

IS TOLERANCE TO UV RADIATION IN ZOOPLANKTON RELATED TO BODY SIZE, TAXON, OR LAKE TRANSPARENCY?

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Abstract. Solar ultraviolet radiation (UVR) has been demonstrated to have damaging effects on zooplankton, but little is known about what factors influence UVR tolerance in nature. Here we examined the relationship between UVR tolerance (the sum of photoprotection and photorepair processes) and zooplankton taxon, body size, and source lake UVR transparency. Zooplankton of various sizes and taxa from lakes of different UV transparency were exposed to different intensities of a constant artificial UVR source. UVR tolerance was expressed as the UVR dose at which 50% mortality was observed for a given species. Smaller zooplankton species showed a uniformly high UVR tolerance, while larger zooplankton varied in their UVR tolerance both among and within species. The smaller rotifers, *Keratella* in particular, showed a high UVR tolerance while the larger, more transparent rotifer (*Asplanchna*) showed an intermediate UVR tolerance. Both cyclopoid and calanoid copepod adults were more highly tolerant of UVR than nauplii. Late-instar larvae of the predatory insect *Chaoborus* were more UVR tolerant than earlier instars. UVR tolerance showed no relationship to the UVR transparency of the source lake. Differential UVR tolerances among zooplankton taxa may alter community and ecosystem structure and function during anticipated changes in underwater UVR environments.

Key words: diel vertical migration; lake transparency; ultraviolet radiation; zooplankton.

INTRODUCTION

Decreases in stratospheric ozone over temperate, as well as polar latitudes, have resulted in increased amounts of UV-B radiation reaching the Earth's surface, with potentially negative effects on natural ecosystems (Kerr and McElroy 1993, Madronich 1994). While substantial advances have been made in our understanding of the effects of UVR on phytoplankton in both freshwater and marine systems (Prezelin 1986, Smith et al. 1992, Moeller 1994, Cullen and Neale 1997), less is known about the effects of ultraviolet radiation (UVR) on zooplankton and higher trophic levels. Solar radiation has been demonstrated to be damaging to zooplankton, as well as to fish eggs and larvae, with a high degree of variability in UVR tolerance both within and among taxa (Siebeck et al. 1994, Williamson et al. 1994, 1997). The reasons for this variability are not well understood.

Organisms at higher trophic levels in aquatic systems have three options for reducing the negative impacts of high UVR that might contribute to the observed variability in UVR tolerance within and among taxa (Zagarese and Williamson 1994). They can reduce exposure to UVR through behavioral avoidance, reduce damage during exposure to UVR through the use of photoprotective compounds, or repair DNA damage during and following exposure to UVR with photoenzymatic repair (PER). Another way to view this is that

organisms can minimize the negative impacts of UVR damage if they have either a high UVR "tolerance" (which we define as the sum of all photoprotection and photorepair processes) or the ability to behaviorally avoid being exposed to high UVR. Here we examine the UVR tolerance of several taxa of zooplankton relative to their body size and the transparency of the UVR environment in which they were collected. Zooplankton body size and lake transparency are related through the diel vertical migration of zooplankton in response to size-selective predation and the anticipated differences in UVR exposure of zooplankton of different body sizes.

Both light and predation are important factors regulating zooplankton abundance and distribution. One of the most widely recognized responses to light and predation is the phenomenon of diel vertical migration (DVM). Light is often recognized as the proximate cause of DVM, although there is some evidence of damage to zooplankton from shorter wavelength solar radiation (Hairston 1976, Williamson et al. 1994). Predation, on the other hand, is well established as both a proximate and an ultimate factor affecting zooplankton abundance and distribution (Kerfoot 1985, Haney 1988, Lampert 1989). Visual predators use light to forage and to selectively consume larger zooplankton prey (Zaret 1980). In response to this, large zooplankton exhibit strong migrations to deeper, darker depths during the day. Smaller zooplankton, in turn, remain in the surface waters during daylight and migrate to the deeper waters at night to avoid predation or interfer-

