Polar Biol (2002) 25: 460–468
DOI 10.1007/s00300-002-0366-y

ORIGINAL PAPER

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# Effects of ultraviolet radiation and dissolved organic carbon on the survival of subarctic zooplankton

Accepted: 27 January 2002 / Published online: 20 March 2002

**Abstract** High intensities of ultraviolet radiation are known to be harmful to aquatic biota, especially for species living in shallow, clear water bodies. Zooplankton species from such habitats are good model organisms to study the effect of changes in UV radiation, and how animals deal with this. We tested experimentally the effect of natural UV radiation, which was controlled by different filters and varying concentrations of UV-screening dissolved organic carbon (DOC), on the survival of the cladocerans, *Daphnia longispina* and *D. pulex*, and a calanoid copepod, *Eudiaptomus graciloides*. All species originated from subarctic Fennoscandia where underwater UV intensity is influenced by ozone depletion, changes in DOC and timing of ice break-up. Measured as mortality, all species were affected by both UVB and UVA radiation. Survival was highest and similar between species in the dark controls and photosynthetically active radiation exposures. Under each UV filter, the highest DOC concentration provided significant and best shelter from UV radiation and led to best survival. Variation in survival was observed between species. *E. graciloides* responded more readily to changes in UV radiation than did the daphnids. In natural environments, species' previous exposure to light and different protection strategies (pigmentation, vertical migration) are probably as important factors controlling the survival of zooplankton as radiation intensity and optical properties of water.

## Introduction

Ultraviolet radiation is the shortest wavelength spectrum reaching the Earth's surface. It is divided into two wavebands: wavelengths from 280 to 320 nm are referred to as UVB, and from 320 to 400 nm referred to as UVA. In most atmospheric situations, the UVB range of the spectrum covers 0.1%, UVA 6% and the visible light (photosynthetically active radiation, PAR, 400–700 nm) 50% of global radiation. Despite the low intensity in ground-level solar radiation, UV radiation can cause biological damage due to the great energy content per photon (Frederik et al. 1989).

In recent years, ozone loss rates in the subarctic and arctic regions have reached values comparable to those recorded over the Antarctic (Rex et al. 1997; Taalas et al. 1997). As a result, in the subarctic region, springtime (February/April) levels of UVB radiation reaching the surface of the Earth have increased by 10–20% between the late 1970s and 1995 (International Arctic Science Committee 1995). During this time, northern ponds and lakes are usully still ice-covered. However, increases in atmospheric carbon dioxide anticipated over the next 50 years account for the warmer temperatures and shorter period of ice-cover (Livingstone 1997; Rouse et al. 1997). Simulation studies by Huttula et al. (1992) and Elo et al. (1998) suggest that doubling of $CO_2$ will lead to a 1–2 month earlier melting of ice-cover in Finnish lakes. Consequently, ice break-up in subarctic lakes would occur earlier, exposing the lake to the most intensive period of UV radiation. In addition, ozone depletion over the poles is considered to be of special ecological concern because the biota may have evolved under UV conditions that are substantially lower in intensity than those experienced at lower latitudes (Vincent and Roy 1993).

The penetration of UV wavelengths into water is highly dependent on the concentration of chromophoric dissolved organic matter (CDOM) in the water body. CDOM absorbs a large part of the radiation between wavelengths 300–500 nm in fresh and coastal waters (Davis-Colley and Vant 1987; Gibson et al. 2000; Laurion et al. 2000). In clear fresh waters, the absorption of radiation by phytoplankton may also significantly contribute to the attenuation of UV radiation

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(Laurion et al. 2000). In general, however, dissolved organic carbon (DOC), which is the most important chromophoric compound, can be used to predict UV transparency (e.g. Laurion et al. 1997; Pienitz and Vincent 2000). With DOC concentration $<2$ mg $l^{-1}$, UVB can penetrate to several metres depth (Schindler et al. 1996). Many northern waters are both poor in DOC and shallow; the median DOC for 45 lakes across the treeline in Finnish Lapland was 3.0 mg $l^{-1}$ (Korhola et al. 1999), and measured maximum depth for 98 northern Finnish lakes was 5.1 m (Blom et al. 1998) while ponds seldom exceed 1 m. In addition, dissolved organic matter (DOM) in water bodies above the treeline is usually autochthonous in origin (Baron et al. 1991) and thus less effective than allochthonous DOM at absorbing UV radiation (McKnight et al. 1994). As a consequence, in shallow subarctic waters, all functional groups within the water body, including the benthos, are often exposed to UV radiation. In addition, many aquatic species stay in the open-water area of the water body. Even species that are considered more benthic or littoral (e.g. many Cladocera) seldom find shelter amongst macrophytes, as subarctic waters usually lack higher vegetation.

