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Vertical distribution of *Daphnia longispina* in a shallow subarctic pond: Does the interaction of ultraviolet radiation and *Chaoborus* predation explain the pattern?

Abstract The adaptive significance of vertical migration by planktonic organisms is often explained in terms of reducing the risk of predation. Observational evidence, however, indicates that migratory patterns may also be triggered by solar ultraviolet (UV) radiation. Such a strategy would allow animals to escape from UV-induced damage into deeper water layers. In this study, we examine the relation of several biotic (invertebrate predators, algae) and abiotic (temperature, radiation) factors to the vertical distribution of *Daphnia longispina* in a 50-cm-deep, fishless pond in subarctic Finnish Lapland. Samples were taken from three depths, on both sunny and overcast days, and at different hours of day. Our results show that, on sunny days, the vertical distribution of *Daphnia* responds to ultraviolet radiation, whereas on overcast days, predator avoidance (phantom midge, *Chaoborus obscuripes*) is a better predictor of *Daphnia* distribution. Juvenile and adult *Daphnia* showed a similar distribution pattern.

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Introduction

Vertical migration (VM) behaviour, whereby aquatic organisms inhabit different layers of the water column at different times of the day, is widespread among zooplankton (Gliwitcz 1986; Neill 1990). The best-known causes for VM, the interaction between visual predation and the dark nights that provide refuge from it, are absent in the subarctic and arctic pond environments. In the far north, ponds usually lack fish, and the period from the ice-break in June to mid-August is characterized by the presence of the midnight sun, with light penetrating to the bottom of the ponds 24 h a day. Consequently, if VM occurs in these environments, alternative factors are likely responsible. One alternative is invertebrate predators using tactile senses instead of visual ones. Nesbitt et al. (1996) reported that in the presence of the phantom midge *Chaoborus*, *Daphnia* moved upward in the water column, thus reducing spatial overlap. The environmental cue responsible for triggering this vertical movement in zooplankton is believed to be chemical, specifically the kairomones released by the predators.

Ultraviolet radiation (UVR) has also been discussed as a stimulus for VM. As early as 1924, Huntsman suggested UVR as a possible reason for VM (Huntsman 1924) and, more recently, Leech and Williamson (2001) and Rhode et al. (2001) have provided more supporting evidence. Results from shallow rock pools on Baltic islands (Ranta and Nuutinen 1985) showed that, during the daytime, *Daphnia* stayed in water layers close to the sediment, while at midnight they were evenly distributed throughout the water column or had a modal peak of distribution in the surface water. The authors did not mention ultraviolet radiation but concluded "the pattern of *Daphnia* vertical migration in shallow rock pools is not satisfactorily explained by predation".

Ambient levels of UVR (280–400 nm) are known to decrease the survival of common zooplankters like *Daphnia* and copepods (Siebeck and Bohm 1994;

Zellmer 1995, 1998; Tartarotti et al. 1999; Rautio and Korhola 2002a). Rapid attenuation of UV by dissolved epilimnetic material means the harmful effects of this radiation, like the effects of visual predation, are typically limited to lighted surface waters. Thus determining whether VM is an avoidance strategy to visual predation, harmful UVR or a combination of both is difficult based solely on measurements of zooplankton vertical distribution. What is needed to separate the two effects is a model system where zooplankton distribution can be evaluated in the presence and absence of the tested variables. We suggest that subarctic ponds in Finnish Lapland provide just such an environment. Many of these high-latitude ponds are both shallow and contain enough dissolved organic carbon (Rautio and Korhola 2002a) for rapid UV attenuation. They therefore simulate radiation extinction patterns similar to those of clear arctic lakes, but on a smaller scale. In addition, many such ponds are in high-altitude mountainous areas of Scandinavia, meaning the UV dose they receive is greater than that calculated by latitude alone. We present a study that takes advantage of conditions in these ponds to evaluate changes in *Daphnia* distribution, in the presence and absence of the hypothesized UV cue. Clear and cloudy days (high and low ambient UVR) are used to separate the roles of predation and UV. The study is a continuation of earlier papers that concentrated on the UV-induced mortality and pigmentation of several subarctic *Daphnia* populations (Rautio and Korhola 2002a, 2002b).