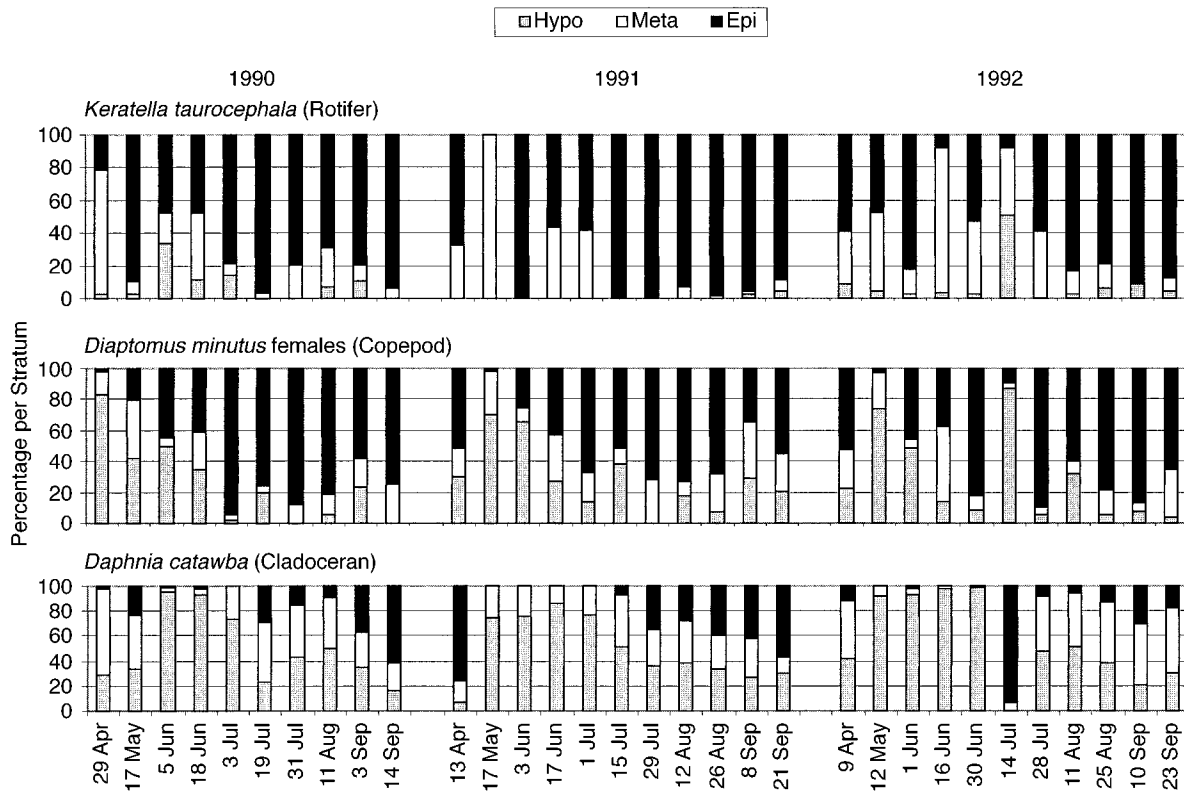


FIG. 1. Mean percentage of population in the epilimnion of Lake Giles for the most abundant species of cladocerans (*Daphnia catawba*), copepods (*Diaptomus minutus*), and rotifers (*Keratella taurocephala*) from April through September. Mean percentages were determined by analyzing a 3-yr (1990–1992) zooplankton database which contains extensive data on zooplankton seasonal and vertical distribution and abundance. Wisconsin bongo-style closing nets (202- μ m and 48- μ m mesh nets) were used to collect the organisms on a biweekly (when temperatures were $>20^{\circ}\text{C}$) to monthly (when temperatures were $<20^{\circ}\text{C}$) basis. The closing mechanisms allowed for separate sampling of the epi-, meta-, and hypolimnion. The depth range of each stratum was determined using a YSI 57 model dissolved oxygen and temperature meter (Yellow Springs Instrument Company, Yellow Springs, Ohio). A change of $>1^{\circ}\text{C}/\text{m}$ depth was used to demarcate the metalimnion. After collection, organisms were preserved in a 4.5% sucrose formalin solution. *D. catawba* were counted from the 202- μ m mesh net samples. *D. minutus* females and *K. taurocephala* were counted from the 48- μ m mesh net samples. The total number of individuals in each stratum was added to determine the number of individuals of each species in the total water column. From this information, the percentage of individuals in each stratum was calculated and plotted as a stacked bar graph.

ence by larger zooplankton (Neill 1990, Ohman 1990, Williamson and Stoeckel 1990). These daytime vertical distribution patterns can be seen clearly in representative species from Lake Giles (Fig. 1). In lakes without visual planktivores, DVM may be absent, and large and small zooplankton are expected to overlap more in time and space. The predation-induced DVM patterns in lakes with visual planktivores cause smaller zooplankton to be more exposed to potentially damaging UVR than larger zooplankton, especially in high UVR systems (Fig. 1).