The central goal of this work was to determine whether natural present-day levels of UVB and UVA could cause increase in zooplankton mortality in northern Fennoscandia, and to test how changes in DOC concentration of water might affect species mortality rates. Of these variables, UVB and DOC are undergoing changes in their intensity and concentration as a result of climate change. A mesocosm experiment was conducted where a survival response of dominant species in subarctic zooplankton communities was tested separately to the combinations of solar radiation and dissolved organic carbon. The two studied daphnids, *Daphnia longispina* and *D. pulex*, are the dominant crustacean zooplankton species in humic shallow ponds in Finnish Lapland (Rautio 2001) while the calanoid copepod, *Eudiaptomus graciloides*, is common in clear lakes in the Fennoscandian Subarctic (Nauwerck 1994). We also discuss how the results of the mesocosm experiment are attributable to the natural water bodies and their fauna in the northern treeline region. This study is one of the first attempts to conduct experimental studies under natural conditions in order to more comprehensively understand the linkages between various environmental factors affecting the UV-induced changes in aquatic ecosystems.

## Materials and methods

Individuals of adult female *D. longispina* and *D. pulex* originating from two shallow (max. depth 50 cm) fishless ponds in the Kilpisjärvi region, northwest Finnish Lapland, were studied in 2 sequential 11-day experiments in late July and early August 1999, respectively. The experiments were run under natural light conditions at Lake Kilpisjärvi in Finnish Lapland (69°03′N, 20°50′E).

The *Daphnia* used in the experiment were collected with a 200-µm townet 24 h before the commencement of the experiment. In the laboratory, 20 female individuals were randomly transferred to the treatment containers using a pipette. Prior to the experiment, containers were kept for 12 h in a lighted 11°C cold room, which equals the temperature of the pond where the population originated.

The following five radiation treatments were set up for *Daphnia* experiments: (1) UVB + UVA + PAR, i.e. full sunlight, using a cellulose diacetate foil (0.13 mm thickness Courtaulds, Derby, UK); (2) UVA + PAR, using Mylar foil (0.1 mm, Ekman, Sweden) to exclude the UVB; (3) PAR, using Wipa foil (Wipa-Technik, Germany) to exclude both UVB and UVA; (4) 70% decrease of total radiation using a white cloth; (5) dark control in which containers were wrapped with black plastic bags (Fig. 1A). The containers under the cellulose foil were considered as full sunlight exposures although the foil absorbed some radiation (Fig. 1A). However, we nevertheless decided to use the cellulose foil in order to minimise the effects of, for example, rain in diluting the DOC media, and to prevent the occasional heavy winds from emptying the exposure containers. The Mylar foil effectively absorbed wavelengths below 320 nm. Transmittance of UV by the Wipa foil was nearly 0%, and thus the foil provided a PAR exposure. The white cloth transmitted 22–55% of the UV, and the transmittance of the black plastic was zero (data not shown). As rain might change the UV penetration of the filters, the transmittance was measured at the start and end of the experiments. In general, no significant changes occurred in the transmittance properties of the filters during the course of the experiments, except in the case of the white cloth, which after being wet several times during the experiment from the rain become more loose. This resulted in the UV penetration increasing approximately twofold during the survey.

Under each filter, survival of *Daphnia* was studied using different DOC concentrations to further manipulate the underwater light intensity (Fig. 1B). Each container (area 11×7 cm, depth 4 cm) was filled with 2 dl of water which corresponded to a water depth of 3 cm. Three replicates of each exposure were carried out. The lowest DOC concentration (4.7 mg $l^{-1}$) represents the most typical DOC value for small treeline waters in the area; the intermediate DOC water (9.5 mg $l^{-1}$) originated from the pond that was initially inhabited by the *D. longispina* population used in the experiment; and the darkest water (DOC 11.3 mg $l^{-1}$) was from one of the most humic waterbodies known in the Kilpisjärvi area. All waters were filtered (Whatman GF/C) prior to the experiment to remove phytoplankton and large bacteria and hence obtain more equal media between different DOC treatments. However, the differences in, for example, nutrient concentration and pH (for information on the values, see Rautio 2001) between the waters could not be compensated.

Water temperature was kept relatively constant at 11°C during the experiment and equal between different *Daphnia* exposures by placing treatment containers in a lake-water bath for the duration of the experiment. An electrical water pump provided a constant flow of water from lake to bath and back to lake (Fig. 1B). Mean UVB and UVA radiation were recorded for each 15-min interval during the experiment. Measurements were made by Solar com gauge 1200 meter (Solar Light, Philadelphia), which was located close to the experimental containers, i.e. the device recorded unfiltered ambient UV radiation. In all containers, all individuals stayed near the bottom, and thus we assume that each individual was exposed to same amount of ambient radiation during the experiment.

The *Daphnia* were examined daily, during the evening. Mortality was recorded, dead organisms and newborns were removed from the containers, and survivors were fed *Scenedesmus* (concentration unknown, each container received 2 ml homogenised media daily) and left in the containers for the duration of the exposure. This routine was continued daily until the termination of the exposures. The main effects of UV, DOC and UV*DOC interactions on the mortality of the population, and the time trends (within-subject effects) were studied using two-way analysis of variance (ANOVA) with repeated measures. ANOVA was performed using Systat 8.0.

