B they were higher (experiment 2) and even positive (experiment 1, Table 1).

Field experiments. Under natural solar radiation, the morphology of *B. saltans* was also affected in the plus-UV-B treatment, but the response was faster than in the laboratory experiments, and after 4 h, almost all cells were spherical (Fig. 6A). After 6 h, also in the control (minus UV-B), 91% of the cells were spherical although they appeared after a longer lag time compared with the plus-UV-B treatment (Fig. 6A). At 6 m, where we registered only 10% of the surface UV-B irradiance at 305 nm (Fig. 2A), this effect was minimal. After 6 h, only 14% of the cells were round in the plus-UV-B treatment while in the control the percentage of spherical cells was very low ($<4\%$) and did not increase with exposure time. In the same experiment, the average FLB ingestion per cell followed a linear increase with time in the treatment without UV-B at 6 m (Fig. 6B). At the same depth but in the plus-UV-B treatment, values were lower, but a positive ingestion rate was still observed. Conversely, in those samples exposed at the surface, the FLB ingestion rate per cell decreased with time. After 6 h, when 100% of the cells were spherical, the uptake in the treatment with UV-B was nearly 0.

DISCUSSION

B. saltans is clearly affected adversely by both artificial and natural UV-B radiation but also by UV-A. The remarkable change caused by UV radiation is the appearance of a nonmotile spherical cell, in contrast to the ellipsoidal-oval shape of moving cells characteristic for *B. saltans*. In the experiments with artificial radiation, this effect was significantly delayed without UV-B, indicating a major role of UV-B. This change also occurred in the samples exposed to solar radiation at a 0.5-m depth. However, compared with the laboratory experiments, the appearance of the spherical cells was observed after a shorter time in both the plus-UV-B and minus-UV-B treatments. At a 6-m depth, where only 10 and 23% of the surface UV-B (305 nm) and UV-A (340 nm) irradiance, respectively, were found, the damage was very low, indicating the existence of an irradiance threshold. The different time response between experiments made with natural or artificial UV radiation is difficult to evaluate, because we had no possibility to calculate the field doses and compare them with the laboratory

FIG. 4. Change in the percentage of motile cells of *B. saltans* versus time of exposure to artificial UV radiation. + UV-B and - UV-B refer to the exposure to UV-B plus UV-A plus PAR or only UV-A plus PAR, respectively.

FIG. 5. Representative time course of the uptake of FLB by *B. saltans* exposed to UV radiation or kept in the dark. Abbreviations are as for Fig. 4. When error bars are not shown, 1 standard deviation was less than the width of the symbols.

experiments. The radiation of the lamps simulated closely that of the natural solar spectrum in the UV-B range, although wavelengths of <290 nm were present. In the UV-A the two spectra differed considerably for wavelengths of >350 nm. Thus, the integrated value for the UV-A radiation emitted by the lamps was 1.4 to 3 times lower compared with those calculated for the solar spectra in October and June, respectively.

Similar changes in motility caused by UV-B and partially by UV-A have been observed in several species of phototrophic flagellates (9). Morphological changes, e.g., in *E. gracilis*, have been attributed to a damage at the cytoplasmic membrane level (6). Low doses of UV radiation can produce rapid changes in the transport across damaged membranes (21). The increasing vacuolization with exposure time observed in *B. saltans* indicates an influx of water into the cells and points also to a damage of the cytoplasmic membrane. The decrease of motile cells observed under the plus-UV-B treatment in the laboratory experiments was clearly associated with the change in morphology. The decrease in swimming speed, however, was noticeable before the morphological change took place. In *E. gracilis*, the mechanism for the reduced motility under UV-B radiation has been attributed to a damage to the tubulin subunits of the microtubules of the flagella (8). Bodonids resemble

FIG. 6. Representative time course of the abundance of spherical cells (A) and FLB uptake per cell (B) when *B. saltans* was exposed to natural solar radiation at a 0.5-m depth (circles) and 6-m depth (squares) in the plus-UV-B treatment (open symbols) and the control without UV-B (closed symbols). When error bars are not shown, 1 standard deviation was less than the width of the symbols.

the euglenoids in several ultrastructural aspects, e.g., regarding the flagellar apparatus, and are phylogenetically closely related (29).

Bodonids possess as a peculiarity the kinetoplast, the largest repository of extranuclear DNA found in eukaryotic cells. Although the role of the kinetoplast in flagellar movement is not clear (30), this DNA may represent also a target for UV-B damage. Nevertheless, photoreactivation of damaged cells was not observed, which suggested that damage at the protein level is very important.

Under environmental stress, different species of bodonids may produce spherical cysts (30). Cysts may be an important strategy for surviving the stress imposed by UV radiation. However, we did not observe that UV stress induced encystation of *Bodo* cells. Characteristically, the encystment process implies the loss of the flagella (30). In our experiments, the spherical cells always retained their flagella even several days after the exposure. Moreover, studies made with the bodonid *Procrystobbia glutinosa* have shown that the kinetoplast DNA in the cyst is dispersed into several nucleoids (30). We could not detect any dispersion of the DAPI-stained kinetoplast.

