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In situ exposure to ultraviolet radiation alters the depth distribution of *Daphnia*

Abstract—Damaging solar radiation was one of the first factors proposed to explain zooplankton diel vertical migrations (DVM), yet other factors such as temperature, food, and especially predation have typically been more widely studied and identified as the primary factors inducing DVM. This is true in spite of the fact that recent experiments have shown that ambient levels of solar ultraviolet radiation (UVR) are potentially lethal to zooplankton and negative phototactic behavior has been demonstrated in the laboratory. Here we present the first evidence from in situ experiments demonstrating that UVR wavelengths influence the vertical swimming behavior of zooplankton under full spectrum solar radiation. Cylindrical acrylic columns that transmitted or blocked UVR were used to examine the behavioral responses of *Daphnia pulex* to UVR. Experiments were conducted in the epilimnion of a high-UV system at midday and in late afternoon. In both experiments, a large proportion of individuals migrated downward in the presence of UVR, whereas those in the UVR-shielded treatments tended to remain closer to the surface.

The water column of lakes and oceans can be thought of as a vertical habitat gradient that varies in many abiotic and biotic factors including temperature, light, food, and predation. Although all of these factors contribute to the vertical distribution of organisms, migrations that involve daily changes in vertical distribution are generally connected with factors that vary on a diel basis, such as light and predation. Some of the earliest works on diel vertical migration (DVM) demonstrated that sunlight was a potential proximate as well as ultimate factor inducing migrations. Both negative phototactic behavior (Moore 1912) and increased mortality rates were observed in freshwater and marine organisms exposed to ultraviolet radiation (UVR) (Huntsman 1924; Klugh 1930).

In spite of this evidence for the potential importance of

sunlight in small-scale experimental studies, no field studies were conducted to demonstrate a clear link between damaging solar radiation and zooplankton migration patterns in nature. In addition, although most investigators agree that multiple factors are important in inducing DVM, damaging light has been given little attention in comparison to other factors, such as temperature, food availability, and especially predation (Haney 1988; Kerfoot 1985; Lampert 1989).

Both intensity and spectral composition of light have been shown to be important in the vertical migration and associated behavioral responses of zooplankton. For example, a strong relationship has been demonstrated between lake transparency and the magnitude of *Daphnia* vertical migrations in nature (Dodson 1990). Laboratory experiments with polychromatic light have demonstrated that cladocerans are negatively phototactic to short-wavelength blue light but positively phototactic to long-wavelength red light (Smith and Baylor 1953). These “color dances” were hypothesized to cue zooplankton to high concentrations of algal food but were also thought to influence DVM. More recent studies with monochromatic light have demonstrated that *Daphnia magna* are positively phototactic to visible light (420–600 nm) and negatively phototactic to UVR (260–380 nm) with maximal sensitivity at 340 nm (Storz and Paul 1998). In addition to these laboratory experiments, field studies have shown that just a few days exposure to natural levels of solar UVR in the surface waters of lakes can be lethal to zooplankton (Williamson et al. 1994).

The combined results of these studies strongly suggest the potential role of damaging solar UVR in influencing diel vertical migration behavior in UVR sensitive organisms; however, no studies have directly examined the role of UVR as a proximate factor of DVM in the presence of full spectrum solar radiation. The contrasting responses of *Daphnia*

to visible and UV components of the spectrum in the laboratory leave open the question of the direction of vertical migration responses to natural sunlight. In particular, what is the role of the shorter wavelength damaging UVR? Here we present the results of an in situ study in which we manipulated UVR in the presence of full spectrum solar radiation and quantified the vertical swimming responses of *Daphnia pulicaria*.

Preliminary experiments were first conducted to observe the vertical swimming response of *Daphnia* under manipulated solar radiation. This study took place in Dutch Springs Reservoir, Bethlehem, Pennsylvania (40.6°N, 75.4°W), an oligotrophic, high-UV system with a dissolved organic carbon concentration of 1.5 mg L⁻¹ and a summer secchi depth of 6–7 m. At the time of the experiments, *Daphnia* were exhibiting a nocturnal migration, with individuals absent from the surface waters during the day but present at night. The fish community of the reservoir includes both planktivorous and piscivorous fish such as *Lepomis macrochirus*, *Salmo* spp., *Cyprinus* sp., and *Micropterus salmoides*.