Based on these relationships between predation, DVM, and lake UVR transparency, we predict that UVR tolerance in zooplankton will be related to body size. From this prediction, two central hypotheses arise (Fig. 2). First, in high UVR lakes with visual predators (fish), tolerance to UVR damage will be inversely related to zooplankton body size. Because smaller zooplankton occupy the surface waters during daylight in

avoidance of invertebrate predators, they are more likely to receive greater UVR exposure than larger zooplankton that occupy the darker, deeper depths. Prior UVR exposure may lead to increased UVR tolerance in these smaller zooplankton. Second, in high UVR lakes without visual predators, zooplankton UVR tolerance will be higher for all body sizes than the UVR tolerance of zooplankton inhabiting low UVR lakes with or without visual predators. Zooplankton of all body sizes have the potential to disperse throughout the water column in lakes without visual predators; thus UVR tolerance is expected to be similar for all body sizes. In high UV systems, tolerance is predicted to be higher because of increased UVR exposure, while in low UV systems with or without visual predators UVR tolerance is hypothesized to be lower because of little to no prior UVR exposure.

Alternatively, the UVR tolerance of zooplankton will not be related to body size and lake UVR transparency,

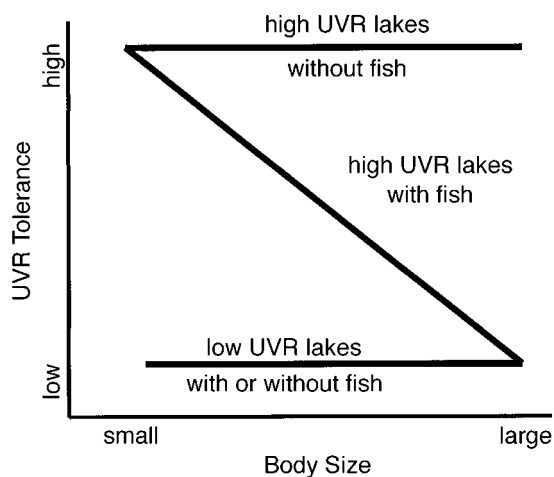


FIG. 2. A conceptual model relating zooplankton UVR tolerance to body size based on lake UVR transparency and size-selective predation pressures. See *Introduction* for details.

but will be species- or taxon-specific due to differences in inherent tolerance mechanisms (photoprotection or PER). Here we test our hypotheses pertaining to lakes with visual predators. UVR tolerance of a variety of zooplankton taxa that differ in their size and in the UVR transparency of the lake of origin are examined.

METHODS

Dissolved organic carbon (DOC) absorbs UVR and is the major factor regulating variation in UV attenuation among lakes (Scully and Lean 1994, Morris et al. 1995). In this study, lakes of varying DOC concentrations and thus varying UVR environments were chosen to examine differences in zooplankton UVR tolerance in relation to zooplankton size (body length) and taxon.

Study sites

Six lakes located on the Pocono Plateau of northeastern Pennsylvania, USA, were sampled in this study. Three were selected for their low DOC concentrations and consequently high UVR transparency (Giles, Silver, and Wildcreek), and three for their moderate DOC and low UVR transparency (Lacawac, Waynewood, and Paupac). In order to characterize the optical properties of the study lakes, DOC concentrations and light attenuation (within each lake) data were collected on a monthly basis from April–July, 1996 (Table 1). Although there is some variation in DOC concentration and lake transparency among months, these lakes provide a strong contrast in UV environments ranging from low to high UV levels. In both years, the lakes were thermally stratified from early May to mid-September. Breakdown of stratification began in late September. In the low UV lakes, the metalimnion and especially the hypolimnion became increasingly anoxic throughout the summer months, while the high UV lakes remained well-oxygenated at all depths.