Materials and methods

Study site

The study pond lies at 510 m a.s.l. (69°06′N, 20°45′E) in a mountain birch (*Betula pubescens* var. *tortuosa*) woodland valley. The surface area is small (0.2 ha) with a maximum depth of about 50 cm. The water is humic with a dissolved organic carbon (DOC) content of 11.3 mg l^{-1} and has a bottom of dark, coarse detritus, all relatively common features in boggy areas across the treeline in northern Fennoscandia. In addition to *Daphnia longispina*, 20 other crustacean zooplankton species are found in the pond (Rautio 1998). These stay mainly among the littoral vegetation, leaving *Daphnia* and fairy shrimps (*Polyartemia forcipata*, Anostraca) to dominate the open-water area. The pond is fishless, so that the only predators are phantom-midge larvae (*Chaoborus obscuripes*) and water boatman (Corixidae). The pond is surrounded by thick macrophyte stands of *Carex* and *Eriophorum* species, but the catchment area consists mainly of a subalpine mire of *Sphagnum* mosses. The pond is frozen solid from October to mid-June. The summer water temperature closely follows air temperature, thus exhibiting a large diel and seasonal variation. Measured minimum and maximum water temperatures in July 1998 were 13.6 and 22.0°C, respectively.
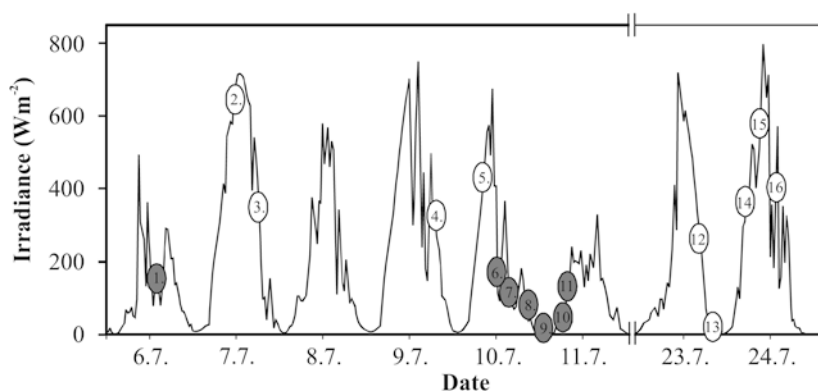
Sampling

Sampling was performed in July 1998 on seven different days in both sunny and overcast weather. For analysis, weather was considered sunny when no clouds occurred, and cloudy when the sky was completely covered with heavy clouds. During intermediate conditions, no sampling was performed. In most cases, cloudy weather also meant rain. Samples were taken during two consecutive 24-h cycles at 4-h intervals, and five additional single measurement days (Fig. 1). Samples of *Daphnia*, *Chaoborus* and Corixidae, and measurements of chlorophyll-*a* and temperature were taken from three depths (0, 25, 50 cm) using a Limnos water sampler (volume 2 l, tube diameter 7 cm). The sampler was used horizontally and closed manually in order to get a sample that best represented the water layer in question. All samples were taken in front of an inflatable boat with a flat bottom, and special attention was paid to not disturbing the water column before taking the sample. As the boat was drifting while the sampling was performed, each sample was taken from an undisturbed water column, thus reducing potential escape reactions of the animals. Depending on the density of *Daphnia* (judged by eye), three to seven additional 2-l samples were taken. Samples containing *Daphnia*, *Chaoborus* and Corixidae were preserved with formaldehyde (4% final concentration), and later counted under a stereo microscope at ×25–50 magnification. *Daphnia* were divided into neonates, juveniles, adults, gravid adults and adults with ephippia. Water (1 l) from each of the three depths was immediately filtered in the field through a Whatman GF/C filter, and frozen for the determination of chlorophyll-*a*. Chlorophyll-*a* was determined within 4 months of sampling with a spectrophotometer using a 96% ethanol extraction method. Because the green colour of their intestines suggested *Daphnia* feed on algae, chlorophyll-*a* was used as a rough measure of food availability. Temperature was measured at the surface and bottom of the water column.