Two cylindrical acrylic columns (7.6 cm diameter × 4 m depth) were placed in the water column of Dutch Springs Reservoir. One column was constructed of a UV-transparent acrylic (UVT, Spartech, formerly Townsend/Glasflex) that had a 50% transmittance at approximately 287 nm (curve rising from 0.32% transmission at 257 nm to 91% transmission at 400 nm, with a small dip in the curve from approximately 300–400 nm). The other column was made of a UV-blocking acrylic (“extruded,” Thermoplastic Processes) with 50% transmittance at approximately 387 nm (curve rising from 0.31% transmission at 345 nm to 90% transmission at 412 nm). Columns were sealed at the ends with a flat sheet of acrylic that was also either UV transparent (OP-4, CYRO) or UV blocking (OP-2, CYRO). (Detailed spectral scans of the acrylics are available from the authors upon request.)

To determine the total energy transmitted by each acrylic column within the UV to PAR range, the transmittance spectrum of each was multiplied by a modeled solar irradiance spectrum for the day and location of the experiment. The transmittance of the acrylic columns was determined in the laboratory using a scanning UV-1601 Shimadzu spectrophotometer from 200 to 800 nm. Solar irradiance spectra for 295–800 nm were generated using the RTransfer95 model developed by R. Booth at Biospherical Instruments. This model generates irradiance based on date, latitude, longitude, and ozone levels, as well as several other important factors. These modeling efforts indicated that the UV-blocking columns transmitted 7–8% less solar energy than the UV-transmitting columns at the water surface. If infrared wavelengths were included, this number would be approximately cut in half. In addition, this percentage will decrease exponentially with depth as the lake water and the dissolved and particulate substances in it selectively attenuate the UV portion of the spectrum.

Experiments were conducted at midday and late afternoon on 22 June 1999. Columns were filled with unfiltered lake water and were suspended from a wooden rack approximately 15 cm from the surface near the center of the lake. *Daphnia pulicaria* were collected from the lake with a single

Table 1. Percent of surface irradiance (E_d) at 1.5 m, attenuation coefficients (K_d), and $Z_{1\%}$ attenuation depths (depth to which 1% of surface irradiance penetrates) for 305, 320, 340, 380 nm and PAR for Dutch Springs Reservoir, Bethlehem, Pennsylvania. Irradiance measurements were taken on 30 June 1999 with a profiling ultraviolet radiometer (PUV) near the center of the lake. $Z_{1\%}$ attenuation depths were estimated from epilimnetic K_d data.

	Wavelength (nm)				
	305	320	340	380	PAR
Percentage of surface E_d at 1.5 m	30	48	65	68	69
K_d	1.00	0.65	0.35	0.29	0.25
$Z_{1\%}$ (m)	5	7	13	16	19

deep tow of a 363- μ m plankton net and were introduced to the top of each column. Individuals were allowed to migrate freely throughout the length of the columns while visual observations were carefully made of their distributions with SCUBA and snorkeling. During both time periods, *D. pulicaria* were observed to migrate rapidly to the bottom of the column in the presence of UVR; however, in the absence of UVR, individuals migrated downward more slowly with many remaining closer to the surface. These striking differences in the distributions of individuals in the presence and absence of UVR led us to do further experimentation using traps placed inside the columns.

The design of the columns was modified from Leibold and West (1993). Three replicate columns were constructed for each light treatment using the same acrylics as described above. Each acrylic column was divided into three 0.5-m sections (total length = 1.5 m) separated by conical traps, or funnels, with a 0.5 cm opening. Funnels permitted unidirectional downward migration and were constructed of UV-transparent cellulose acetate to avoid UV shading. Columns were assembled by taping alternating sections and funnels with UV-transparent, waterproof polyethylene tape. An additional funnel leading to a small collecting cup was placed at the bottom of each column to determine the percentage of animals that would migrate deeper than 1.5 m. Longer columns proved to be more difficult to disassemble in the field and increased the time it took to take down an experiment.

Two experiments were conducted on 30 June 1999 in Dutch Springs Reservoir. The weather was partly cloudy to overcast with an air temperature of 35°C and a surface water temperature of 24.5°C. PAR irradiance was measured at the surface with a LiCor L-I1905A quantum sensor. At solar noon, or 1300 h, PAR irradiance was 1740 μ mol m⁻² s⁻¹. At 1630 h, PAR was 669 μ mol m⁻² s⁻¹, which is equivalent to 38% of the total irradiance at solar noon. Underwater light profiles of UVR and PAR were taken from the surface to 4 m with a Biospherical Instruments PUV 501B at midday and late afternoon (Table 1). Both of these measurements were used to characterize the optical properties of the epilimnion.