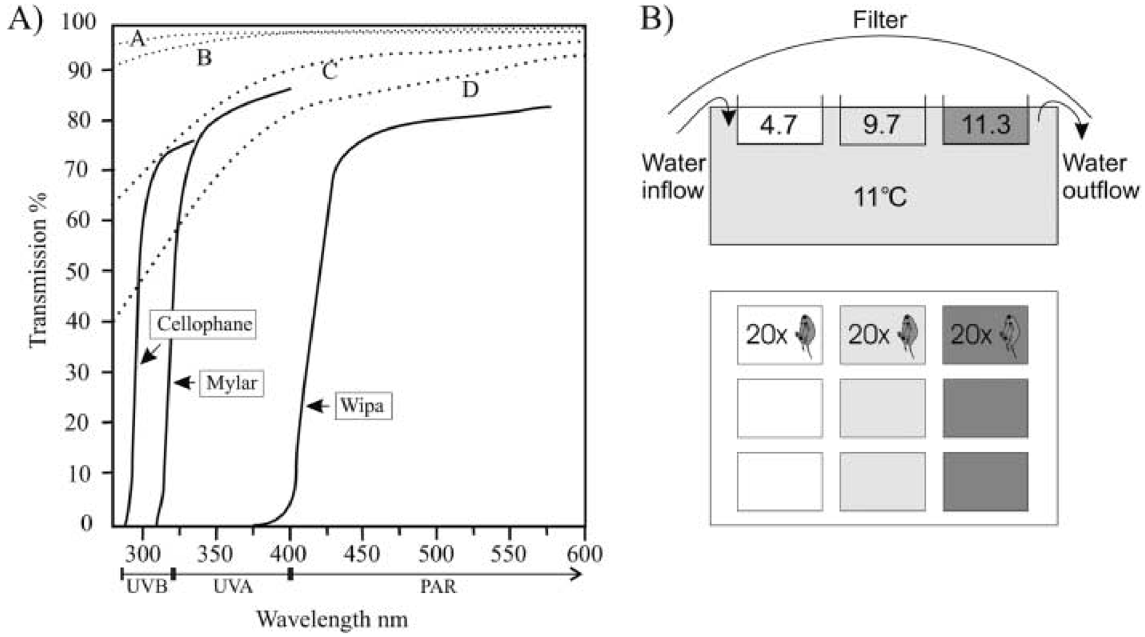


**Fig. 1.** **A** Spectral transmission of different filters and DOC waters used in the experiment. *A* denotes DOC = 1.6 mg $l^{-1}$, *B* DOC = 4.7 mg $l^{-1}$, *C* DOC = 9.5 mg $l^{-1}$ and *D* 11.3 mg $l^{-1}$, respectively. **B** Side and top view of the experimental set-up during *Daphnia* experiments. Numbers inside the containers refer to the DOC concentration (mg $l^{-1}$). Each DOC treatment was performed in triplicate

We also studied the UV-induced mortality of *E. graciloides* (Copepoda) in May 2000 for a 1-day course. Egg-carrying females of *E. graciloides* were collected from Lake Saanajärvi, a 24-m deep, clear-water lake located at 679 m a.s.l. in barren tundra. *Eudiaptomus* populations reproduce and have a biomass maximum in late spring under ice and during the ice break-up in June when the population comprises egg-bearing females, males and newborn nauplii (Rautio et al. 2000).

The experimental set-up varied slightly from the *Daphnia* experiments. The radiation treatments included: (1) full sunlight; (2) UVA + PAR; (3) PAR; (4) dark control. Under each filter, the survival was studied in three replicates but only in one DOC medium (1.6 mg $l^{-1}$), which originated from Lake Saanajärvi; water was used unfiltered in the experiment. Additional DOC treatments for *E. graciloides* could not be conducted for logistic reasons; ponds with humic-rich waters were frozen solid at the time of the experiment.

Females of *Eudiaptomus* were collected from 2°C lake water and kept at 5°C in the cold room for 5 days before the experiment. Twenty individuals in each container were studied in the experiment. During the experiment, the treatment containers were surrounded by snow to keep water temperature at 2°C. The *Eudiaptomus* was usually observed once an hour until all individuals in the UV treatments were dead.

$LD_{50}$ doses (UV dose at which 50% mortality was observed for a given species) of UVB and UVA for each species were calculated from the UV dose at a 3 cm depth (position of the individuals) of each of the treatment waters. Mortality in the control treatments was first subtracted from the mortality in the UV treatments. $LD_{50}$ doses were then achieved as a product of the ground-level radiation intensities of UVB and UVA, which had been measured during the experiments with a Solar com gauge 1200 meter, and a solar attenuation ($K_d$) of UVB and UVA in the study pond using the equation:

$$E_d(z) = E_d(0)e^{-K_d z}$$

where $E_d(z)$ and $E_d(0)$ are the values of downward irradiance at z m and just below the surface, respectively, and $K_d$ is the vertical attenuation coefficient for downward irradiance. The vertical attenuation coefficients at wavelengths 320 (UVB) and 365 nm (UVA) were determined from measurements at 2 depths for each of the waters used in the experiment. This was done in the field at bright sunshine in 5-nm intervals at approximately 1600 hours on 27–28 July 2000 (submersible Macam Spectroradiometer SR-9910-PC). Obtained $K_d$-values (Table 1) were used in the above equation. Constant values of $E_d(0)_{UVB}$ and $E_d(0)_{UVA}$ were determined by comparing above and subsurface measurements for both UVB and UVA from the spectral distribution of downward irradiance curves that were measured in the field simultaneously with the $K_d$ measurements. Obtained values are shown in Table 1.