Zooplankton were collected from the lakes during the months of April–September in 1996 and 1997. Collections from high and low UVR lakes were alternated in order to avoid seasonal bias in the exposure experiments. Collections from Lake Paupac and Wildcreek Reservoir were made only in 1996, and Paupac was sampled only once.

Experimental protocol

Zooplankton were collected during the day (early afternoon) with a vertical tow of a “bongo” style plankton net through both the epilimnion and the metalimnion. *Chaoborus* larvae were collected in the same manner as the zooplankton, except *Chaoborus* were collected at night. Both 48- μm and 202- μm mesh nets were used to ensure adequate collection of both small

TABLE 1. DOC concentrations, attenuation depths (1% of surface irradiance) for UV-B (Z_{a305}) and UV-A (Z_{a380}), collection temperature range, epi–metalimnion depth range from which samples were collected, and maximum depths of study lakes.

Lake	DOC (mg/L) (range)	Z_{a305} (m) (range)	Z_{a380} (m) (range)	Collection temp. range (°C)	Collection depths (m)	Z_{max} (m)
Giles	2.31 (1.38–3.6)	4.51 (2.53–7.56)	8.86 (5.69–12.46)	10–24	0–12	22
Silver	3.39 (3.01–3.62)	1.55 (0.97–1.73)	4.17 (2.90–5.69)	12–24	0–9	13
Wildcreek	2.80 (1.56–4.41)	1.03 (0.91–1.55)	2.44 (1.73–3.63)	14–26	0–13	20
Lacawac	5.17 (3.89–6.12)	0.31 (0.23–0.35)	0.84 (0.71–1.09)	10–26	0–8	13
Waynewood	6.23 (5.41–7.44)	0.26 (0.21–0.32)	0.69 (0.60–0.77)	10–25	0–8	12
Paupac	5.87 (4.82–6.42)	0.27 (0.22–0.35)	0.48 (0.43–0.52)	12–26	0–5	6.8

Notes: The DOC concentrations and attenuation depths are means calculated from monthly measurements during April–July 1996. Ranges for DOC concentrations, Z_{a305} , and Z_{a380} are provided in parentheses. The metalimnion was defined as the range of depths over which the temperature gradient was 1°C or greater per meter. The collection temperature and depth ranges represent the temperatures and depths at which collections were made during April–September 1996 and 1997. Epi–metalimnetic temperatures were generally coldest in April, increased during May–July, and slowly decreased in September.

and large organisms. Dissolved oxygen and temperature profiles were taken using a YSI model 57 or 58 meter to determine the depths of the stratified layers. At least three vertical tows were taken, and samples were stored in 3.8-L polyethylene bottles. Zooplankton were brought back to the laboratory, fed a moderate concentration of *Cryptomas* sp. to provide excess food, and allowed to acclimate overnight inside a growth chamber at 19°C. The following day, the experiment was started by placing zooplankton in their source-lake water filtered through 48- μ m mesh in 31-mL petri dishes (~2 cm deep \times 5 cm wide) with quartz lids. Treatments included five replicates per species, each with 10 individuals per dish except for the *Chaoborus* instars which had only five individuals per dish. When conducting experiments with copepods, adults were primarily selected, but it is possible that a few copepodids may have been included in some treatments. Cyclopoid and calanoid nauplii were not distinguished.

Each experiment consisted of three UVR exposure treatments. Nylon window screen was used as a neutral density filter to vary transmittance from 100% (zero screens) to 41% (two screens), plus a 0% transmittance dark control (foil-covered cardboard box). Because of limited space on the experimental apparatus and the need for adequate replication, other treatments could not be added. Preliminary experiments included a fourth treatment with a transmittance of 11% (four screens). The results of the fourth treatment were consistently similar to the dark control and the fourth treatment was therefore eliminated.

In general, two species of different sizes (one large and one small) were run at the same time. There were five replicate dishes per treatment and species. The treatments were placed inside a walk-in growth chamber on a horizontally rotating (2 rpm) transparent Plexiglas wheel (60 cm diameter) beneath a Spectronics XX15-B UV lamp (Spectronics, Rochester, New York, USA). The rotating wheel provided all dishes with similar, fluctuating UV levels of exposure to simulate mixing in the water column. The UV lamp was placed 23 cm above the wheel, measured from the lamp face to the top of the petri dish. A new piece of clear cellulose acetate was placed over the UV lamp before each experiment to block radiation in the UV-C range. In addition to the UV lamp, eight 40 W cool white fluorescent bulbs were also placed inside the chamber to supply longer wavelengths of light to permit photorepair. Four of these fluorescent bulbs were placed 50 cm above the plankton wheel, measured from the lamp face to the top of the petri dish. The other four fluorescent bulbs were placed 30 cm from the sides of the plankton wheel, measured from the lamp face to the edge of the plankton wheel.