The results from short-term exposure (30 min) to artificial UV radiation showed no effects on bacterivory; however, this may not be the case under natural higher UV radiation. As discussed above, also in those experiments performed in autumn under natural solar radiation, damage of *B. saltans* was visible after a short time. *B. saltans* is an interception-feeding flagellate, and its mechanism of prey capture is well known (20). Either *B. saltans* can be attached to a substratum and use the anterior flagellum to produce feeding currents, or it can

TABLE 1. Grazing rates of *B. saltans* (g , per hour), bacterial growth rates (a , per hour), and total bacteria consumed (TG , in bacteria per milliliter in 6 h) in the three treatments^a

Expt no. and treatment	Parameter			Ratio ^a
	a	g	TG	
1	+UV-B	0.007	0.003	3.3:1
	-UV-B	-0.008	0.011	
	Dark	-0.007	0.014	
2	+UV-B	-0.009	0.012	2.6:1
	-UV-B	-0.014	0.030	
	Dark	-0.016	0.033	

^a Ratio is that of TG in the -UV-B treatment to TG in the +UV-B treatment. *B. saltans* concentrations were 10^3 and 10^4 ml⁻¹ in experiments 1 and 2, respectively. +UV-B and -UV-B refer to the exposure to UV-B plus UV-A plus PAR or only to UV-A plus PAR, respectively.

swim freely. The mastigonemes of the anterior flagellum propel particles toward the cytostome as the cell makes sweeping movements. Therefore, the effects of UV radiation on motility may have consequences for the bacterivory of this species. In the free-swimming mode, a decrease in speed will reduce the encounter rate of prey. A subsequent change to a spherical, nonmotile cell will strongly affect its feeding capacity. This is indicated by the negative relationship between the percentage of spherical cells and the average FLB ingestion per cell (Fig. 6) as well as by the lower specific grazing rate (g) and total number of bacteria consumed (TG) in the treatment with UV-B (Table 1). Although the existence of different species-specific sensitivities to UV is possible, these results suggest the potential role of UV radiation in decreasing the carbon flux between bacteria and HNF. Interestingly, in the plus-UV-B treatment, bacterial mortality was significantly reduced or even growth was possible, indicating the existence of a positive feedback between UV-B and bacteria as a result of the reduced bacterivory in *B. saltans*. Positive feedback mechanisms like the one described here stress the need to consider the trophic interactions in the assessment of the UV-B impact.

Because of physical mixing processes in the water column, planktonic organisms may be exposed to high and low UV irradiances for variable periods of time throughout the day. Unfortunately, the rate of mixing processes in lakes is poorly known. Yet, in lakes where the attenuation of UV radiation is significant, mixing may be an important factor to reduce cell damage. Excluding the mixing effect in our field experiments may have led to an overestimation of the UV impact. Our results show, however, that damage on *B. saltans* appeared already after 2 h, suggesting that in the upper layers of a stratified water column the impact will be considerable.

Considering the sensitivity of *B. saltans* to UV radiation, the question arises where does this species, or bodonids in general, preferentially live and how common are they in their habitats? Many bodonids or at least morphologically indistinguishable species have been reported from marine, freshwater, and terrestrial habitats (33). *B. saltans*, in particular, is typically found in wastewaters (15) or associated with aggregates (2) where it may find protection from UV radiation, but it occurs also in lakes. Very few studies have examined the HNF species composition and their spatiotemporal distribution. For freshwater, some information is available and has recently been reviewed (16). In Lake Constance, chrysomonads, e.g., *Spumella* sp., are the dominant group (74% of the mean annual abundance) in the HNF assemblage (28a). In the mesoeutrophic Neumühler See (Germany), the biomass of HNF was also dominated by chrysomonads with kathablepharids as the second most important component (19). Bodonids and also colorless euglenids were of only minor and sporadic importance. In a seasonal study on lake community bacterivory, *Bodo* spp. were also not common in the eutrophic Lake Oglethorpe (25). In a very detailed study on taxonomical composition and spatiotemporal distribution of HNF from Mondsee (Austria), bodonids had the maximum contribution to the total biomass (40%) in January (23). During the rest of the year, their abundance was negligible with only minor contributions in autumn. The maximum abundance in January at 3 m was associated with a high load of particles caused by heavy rains. Also, in this lake chrysomonads were the most important HNF group. The results from all these studies indicate that bodonids are not common within the HNF assemblage living in the pelagic region of freshwater lakes. Caron (2) has argued that the pelagic existence of HNF that feed preferentially on attached bacteria, like, e.g., on *Bodo* sp. isolated from the Sargasso Sea, may be strongly linked to the distribution of suspended particles and

their associated bacteria. Therefore, one possible explanation for the low share of bodonids in the HNF assemblage is that they are numerically important only at times or places where suspended particles are abundant. In addition, the results of this study show that the high sensitivity of *B. saltans* to solar UV-B and UV-A radiation strongly reduces its ability to live near the surface at times of high UV radiation.

The next step will be to investigate whether various HNF species differ in their sensitivity to UV radiation. Preliminary experiments with the chrysomonad *Spumella* sp. indicate that this species is not adversely affected by even a higher UV-B dose than that supplied to *B. saltans*. More research is required to decide whether the commonly observed dominance of chrysomonads and the low share of bodonids in freshwater lakes can be explained by a different sensitivity to UV radiation.

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