Daphnia pulicaria were collected with a single deep tow using a 363- μ m plankton net from 15 m to the surface. Organisms were placed in a 1-gallon polyethylene container that was placed in a cooler until needed. Experiments were

conducted between 1310–1340 h and 1630–1700 h. At the beginning of each experiment, the columns were filled with unfiltered lake water, and a 300-ml aliquot of zooplankton sample (approximately 100–150 individuals) was introduced to the top of each column. UV+ and UV– columns were filled alternately to avoid sample bias. Once loaded, the columns were then suspended from a floating rack near the center of the lake, approximately 15 cm from the surface. Animals were allowed to migrate downward for 30 min. This incubation time was determined during the preliminary experiments. Dramatic differences in distribution between UV+ and UV– columns could actually be seen within 10–15 min within longer (4 m) columns. This time was doubled to determine whether a response could still be detected in a shorter column. At the end of the 30-min incubation, each column was inverted 180° to prevent further downward migration, and the contents of each section were immediately emptied into a pre-labeled sample cup through a 1.4 cm opening in each section that was sealed with a silicon stopper. Samples were preserved in a 4.5% sucrose-formalin solution.

The total number of individuals in each section of each column was counted under a dissecting microscope in the laboratory. The percentage of *Daphnia* in each section of each replicate was then calculated for both treatments in each experiment. The mean depth of *Daphnia* in each column was determined by multiplying the number of *Daphnia* in each section of a column by the average depth of that section (e.g., 0.25 m for 0–0.5-m section). Organisms in the >1.5-m sections were multiplied by 1.5. These values were then summed and divided by the total number of individuals in the column to determine the mean depth of all *Daphnia* in each column. A two-way ANOVA was performed using Systat to test for significant differences in the mean depth of *Daphnia* in the UV+ and UV– columns at midday versus late afternoon. Because one of the >1.5-m section replicates from the UV– treatment was lost in the field, the data set was unbalanced ($df = 7$).

Results were similar to those found in the preliminary experiments. The mean depth distribution of *D. pulicaria* differed significantly between the UV+ and UV– treatments ($F = 16.7$, $df = 1,7$, $P = 0.005$). In the presence of UVR, the majority of individuals were found in the lower portion of the columns, whereas those in the UVR-shielded treatment tended to remain closer to the surface (Fig. 1). Mean depth of *Daphnia* in the UV+ and UV– treatments did not differ with time of day ($F = 0.006$, $df = 1,7$, $P = 0.942$) nor as an interaction of time by UV treatment ($F = 0.583$, $df = 1,7$, $P = 0.470$).

The present study provides the first evidence of a vertical response of *Daphnia* to UVR in nature under full spectrum solar radiation. In columns both with and without funnels, a stronger negative phototactic response was detected in the presence of UVR than in the absence of UVR. Differences in migration patterns observed in the presence versus the absence of UVR are unlikely to be related to the quantitative differences, or energy transmission, in the acrylics. These differences were only 7–8% within each experiment. Differences in irradiance between the two experiments were far greater (62% reduction from midday to late afternoon), and