To estimate the effect of UV radiation on organisms inhabiting deeper natural water bodies, we also calculated theoretical UVB and UVA irradiances for the experimental waters in depths of 10, 30, 50 and 100 cm, respectively, using the method described above. These data were used as reference material for a set of 50 northern lakes for which DOC concentration and UVB attenuation (Solar com gauge 1200 meter) were measured.

**Table 1.** Diffuse attenuation coefficients ($K_d$) at 320 and 365 nm, and downward irradiance just below the surface [$E_d(0)$] with corresponding DOC concentrations [$E_d(s)$ = irradiance just above the surface]

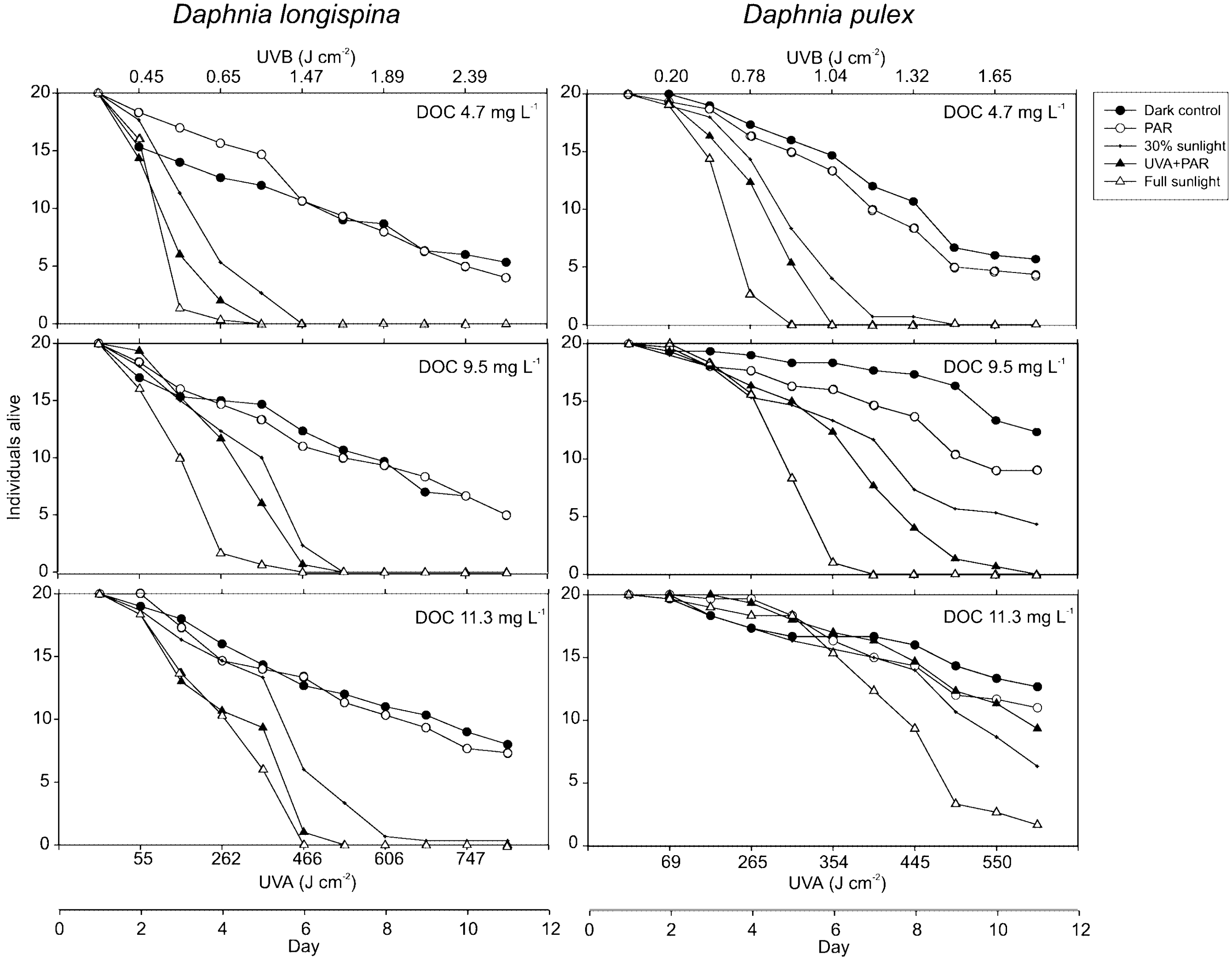
| Lake name | DOC (mg $l^{-1}$) | $K_d$ 320 nm ($m^{-1}$) | $K_d$ 365 nm ($m^{-1}$) | $E_d(0)$ 305 nm | $E_d(0)$ 365 nm |
|---|---|---|---|---|---|
| L. Saanajärvi | 1.6 | 4.76 | 2.37 | $0.49 \times E_d(s)$ | $0.62 \times E_d(s)$ |
| Siilas-3 | 4.7 | 12.18 | 6.34 | $0.41 \times E_d(s)$ | $0.55 \times E_d(s)$ |
| Siilas-4 | 9.5 | 33.38 | 17.10 | $0.29 \times E_d(s)$ | $0.44 \times E_d(s)$ |
| Tsahkal-C | 11.3 | 49.26 | 30.50 | $0.24 \times E_d(s)$ | $0.44 \times E_d(s)$ |