Irradiance measurements

During the sampling period, a global radiation ($I_{305–2000 nm}$) meter (Vaisala) was used at 30-min intervals over the 24-h period at Lake Saanajärvi (10 km from the study pond). Intensities of ground level

Fig. 1 The variation in global radiation (305–2,000 nm) on sampling days in July 1998. *White ovals* determine the sampling periods under clear sky, and *grey ovals* in cloudy weather, respectively. Values in the ovals indicate the number of sequential sampling occasions (Table 1)

UV radiation (UVB + UVA) during the VM study were estimated as a fraction (UV$_{sunny}$ = I×0.025, UV$_{cloudy}$ = I×0.036) of global radiation. The constants were achieved by comparing several contemporary ground-level measurements between UVR (PMA2111, Solar Light Company) and global radiation. As radiation is reflected and returned from clouds, comparisons were made separately for sunny and cloudy days because the relative proportion of UVR in global radiation is greater during overcast conditions than in sunny days (Madronich et al. 1995). As the visible range of the spectrum (PAR) covers approximately 50% of global radiation, we subtracted UV from global radiation level to have an indicator of PAR radiation above the pond. UV and PAR irradiance at the three study depths was calculated as a product of the ground-level radiation intensities of UV and PAR and a solar attenuation of UV and PAR in the study pond using an 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 depth z and just below the surface, respectively, and K_d is the vertical attenuation coefficient for downward irradiance. The vertical attenuation coefficient, $K_d(\lambda)$, was determined for UV and PAR wavebands, which were measured under bright sunshine in 5-nm intervals at 1615 hours on 28 July 2000 (submersible Macam Spectroradiometer SR-9910-PC). As 400 nm is the transition between UV and visible light, summed wavebands below 400 nm were used as a value for UV whereas measurements between 400 and 700 nm were summed to obtain a value for PAR. The obtained $K_{d, UV} = 3.42$ and $K_{d, PAR} = 0.70$ were used in the above equation. As only a global irradiance meter was accessible during the VM sampling, constant values of $E_d(0)$ were used to calculate the irradiance at the three study depths. $E_d(0)_{UV}$ and $E_d(0)_{PAR}$ were determined by comparing above and subsurface measurements for both UV and PAR from the spectral distribution of downward irradiance curves (Fig. 2). $E_d(0)_{UV} = 0.51×UV_{above}$ and $E_d(0)_{PAR} = 0.68×PAR_{above}$ were obtained. This method gives a usable but slightly robust estimate of UV radiation because the effect of solar angle could not be taken into account. The values for midday are therefore probably a slight underestimate, whereas the opposite is true for the values at morning and evening.

Data analysis

We used a linear-based direct ecological gradient analysis technique of redundancy analysis (RDA, ter Braak 1994) to identify which physical and biological factors influenced the vertical distribution of *D. longispina* in our study pond. RDA is a multivariate form of regression analysis (i.e. a multiple regression) for all species simultaneously with linear constraints on the regression coefficients, in which the species data are modelled as a function of the environment data. We decided to use RDA because of the limited range of variation in the response variables and the observed linear relationships between the response and predictor variables [analysed by detrended correspondence analysis, DCA, gradient length 1.2 standard deviation (SD) units]. In all RDA analyses, the abundance of the five life-history stages of the *Daphnia* population (neonates, juveniles, adults, gravid adults, adults with ephippia) were considered as response or dependent variables, whereas the physical (UV, PAR) and biotic (chlorophyll-*a*, *C. obscuripes* and Corixidae) variables were treated as predictor or explanatory variables. Temperature was not included in the analyses as it was measured only from surface and bottom. Multivariate analyses were performed on log-transformed [log (n + 1)] species values (standardized to a sample volume of 1 l) in order to reduce statistical noise in the data. A slightly reduced data set was used in the case of chlorophyll-*a* because the variable was not determined on all sample dates.