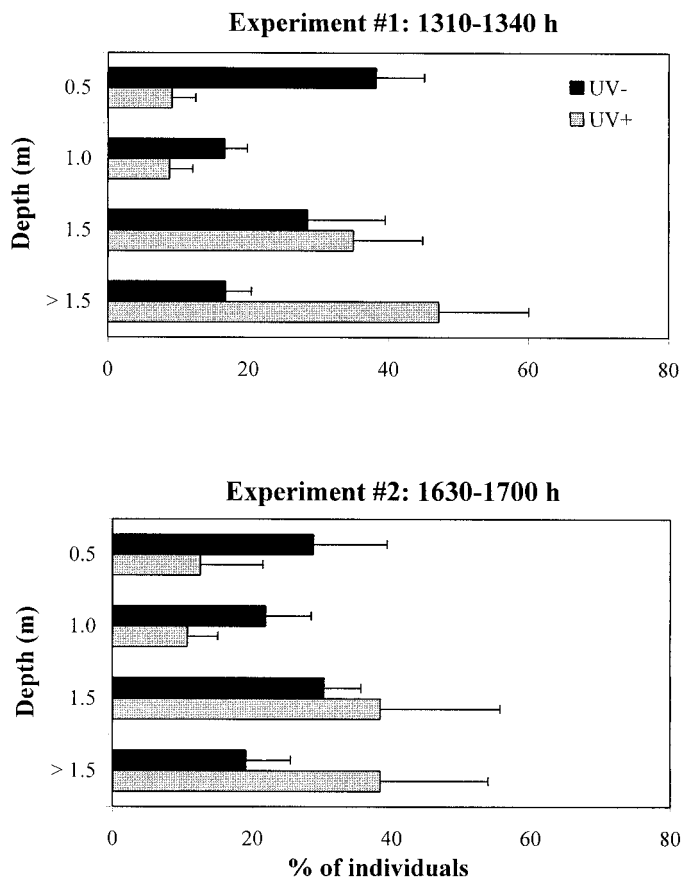


Fig. 1. The vertical distribution of *Daphnia pulicaria* in the presence and absence of UVR. The mean percentages of *Daphnia* in each section of the columns are reported for both experiments at midday and late afternoon. There were three UV-transmitting columns and three UV-shielding columns with approximately 100–150 individuals introduced to each. Error bars represent the standard errors. Experiments were conducted in Dutch Springs Reservoir, Bethlehem, Pennsylvania on 30 June 1999.

yet similar migration patterns were observed. An alternate explanation is that *Daphnia* swam faster in random directions in the presence of UVR, and the unidirectional funnels ultimately resulted in more animals at deeper depths. However, similar results were found using columns without funnels in which *Daphnia* could move freely throughout the length of a 4-m column.

During this study, *Daphnia* were not found in the surface waters during the day but did migrate upward into the surface waters at night. Given that there are fish present in this system, predation is likely to be a driving force in inducing migrations. However, it is interesting that in our study *Daphnia* remained in the surface waters during the day in the absence of UVR in spite of the likely high kairomone concentrations in the untreated whole lake water.

Daphnia are known to detect UVR. UV photoreceptors have been reported in the compound eye of *Daphnia magna* with peak sensitivity at 348 nm (Smith and Macagno 1990). In addition, many laboratory studies have demonstrated negative phototaxis in *Daphnia* in response to potentially damaging UV wavelengths (Moore 1912; Smith and Baylor

1953; Storz and Paul 1998). Rapid downward swimming was invoked in *Daphnia pulex* when exposed to an artificial, broadband UV light source from above (Hessen 1994), and similar UVR avoidance behavior was detected in the marine echinoid larvae, *Dendraster excentricus* (Pennington and Emler 1986). Based on these results, as well as those of the present study, UVR appears to be a potentially important proximate cue for DVM.

UVR is also known to be lethal to both freshwater and marine zooplankton, which suggests that UVR may also be an ultimate cause of DVM (Ringelberg 1999; Storz and Paul 1998). Both laboratory and field experiments have demonstrated that increased exposure to UVR leads to a decrease in survival as well as a decrease in growth and reproduction in both freshwater and marine zooplankton (Karanas et al. 1979; Siebeck et al. 1994; Williamson et al. 1994; Zagarese et al. 1994). *Daphnia* in particular has a low tolerance to UVR when compared to other taxa (Leech and Williamson 2000). The downward migrations of *Daphnia* in the presence of UVR may therefore be a response to damaging solar radiation.

The negative phototactic behavior detected in *Daphnia* appears to be wavelength dependent. Although both UV-B and UV-A can be damaging, UV-B (280–320 nm) is generally more damaging than UV-A radiation (320–400 nm). Interestingly, the UV photoreceptors in *Daphnia* peak in the UV-A range (approx. 340 nm) (Smith and Macagno 1990; Storz and Paul 1998). If *Daphnia* are cueing to UV-A wavelengths that penetrate more deeply into the water column, they would be protected from potentially more damaging UV-B light found closer to the surface. A vertical response of *Daphnia* to UV-A wavelengths is also of interest because of the possible link to predation. Many species of larval fish have retinal cones that perceive UV-A light (350–370 nm) and are thought to help larvae locate and capture their prey (Loew et al. 1993; Browman et al. 1994). *Daphnia*'s response to UV-A wavelengths may therefore also be a means of predator avoidance in the surface waters. In this case, predation may be the ultimate cause of DVM but UV-A light would be the proximate cue.