## Results

The three zooplankton species showed a similar ranking of treatments. Mortality of each species was highest in full sunlight treatment and decreased with declining UV intensity (Figs. 2, 3). Not only the presence of UVB, but also UVA, resulted in high and rapid mortality. In all treatments, survival was already affected at the beginning of the experiment and the influence remained high for the duration of the experiment, as shown by the slope of the survivorship curves. Zooplankton mortality was lowest and similar in both non-UV exposures (PAR and black control). Treatment comparisons by ANOVA revealed significant differences in the survival slopes between the non-UV and UV treatments ($P < 0.001$ for all species). An exception to this pattern was the survival of *D. pulex* in the highest DOC concentration (DOC = 11.3 mg $l^{-1}$), where none of the UV-treatments differed significantly from the non-UV treatments. In generally, the mortality of both *Daphnia* species increased with decreasing DOC concentration. The highest DOC concentration was most favourable to *D. pulex*, reducing its mortality greatly so that at the termination of the experiment some *D. pulex* were still alive in all exposures (Fig. 2). The differences were statistically significant for both species (ANOVA, *D. longispina* $P < 0.004$, $df = 2$; *D. pulex* $P < 0.001$, $df = 2$).

Despite the same general trend in their response to the changes of UV radiation, the susceptibility of species differed. *E. graciloides* responded most rapidly to UV light; in the presence of UV nearly all individuals died within 7 h. The survival of *D. longispina* and *D. pulex* was better; in full sunlight *Daphnia* lived for 4–5 days (DOC = 4.7 mg $l^{-1}$ exposure). By calculating the depth-specific (3 cm) irradiance, we were able to remove the effect of DOC and achieve $LD_{50}$ values of UVB and UVA for each species. The values differed between species but also within the species, depending on the DOC treatment (Table 2). *Daphnia* in low DOC concentration had higher $LD_{50}$ values, i.e. they tolerated higher UV doses than *Daphnia* that were

**Fig. 2.** Survival of *Daphnia longispina* and *D. pulex* in relation to radiation and DOC. Values of UVB and UVA represent cumulative natural unfiltered radiation dose



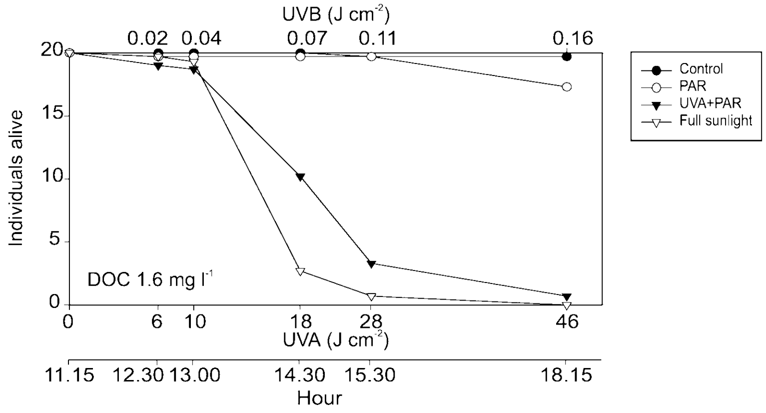


**Fig. 3.** Survival of *Eudiaptomus graciloides* under different spectral conditions

**Table 2.** $LD_{50}$ doses (J cm$^{-2}$) of UVB and UVA radiation for *Daphnia longispina*, *D. pulex* and *Eudiaptomus graciloides* in the corresponding DOC concentrations of 1.6, 4.7, 9.5, and 11.3 mg l$^{-1}$

| | DOC (mg l$^{-1}$) | $LD_{50}$ (J cm$^{-2}$) | | |
|---|---|---|---|---|
| | | *D. long* | *D. pule* | *E. grac* |
| UVB | 1.6 | | | 0.025 |
| | 4.7 | 0.16 | 0.18 | |
| | 9.5 | 0.08 | 0.10 | |
| | 11.3 | 0.06 | 0.08 | |
| UVA | 1.6 | | | 11.5 |
| | 4.7 | 93 | 136 | |
| | 9.5 | 92 | 113 | |
| | 11.3 | 70 | [a] | |

[a] Not enough dead individuals to calculate the $LD_{50}$ dose

in high DOC concentration treatments. *E. graciloides* was almost 10 times as susceptible to UV as the daphnids.