Exposures lasted for 12 h, followed by a 24-h dark incubation inside the growth chamber, all at $20 \pm 1^\circ\text{C}$. At the end of the 36-h incubation period, mortality was scored in each dish. Zooplankton from each treatment

TABLE 2. Comparison of the output of the UV Spectronics XX-15B and fluorescent lamps with solar radiation.

Waveband (nm)	305	320	340	380
Output of UV lamp combined with eight 40-W Cool white/fluorescent bulbs	0.097	0.089	0.032	0.0036
Solar radiation (based on mean monthly max.)				
Minimum	0.024	0.202	0.404	0.146
Maximum	0.043	0.255	0.496	0.175

Notes: Lamp output was determined using an Optronics OL752 scanning radiometer (Optronics, Goleta, California), measuring irradiance at each wavelength from 280 nm to 400 nm. Solar radiation was measured with a Biospherical GUV 521 coupled with a Campbell CR-10 data-logger. The GUV has a 10-nm bandwidth (full width at half maximum) at the four UVR wavelengths. The mean maximum irradiance value, expressed in $\text{W}\cdot\text{m}^{-2}\cdot\text{nm}^{-1}$, was determined for each day of the study months (April–September) for both 1996 and 1997 (see *Methods*). Presented here are the minimum and maximum seasonal irradiance values during the study period. UV lamp irradiance was higher for the UV-B waveband (305 nm) but lower for the UV-A wavebands (320, 340, and 380 nm).

were then preserved in a 4.5% sucrose formalin solution, and body length measurements were later made with an ocular micrometer and either a compound microscope (rotifers and nauplii, to the nearest 0.01 μm) or a dissecting microscope (all other species, to the nearest 0.1 μm).

Optical measurements of solar radiation and lamps

Ambient solar radiation data were collected during the study period at Lacawac Sanctuary, using a Biospherical Global Ultraviolet Imager (GUV) 521 (Biospherical Instruments, San Diego, California, USA) coupled with a Campbell CR-10 data logger (Campbell Scientific, Logan, Utah, USA). The GUV has a 10-nm bandwidth (full width at half maximum) in 4 UV wavelengths (305, 320, 340, 380 nm) and PAR wavelengths (400–700 nm). These data were used to determine mean monthly maximum values for each of the study months in both years (April–September, 1996 and 1997). Little variability in solar radiation was seen across months for both UV-B (305 nm) and UV-A (320, 340, and 380 nm) wavelengths (Table 2). Solar radiation for both years was least in April and September (solar radiation at 305 nm = $0.022\text{--}0.029 \text{ W}\cdot\text{m}^{-2}\cdot\text{nm}^{-1}$), slightly greater in May, June, and September (solar radiation at 305 nm = $0.034\text{--}0.039 \text{ W}\cdot\text{m}^{-2}\cdot\text{nm}^{-1}$), and greatest in July (solar radiation at 305 nm = $0.040\text{--}0.046 \text{ W}\cdot\text{m}^{-2}\cdot\text{nm}^{-1}$). A more complete UV solar spectrum was generated using a modified model developed by B. R. Hargreaves (Lehigh University) based on solar data collected in July 1997. This model has been previously used in an intercomparison study of optical UV-B measuring instruments (Kirk et al. 1994) where it is described more fully, as well as in comparing seasonal photodegradation rates of dissolved organic carbon in lakes (Morris and Hargreaves 1997). The modeled solar spectrum was plotted against that of the experimental lamp con-