In systems with low concentrations of dissolved organic carbon, UVR may penetrate deeply into the water column (Morris et al. 1995). In 25% of lakes in several regions of North America, 1% attenuation depths (depth to which 1% of surface irradiance penetrates) were estimated to be greater than 4 m for 320 nm UV-B and greater than 10 m for 380 nm UV-A (Williamson et al. 1996). This is similar to the UVR transparency of Dutch Springs Reservoir (Table 1). UVR may be present up to 25 m depth in clear marine waters (Fleischmann 1989), and signs of increased levels of UV-B radiation entering the oceans are apparent as stratospheric ozone is depleted (Kerr and McElroy 1993).

Based on the results of the present study, *Daphnia* appear to be responding to these natural levels of UVR. Under full spectrum solar radiation, *Daphnia* were found to be negatively phototactic to UVR in spite of the presence of longer wavelength PAR to which they are known to respond with positive phototaxis (Storz and Paul 1998). However, it may be that in Dutch Springs light intensities were too great to invoke positive phototaxis. Contrasting intensity- and wave-

length-dependent phototactic responses in zooplankton are of great interest due to their potential to impact distribution and migration patterns. For example, the spectral composition of underwater solar radiation may vary greatly during different times of day, year, or with changes in DOC, aerosols, cloud cover, or other environmental factors. It is likely that these intensity- and wavelength-specific responses will also interact with predation and other important selective pressures. We are currently investigating how phototactic responses to UVR interact with predation and other factors known to be important in DVM.

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Identification of a natural desferrioxamine siderophore produced by a marine bacterium

Abstract—Desferrioxamine B (DFOB, a terrestrial bacterial siderophore) has been used in experiments on waters from iron-replete areas of the oceans to manipulate the levels of iron available to the biota. Addition of DFOB complexes the available iron (III) and has been suggested to render this complexed iron unavailable to marine microorganisms. We have identified a marine bacterium belonging to the genus *Vibrio* that produces the siderophore desferrioxamine G. Desferrioxamine G, another known terrestrial siderophore, is very similar in structure to DFOB, differing only by the substitution of a terminal methyl group by a propionic acid moiety. These results could affect the interpretation of DFOB iron-removal experiments and further suggest that addition of DFOB might not impose iron stress uniformly across the biological community.

Iron is arguably the most important transition metal ion for living systems. Although iron is one of the most abundant crustal elements, Fe (III) is highly insoluble in aerobic aqueous conditions, making iron acquisition difficult for microorganisms. The difficulty of iron acquisition is further compounded for marine organisms, since total iron concentrations in surface seawater are 20 pM to 1 nM with >99% of the dissolved iron complexed by organic ligands (e.g., Rue and Bruland 1995; Wu and Luther 1995). This low level of iron is known to limit primary production by phytoplankton in regions characterized by high levels of nitrate and low levels of chlorophyll (HNLC regions) such as the subarctic Pacific, equatorial Pacific, Southern Oceans, and certain

coastal upwelling regions (e.g., Coale et al. 1996; Boyd et al. 2000). HNLC regions of the ocean are rich in nutrients for phytoplankton such as phosphate, nitrate, and silica; however, phytoplankton growth is depressed in these areas. To test the hypothesis that the low iron concentration limits primary production, IronEx experiments were carried out by seeding surface waters with low concentrations of dissolved iron (e.g., Coale et al. 1996). These iron addition experiments provided strong evidence for iron limitation of biological productivity in areas with low levels of iron (0.05 to 1 nM). Iron may also influence community structure and primary production in iron-replete waters (Wells 1999). Consequently, iron-removal experiments have been completed by addition of desferrioxamine B (DFOB) to seawater samples to complex Fe (III) (Hutchins et al. 1999; Wells 1999). The addition of desferrioxamine B to seawater from certain iron-replete regions in on-deck experiments causes a decrease in iron availability to both phytoplankton and heterotrophic bacteria and makes the sample artificially iron limited. Iron removal via DFOB addition is a valuable complement to Fe addition experiments because it can induce differing levels of iron stress in natural populations without affecting the availability of other bioactive metals.

Desferrioxamine B is a siderophore commonly produced by terrestrial bacteria (Keller-Schierlein et al. 1965). Siderophores are low molecular weight compounds that typically have very high affinity constants for ferric ion (10^{25} – 10^{50}). The role of siderophores is to scavenge extracellular iron from the environment and transport it into microbial cells.