RDA was used first to identify a subset of environmental variables that explained statistically the greatest proportions in the species variation. This involved a series of constrained RDAs, in which species composition was constrained to only one explanatory variable at a time. The significance of each variable in explaining the variance in the *Daphnia* data was determined by testing the significance of the first ordination axis by means of a Monte Carlo permutation test (199 unrestricted permutations). Because many of the environmental variables in our data set are highly correlated with each other, the relative statistical strength and independence of each explanatory variable was assessed by performing a series of variance decomposition analyses by means of partial RDAs, in which the total variance in the *Daphnia* data was decomposed into fractions representing the unique and covariance contributions (Borcard et al. 1992). The analysis was done by constraining the first ordination axis to the environmental gradient of interest and by using other relevant parameters as covariables. All ordination analyses were done with the program CANOCO for Windows version 4.0 (ter Braak and Smilauer 1998). Earlier work has shown that the synthesis of photo-protective melanin pigment is induced when the dissolved organic carbon concentration declines below 3 mg l^{-1} (Rautio and Korhola 2002b). Thus it is probable that the response of zooplankton to UVR is not linear but instead there is a threshold value that triggers the different protection strategies. To test this idea, we divided the data set into two parts, sunny and cloudy days. Although the radiation values for cloudy and sunny days overlap slightly, we chose to separate them and argue that it is more relevant to do this than to try to estimate the actual ecologically important UV threshold for the studied pond.
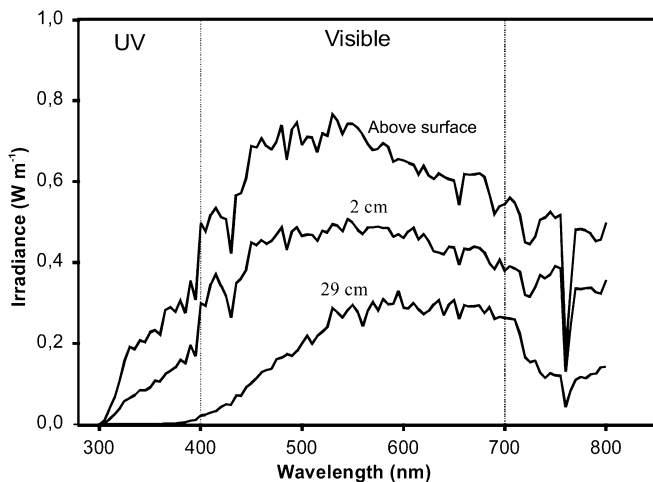

Fig. 2 The spectral attenuation of irradiance on 28 July at 1615 hours in bright sunshine