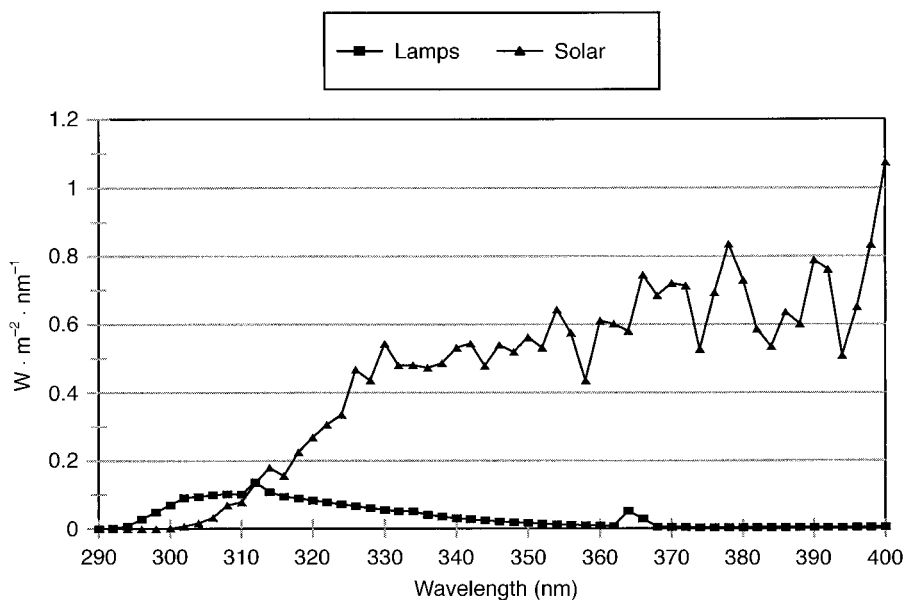


FIG. 3. Spectral composition of solar radiation and the experimental lamps. The solar spectrum was generated by applying the average monthly maximum irradiance for July 1997 at the four UV wavelengths and PAR, as determined by the GUV, to a model which uses these five points to calculate a complete spectrum (see *Methods*). The spectrum of the experimental lamp configuration (Spectronics XX-15B UV lamp covered with cellulose acetate and eight 40-W cool white fluorescent bulbs) was collected with an Optronics OL752 scanning radiometer.

figuration for comparison (Fig. 3). In the past, a scanning radiometer was used to accurately characterize the experimental lamp output (Fig. 3); however, no scanning instrument was available during the current study. Comparisons of the exposure regimes were made with a Biospherical Instruments Psoralen Ultra-Violet (PUV) 501 (using an appropriate air calibration correction) twice during the study. Although these measurements are crude due to the 10 nm bandwidth (full width at half maximum) of the instrument, they indicated that the UV exposure varied by no more than 8–10% throughout the study period. Compared to solar radiation, the UV lamp was higher in the 305-nm waveband but lower for 320-, 340-, and 380-nm wavebands (Table 2; Fig. 3).

Statistical methods

Transformed data were used to estimate a 12-h LD_{50} (exposure level at which 50% mortality occurs after a 12-h UVR exposure) for each species in each experiment using linear regression analysis. An arcsine-square-root transformation was performed on percentage survival data for each species in each experiment with <10% mortality in the dark controls. Linear regression analysis was used to calculate LD_{50} values which were expressed as percent transmittance of the UVR lamp as adjusted with the neutral density filters. These 12-h LD_{50} values were used to indicate UVR tolerance.

Regression, *t* tests, and one-way ANOVAs were used to determine if LD_{50} values (UVR tolerance) depended

on body size, lake transparency, and taxon. Zooplankton were grouped into six body size categories to permit estimates of the minimum, maximum, and variance in tolerance values for different size classes. Differences in variance invalidate a simple regression analysis approach to analyzing the overall data. However, given that regression analysis is often robust in spite of invalid assumptions, we ran regressions on the maximum and minimum tolerance values determined for each of the six body size classes as well as the maximum and minimum tolerance values from the full 22 experiments on 12 different zooplankton species. A *t* test was used to examine differences in LD_{50} values among lakes to test the hypothesis that UVR tolerance is related to UVR transparency of the source lake. To test for differences in UVR tolerance among taxa, LD_{50} values were grouped by taxon, and a one-way ANOVA was performed. In addition, mean LD_{50} values for each taxon were calculated giving equal weight to species or genus to compare UVR tolerance across species and genera. Separate ANOVAs were carried out on four paired experiments in which different life history stages of a single species were exposed together to examine differences in UVR tolerance related to life history stage. Mean LD_{50} values for each species were compared across months for possible monthly differences in UVR tolerance.