Figure 4 shows how deep in the water column UV radiation would theoretically penetrate in natural water bodies containing the same concentrations of DOC as used in the mesocosm experiments. The cumulative UV irradiance as a function of time is also shown. The reference ambient UV irradiance is from the *D. longispina* experiment. The calculated penetration of UV is clearly dependent on the DOC concentration, indicating that only the clearest water bodies are exposed to high UV irradiances just below the surface. In the lowest DOC concentration (1.6 mg l$^{-1}$), the $LD_{50}$ dose of UVA is reached only within 4 days for *E. graciloides* individuals that stay at 100 cm depth. The less susceptible *Daphnia* would survive better during the 10-day period but would still be exposed to UVA doses that exceed the $LD_{50}$ values if placed at 50 cm depth. As UVB attenuates faster in the water column, only the lowest DOC water of the uppermost 50 cm would receive enough radiation to cause significant death among zooplankton (Fig. 4). Individuals in darker water are quite well protected from the UV.

Most of the natural lakes in the region above the treeline were very clear with DOC concentrations between 0.5 and 2 mg l$^{-1}$ (Fig. 5A). The measured penetration of UVB radiation into these lakes is shown in Fig. 5B. Higher DOC concentration results in a rapid UVB attenuation whereas a lower DOC significantly increases UV penetration into the water column.

## Discussion

UV investigations often only take into account the effects of UVB radiation (280–320 nm) on biota. This is reasonable because DNA's absorption maximum near 260 nm makes UVB biologically the most dangerous spectrum of radiation (Caldwell 1979). All studied species in our experiment also had the lowest survival in full sunlight exposure, which was the only treatment to include UVB radiation. However, the longwave portion of UV band (UVA, 320–400 nm) can also be harmful to organisms, for example, by causing reductions of photosynthesis (Helbling et al. 1992) and increasing mortality in zooplankton. Zellmer (1998) showed that survival was 80% higher in *D. pulicaria* in natural habitats when both UVB and UVA were excluded, as opposed to only UVB exclusion. Our results also convincingly show that only the reduction of both UVB and UVA substantially increased species survival, and indicate that natural levels of UV radiation, even in high latitudes in subarctic Fennoscandia, can increase mortality in zooplankton.

*Daphnia* mortality was also relatively high in the visible light (PAR, 400–700 nm) exposure. Although PAR has been shown to cause reductions in photosynthesis rates (Helbling et al. 1992), the similar survivorship curves of PAR and the dark control indicate that mortality of zooplankton was not influenced by the presence of PAR. The high mortality in the two non-UV treatments probably resulted from the experimental setup that may have caused stress for individuals originating from natural habitats. We altered, for example, the interactions between individuals by keeping them at high density. Since the water was not changed during the 11-day course of the experiment, it is probable that chemical accumulation occurred, which may have been unfavourable to the studied individuals and hence caused high mortality in the controls.