Results

The total density of *Daphnia* in the water column during different sampling occasions varied between 1.6 and 24.0 ind. l^{-1} (Fig. 3A). *Polyphemus pediculus*, *Streblocerus serricaudatus* and *Alona* sp. were found in some of the samples but they always formed <1% of the zooplankton community. The distribution of *Daphnia* in the water column varied both as a function of depth and weather. Under high ambient radiation, the *Daphnia* population avoided the surface (Fig. 3B) and the majority stayed in the middle of the water column around 25 cm or near the bottom (Fig. 3A). In contrast, on cloudy days, the largest proportion of the population was found in the uppermost layers of the water column. The only exception to this pattern was around midday on 10 July when the surface was
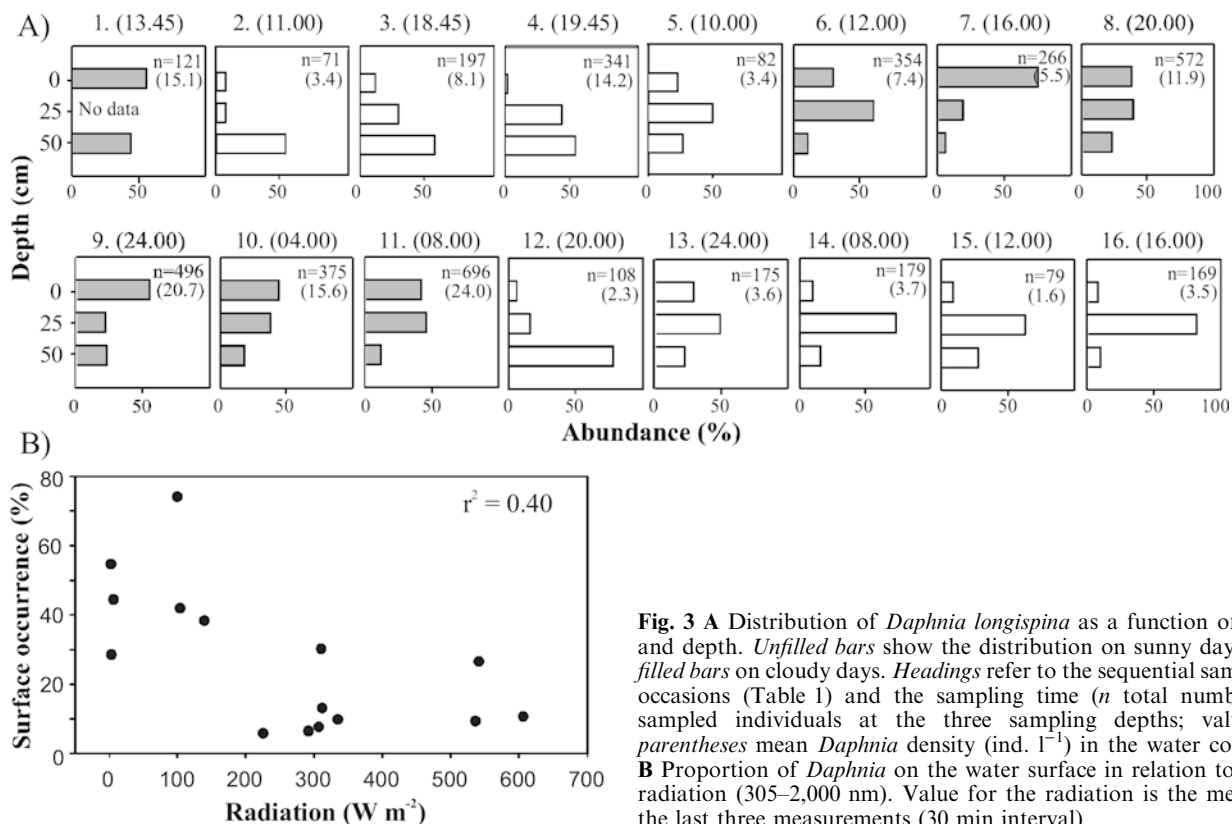
Fig. 3 A Distribution of *Daphnia longispina* as a function of time and depth. *Unfilled bars* show the distribution on sunny days and *filled bars* on cloudy days. *Headings* refer to the sequential sampling occasions (Table 1) and the sampling time (*n* total number of sampled individuals at the three sampling depths; value *in parentheses* mean *Daphnia* density (ind. l^{-1}) in the water column. B Proportion of *Daphnia* on the water surface in relation to total radiation (305–2,000 nm). Value for the radiation is the mean of the last three measurements (30 min interval)

avoided, just as on sunny days. Juveniles (neonates + juveniles) and adults (adults, gravid adults and adults with ephippia) did not differ in their vertical distribution in the water column in response to the measured environmental variables (RDA ordination, data not shown).

Radiation (305–2,000 nm) varied greatly between the studied days depending on the weather conditions (Fig. 1). On sunny days, the maximum values of total radiation were almost twice that of the cloudy days (350 vs 700 Wm^{-2}). During the night (2300–0400 hours), the radiation declined to nearly zero although the sky was never completely dark. Transmission of different wavelengths in the water column varied greatly (Fig. 2). While at 29 cm depth, nearly all UV wavelengths (305–400 nm) were extinguished, wavelengths of the visible spectrum were reduced by 60% only (Fig. 2). Changes in radiation intensities were reflected in the water temperature. Mean temperatures on sunny days were constant around 19–21°C, except for the first sampling occasion in early June. On cloudy days, the values declined, ranging from 13.6 to 20.3°C (Table 1).