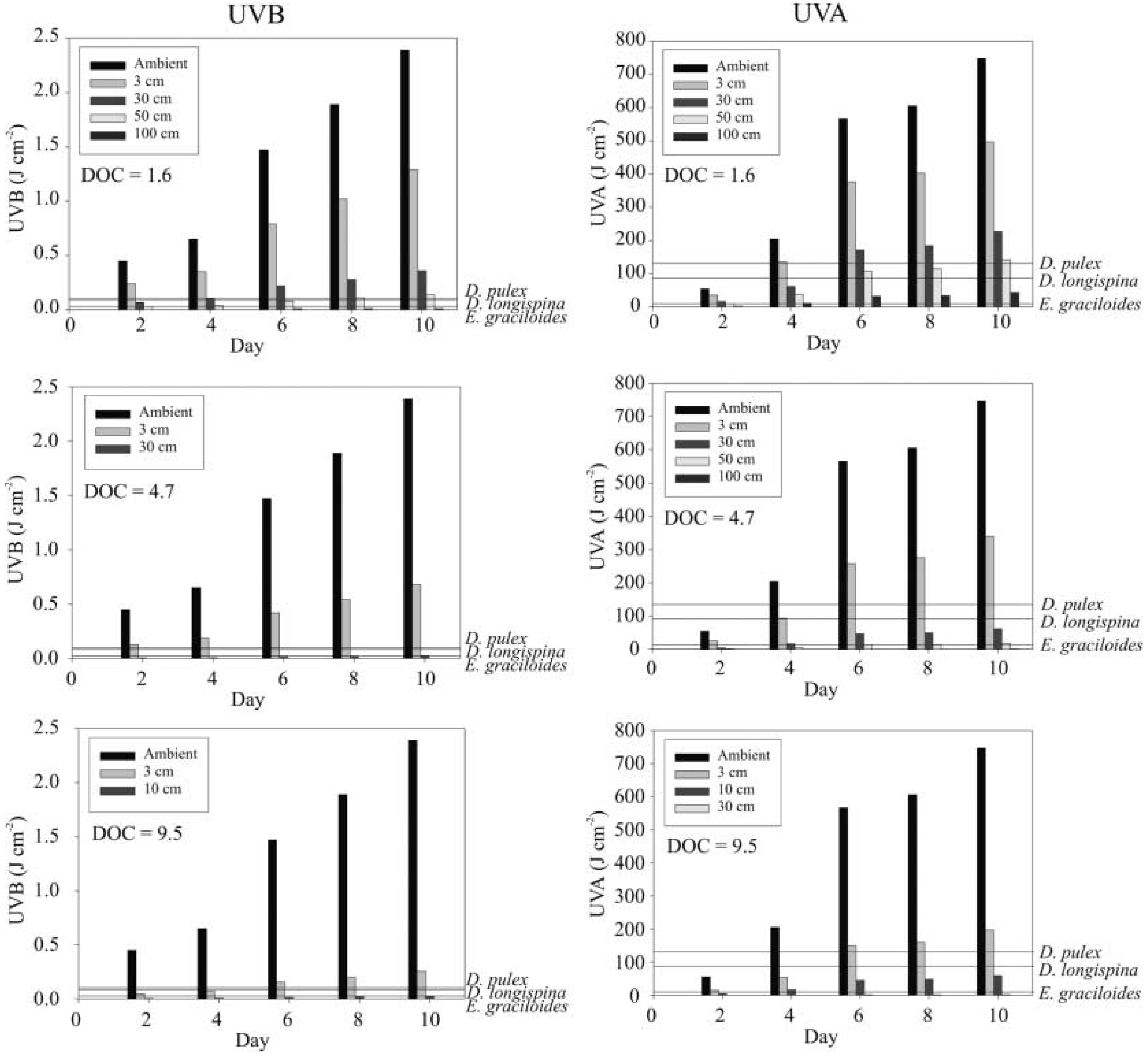
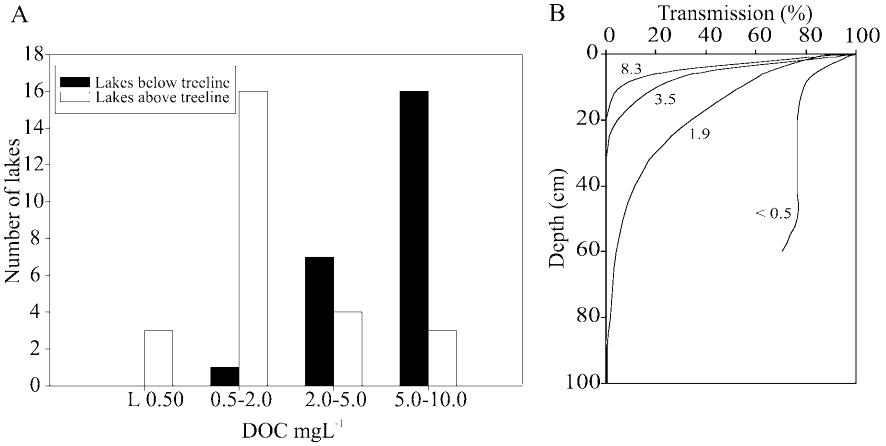


**Fig. 4.** Calculated cumulative subsurface UVB and UVA doses for waters with different DOC concentrations. The ambient UV radiation is from the *Daphnia longispina* experiment. UV-doses are calculated for depths between 10 and 100 cm. The mean level of $LD_{50}$ dose is shown for *D. longispina*, *D. pulex* and *Eudiaptomus graciloides*

Several studies have shown that the tolerance and hence $LD_{50}$ dose to UV radiation vary between different zooplankton species. In contrast to our study, adult calanoid and cyclopoid copepods exhibited high, and cladocerans low UV tolerances in the study by Leech and Williamson (2000). The species in their study, however, were different than in the present study. In addition, as Siebeck and Böhm (1994) argued, spot measurements of $LD_{50}$ may not be directly attributable to other seasons or water bodies. This results from, for example, a different UVB:PAR ratio between the experiments. During cloudy days and towards the autumn, physiological damage may be repaired by short wavelength PAR (390–470 nm, recovery radiation) more efficiently than in sunny weather or in early summer. Chemical properties of water may also have an effect on the $LD_{50}$ doses. Although the role of humic substances in protecting aquatic ecosystems from UV is well recognised, DOC may also introduce stress to organisms in highly irradiated surface waters. Harmful free radicals such as $H_2O_2$ are formed in humic waters that are exposed to UV radiation (Cooper et al. 1994). In the present study, although the daphnids survived longest in UV exposures with the highest DOC concentration, the $LD_{50}$ dose for both *Daphnia* species studied decreased with increasing DOC concentration. This suggests that the formation of reactive oxygen species (ROS) might have influenced the survival of the daphnids by

**Fig. 5.** **A** The frequency distribution of lakes below and above treeline in northern Finland in relation to dissolved organic carbon (*DOC*) concentration. **B** The penetration of UVB (erythema action spectrum) in relation to depth in selected waters with different DOC concentrations



overcoming some of the positive effects of DOC against UV radiation. However, the DOC-dependent $LD_{50}$ results in our experiment must be regarded with some caution as DOC concentration may have slightly changed during the experiment. UVB causes photochemical mineralisation of DOC (Vähätalo et al. 2000), which leads to a deeper penetration of UV radiation. The daily additions of 2 ml *Scenedesmus* into the containers might also have changed the DOC concentration, although the effect here is probably minor as the water volume only increased by 10% during the 11-day experiment.