The study site was characterized by two potential predators of *Daphnia*: *C. obscuripes* and Corixidae. *C. obscuripes* larvae avoided the surface on sunny days, like *Daphnia* (Fig. 4). Except for the evening of 9 July, the majority of the population stayed in the middle of the water column or close to the bottom during the sunny days. On cloudy days, the vertical distribution of *Chaoborus* was relatively even in the water column and

Table 1 Temperature and mean chlorophyll-*a* values ($\pm$SD) for the sampled three depths and different occasions. Concentrations of chlorophyll-*a* were highest near the bottom for all but one sampling occasion (occasion 11) when the maximum was close to the surface

Occasion	Date	Time (hours)	Weather	Temperature (°C)		Chlorophyll-*a*
				Surface	Bottom	
1	6/7	1345	Cloudy	13.7	8.5	No data
2	7/7	1100	Sunny	16.0	15.4	No data
3	7/7	1845	Sunny	20.7	20.1	No data
4	9/7	1945	Sunny	22.0	22.0	No data
5	10/7	1000	Sunny	20.0	19.6	1.7 ± 0.4
6	10/7	1200	Cloudy	20.8	16.6	2.3 ± 0.4
7	10/7	1600	Cloudy	20.5	19.5	1.9 ± 0.1
8	10/7	2000	Cloudy	19.0	19.0	1.3 ± 0.1
9	10/7	2400	Cloudy	18.0	18.0	No data
10	11/7	0400	Cloudy	16.6	16.4	No data
11	11/7	0800	Cloudy	15.4	15.4	1.1 ± 0.2
12	23/7	2000	Sunny	20.2	18.6	2.2 ± 0.4
13	23/7	2400	Sunny	19.0	18.9	2.7 ± 0.2
14	24/7	0800	Sunny	19.0	19.0	2.7 ± 0.5
15	24/7	1200	Sunny	20.0	19.6	2.6 ± 0.6
16	24/7	1600	Sunny	20.0	19.6	1.7 ± 0.1

none of the three studied depths was favoured. The number of Corixidae in the samples was low and all individuals encountered were from the bottom samples (Fig. 4). Chlorophyll-*a*, which was used as a rough measure of the food availability for *Daphnia*, was relatively evenly distributed in the water column, regardless of the weather or the time of the day (Table 1).
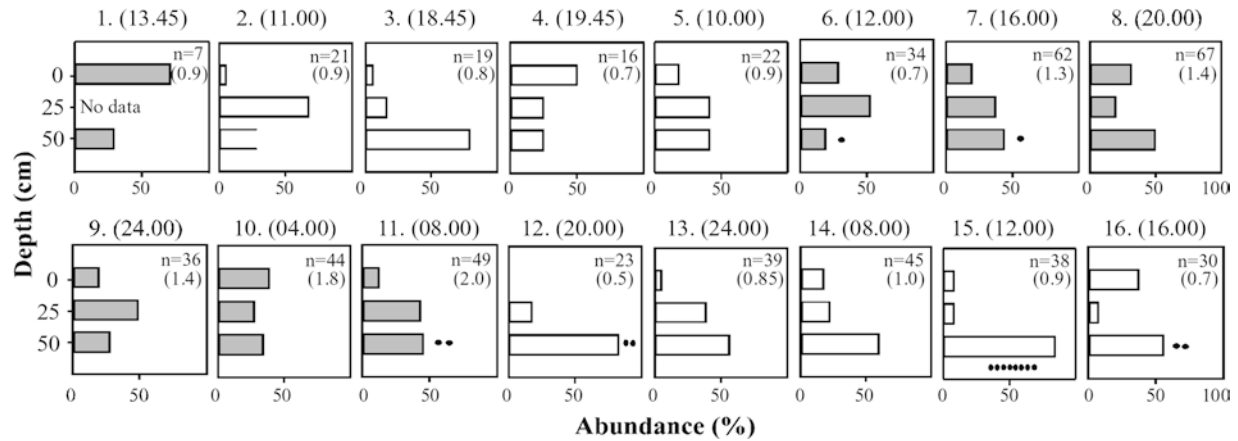
Fig. 4 Distribution of *Chaoborus obscuripes* and Corixidae as a function of time and depth. *Chaoborus* distribution is shown in *bars* (for further explanation see Fig. 3A) and Corixidae in *dots*. Each *dot* indicates one corixid

Table 2 Percent variance explained by Monte Carlo permutation tests (199 unrestricted permutations) in a constrained RDA of the *Daphnia* data where each predictor variable is used as the sole constraining variable at a time. Statistically significant ($P < 0.05$) explanatory variables are indicated by an *asterisk*