Cold temperatures, under certain environmental conditions, may also increase the susceptibility of subarctic and arctic biota to UV-induced damage. Decreasing temperatures have been shown to reduce biosynthetic repair from photochemical damage in antarctic cyanobacteria (Roos and Vincent 1998). It has also been assumed that DNA repair, and detoxification effects of ROS, might decrease in cold environments among poikilotherms (Hessen 1996). However, the recent study by Borgeraas and Hessen (2000) indicated that low temperatures reduce sensitivity to UVB radiation. Hence, UV-induced damage may actually be greater in warm than in cold, especially among subarctic and arctic biotas, which are adapted to cold temperatures. In our study, the studied species were exposed to the temperature that was close to the temperature of the water from which they originated. In the *Eudiaptomus* experiment, the temperature was much lower than in the *Daphnia* experiments (2 vs 11°C), and the species suffered from higher mortality. However, the role of temperature, if any, on UV-induced mortality remains unresolved in the present study.

An organism's susceptibility to UV radiation is, in addition to present levels of radiation, dependent on the UV exposure it has experienced before. Studies on phytoplankton have shown that previous exposure to UV light affects the succeeding photosynthesis rates. Communities originating from highly irradiated surface layers of tropical water show only a small enhancement of photosynthesis after UV has been filtered out, whereas communities from deeper water layers are much more affected (Helbling et al. 1992). In our study, *E. graciloides* females used in the experiment originated from the under-ice population of Lake Saanajärvi, where they had been sheltered from light for 7 months. As a result of the absence of UV radiation for a long time, they might have possessed reduced concentrations of molecular sunscreens, both coloured (carotenoids) and colourless (mycosporine-like amino acids), or reduced repair capabilities and, consequently, they may have been more susceptible to UV damage than *Daphnia* that had been exposed to UV in their natural environment before the experiment took place. We are currently investigating how UV susceptibility and activation of various UV defence mechanisms are related to the light exposure the organism has experienced in the past.

Although $LD_{50}$ data obtained from one depth cannot be transferred to other depths without using caution (Siebeck and Böhm 1994), we calculated the theoretical values for various depths of the studied waters to get an idea of the relevance of our results to natural, subarctic water bodies. The calculations suggested that in shallow ponds, if low in DOC concentration, the cumulative UV dose during natural July weather may exceed the UV tolerance of many species after only few days. This is in accordance with our previous studies, which have documented that *Daphnia* inhabit only relatively humic ponds (DOC > 5 mg $l^{-1}$) in the treeline region in northern Finland, and are still melanic, avoiding the surface water layer in sunny weather (Rautio and Korhola 2002; Rautio et al., unpublished work).

Although the present experimental set-up could not mimic natural conditions with respect to water-column depth, the calculations by which we took the data to a natural lake setting still suggest that, with reduction in ozone, changes in precipitation or in catchment vegetation characteristics and earlier ice break-up, zooplankton may be at risk of injury in the Subarctic. Although different zooplankton species vary in their sensitivity to UV radiation and many species possess protection mechanisms such as vertical migration and pigment production or accumulation, survival could be reduced if underwater UV intensities continue to increase. Ecosystems in northern Europe are especially exposed to increases in UV radiation. Ozone is being depleted more rapidly over Scandinavia than over most geographical regions at corresponding latitudes (Björn et al. 1998). Furthermore, as a result of ocean circulation (Gulf Stream), the climate in this area is warmer than at corresponding latitudes in North America and Asia, resulting in longer open-water periods and hence longer exposure to radiation. However, increase in precipitation and resulting DOC load from the catchment may overcome some deleterious effects of radiation in aquatic biota that habit water bodies that are surrounded by catchment with a top soil. The recent report from IPCC indicates that, in northern Fennoscandia, precipitation has increased and this trend will continue according to climate models (Watson et al. 2001), suggesting that water bodies may become better protected from UV. Lakes with a bare rocky watershed, however, would probably not gain any additional UV-screening DOC even with increasing precipitation. It is likely that climate-driven changes also reflect the influence of interactions with other species (Davis et al. 1998). One of our future objectives is to investigate how these interactions modify changes arising directly from changes in the intensity of UV radiation.

**Acknowledgements** We thank Kilpisjärvi Biological Station for logistic help and Professor Juha Merilä for providing the transmission data for UV filters. The students from the Spring Ecology course are greatly acknowledged for assistance during the *Eudiaptomus* experiment. The Academy of Finland supported this work.

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