Variable	Variance explained (%)	P
Sunny days		
UV	19.6	0.020*
PAR	5.6	0.330
Chaoborus	1.0	0.885
Corixidae	1.2	0.935
Chlorophyll-*a*	20.8	0.130
Cloudy days		
UV	2.0	0.725
PAR	14.7	0.060
Chaoborus	20.7	0.025*
Corixidae	0.9	0.940
Chlorophyll-*a*	0.5	0.955

In order to test which environmental variables influenced most significantly the distribution patterns of *D. longispina*, a series of explanatory RDAs and associated Monte Carlo permutation tests were carried out on each predictor variable separately (Table 2). When interpreting these results, one should keep in mind that instead of looking at the percentages of variance accounted, the more important tests are the associated permutation tests, which demonstrate which of the measured variables make a statistically significant contribution to the explained variance. The analyses revealed that, on sunny days, only UV explains a statistically significant portion (19.6%, $P < 0.020$) of the variance in the *Daphnia* data, whereas on cloudy days, *Chaoborus* (20.7%, $P < 0.025$) was clearly the most powerful predictor variable.

We also calculated the variance that can be uniquely attributed to the relevant predictor variables (as determined by constrained RDA), with a series of partial RDAs (Table 3). Here again, on sunny days, only UV explains the statistically significant portion of the variance in the *Daphnia* data, as determined by a constrained RDA (Table 2). When the effects of all other predictor variables are partialled out (taken as covariables), UV still makes a significant, unique contribution of 29.9% to the *Daphnia* data, whereas other variables explain a non-significant proportion of 23.8% after adjustment for UV (Table 3). In contrast, *Chaoborus* explains a statistically significant amount of variation in the *Daphnia* distribution on cloudy days only.

Discussion

In the subarctic pond we studied, *Daphnia* distribution in the water column was found to vary considerably between different sampling times. Under high radiation, the *Daphnia* avoided the surface, whereas under low radiation most of the population stayed close to the surface. In this study, we tried to identify the ultimate cause for this behaviour. Frequent changes in the intensity of visible light are accepted as the primary cue for zooplankton VM (e.g. Ringelberg 1991). The ultimate purpose of this behaviour is to improve individual fitness by either escaping deleterious conditions such as heavy predation or high UV exposure, or to take advantage of zones with better resources, such as food availability or temperature (Enright 1977; Gliwitcz 1986; Neill 1990). In the pond we studied, the entire water column was illuminated for 24 h a day. Thus there were no refugia against visual predation for *Daphnia* in the open-water area. Sampling in areas of vegetation and those of open water did not reveal differences in the numbers of *Daphnia* (data not shown). We concluded from this that *Daphnia* did not hide between water plants from visual predators. In our pond, *Chaoborus* are the principal *Daphnia* predator. They are known to cause a migration response in zooplankton (Kleiven et al. 1996; Nesbitt et al. 1996) although their feeding strategy is primarily tactile and not visual. Thus, response to visible light was not a meaningful strategy to avoid predation by *Chaoborus* on *Daphnia*. This suggests that *Daphnia* may have used predator kairomones as

Variable	Covariables	Variance explained (%)	P
Sunny days			
UV	PAR, *Chaoborus*, Corixidae	29.9	0.006
PAR, *Chaoborus*, Corixidae	UV	23.8	0.115
Cloudy days			
Chaoborus	UV, PAR, Corixidae	6.6	0.020

indicators of *Chaoborus* location instead of light cues. On cloudy days, *Daphnia* often stayed closer to the surface than *Chaoborus*, in agreement with findings by Nesbitt et al. (1996). On sunny days, such a difference was not detectable as *Daphnia* moved downward in the water column, closer to the maximum density depth of *Chaoborus*. The predation pressure of *Chaoborus* is usually higher on neonates and juveniles than on adults, whose large size provides protection against *Chaoborus* attacks (Repka and Walls 1998; Riessen 1999). Therefore we expected young *Daphnia* to avoid water layers with a high density of *Chaoborus* more than adult *Daphnia*. However, the whole population of *Daphnia* was distributed in the water column in a similar manner both on sunny and cloudy days. Further experiments in ponds with and without *Chaoborus* are needed before concluding that *Chaoborus* distribution predicts *Daphnia* distribution. Other predators in the system we studied, water boatmen, did not have any effect on *Daphnia* vertical distribution. They were found in low numbers in the samples (Fig. 4) and, furthermore, preferred fairy shrimps (*Polyartemia forcipata*, Anostraca) to *Daphnia* (unpublished data) as prey items. We suggest that, during high radiation intensity, UV levelled out the *Chaoborus* predation effect or any other ecologically important effect on *Daphnia* vertical distribution by forcing *Daphnia* to move downward from the brightly lit surface.

Studies by Smith and Macagno (1990) and Storz and Paul (1998) have shown that photoreceptors of *Daphnia* peak in the UV range at 340 nm. Hessen (1994) also suggested that UV detection is possible in *Daphnia* by showing an immediate downward migration response when animals were exposed to UV radiation. Our field data suggest that, on sunny days, *Daphnia* may be using ultraviolet radiation as a proximate cue to avoid the harmful surface waters. Similar indications of zooplankton UV-inhibition in natural habitats have been observed before (Hessen 1993; Tartarotti et al. 1999) although some studies indicate that UV does not play any role in inducing VM (Bollens and Frost 1990). Our data agree with the recent findings of Rhode et al. (2001) and Leech and Williamson (2001) who showed *Daphnia* responding to UV exposure with downward migration.

In humic waters, the harmful effects of UVR can result for reasons apart from direct "sunburn" effects. Despite their roles in quenching UV radiation, dissolved organic carbon and humic substances can also create an acute chemical stress in the UV-irradiated surface zone in humic waters. Toxic photochemical products such as reactive oxygen species (ROS) are formed by exposure of

humic waters to UV (Cooper and Lean 1989; Shtamm et al. 1991). In our earlier paper (Rautio and Korhola 2002a) we showed that, under experimental conditions, the same *Daphnia* population of this study suffered from rapid mortality in shallow humic water (DOC > 10 mg l^{-1}) when exposed to natural levels of UV radiation. Humic substances also effectively absorb heat, leading to the formation of a thermally stratified layer that prevents dilution of ROS with the rest of the water column. Even in shallow ponds, where periodic wind events may mix the whole water column, short-term thermoclines may be formed in calm periods. However, in our study the temperature measurements were not fine-scaled enough for detection of any such thermoclines (0.1° intervals).

Another recent study by Rautio and Korhola (2002b) showed that in subarctic ponds in Finnish Lapland, *Daphnia* were present only if the DOC concentration was > 5 mg l^{-1}. Despite this high concentration of UV-screening DOC, these *Daphnia*, including the population from this study, were also pigmented with UV-absorbing melanin. This indicates that UV-protection mechanisms are required even in brown waters with high DOC concentrations. Since melanin does not provide protection against ROS, these must be avoided by escape from areas of high accumulation. Therefore the abundance of ROS may play a role in inducing downward movement of *Daphnia* in the water column during calm sunny days. However, wind is a very prominent factor at the studied pond site.

In summary, results of the partial RDAs (Table 3) show that on sunny days the largest amount of the variation in the *Daphnia* data (29.9%) is explained by UV alone. The analysis further suggests that the variance explained by UV is not conditional on other variables. Thus we conclude that UV is the most important factor affecting *Daphnia* distribution on sunny days. On cloudy days with low UV intensities, predation (*Chaoborus*) largely determines the distribution patterns of *Daphnia*. The cloudy-day results suggest that VM may be a general adaptive response used to avoid the effects of either predation or UV. We therefore propose that *Daphnia* VM behaviour in our system is a result of two fundamentally different factors, a biological one (predation) and a physical one (UV-induced damage). The relative importance of these two factors to *Daphnia* distribution changes depending on ambient UV levels (i.e. sunny vs cloudy conditions), the net effect being to minimize the negative impacts of both. Carefully designed factorial experiments that control both predator and radiation cues are needed to assess the ultimate cause of the vertical

distribution patterns of zooplankton. However, data sets from natural environments are still important and useful, and multivariate analyses provide a powerful tool for an interpretation of this type of data.

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