RESULTS

There was no clear relationship between LD_{50} values and body size (Fig. 4). Smaller zooplankton generally

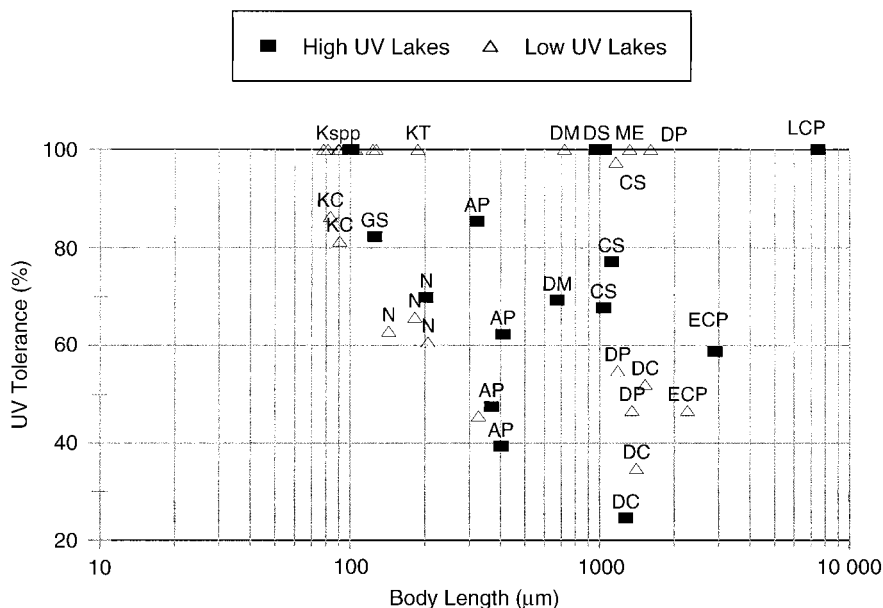


FIG. 4. UVR tolerance of zooplankton from both high- and low-UVR lakes vs. body length (μm), plotted on a log scale. Each point represents an LD_{50} expressed as percentage transmittance of the UVR lamp as adjusted with the neutral density filters. LD_{50} values were calculated using linear regression analysis on arcsine-square-root transformed percentage survival data for each species in each experiment. Species codes are as follows: AP = *Asplanchna priodonta*, CS = *Cyclops scutifer*, DC = *Daphnia catawba*, DM = *Diaptomus minutus*, DP = *Daphnia pulex*, DS = *Diaptomus spatulocrenatus*, GS = *Gastropus stylifer*, KC = *Keratella cochlearis*, KT = *Keratella taurocephala*, LCP = late-instar *Chaoborus punctipennis*, ME = *Mesocyclops edax*, N = nauplii, and ECP = early-instar *Chaoborus punctipennis*. Ksp indicates closely overlapping rotifer LD_{50} values from 10 experiments examining *K. cochlearis*, *K. crassa*, and *K. taurocephala*. Data are from Table 4.

had higher tolerances ($\text{LD}_{50} \geq 80\%$), while the tolerances of larger zooplankton ranged from $\text{LD}_{50} < 25\%$ to $\text{LD}_{50} = 100\%$ (Fig. 4). Grouping the zooplankton into six body size categories showed generally increasing sample variance with increasing body size (Table 3). Linear regressions performed on the maximum and minimum tolerances for the six size categories vs. body size gave no significant relationships ($P > 0.39$). Additionally, regression analysis of the entire data set found no statistically significant pattern between UVR tolerance and body size ($R^2 = 0.01$, $P > 0.537$). UVR

TABLE 3. Minimum and maximum LD_{50} values, variance, and number of species represented for each grouped size class.

Size range (μm)	Minimum	Maximum	Variance	No. of species
<300	61	100	224	5
301-600	39	85	341	1
601-900	69	100	468	1
901-1200	55	100	368	3
1201-1500	25	100	1123	3
>1500	52	100	1150	2

Notes: Data derived from Table 4 were broken into size classes of 300 μm in order to estimate variance in UVR tolerance with body size. In two cases, multiple tests on a single species composed the entire size category. *Chaoborus* instars were not included in the largest size class due to their body size being an order of magnitude greater than the other zooplankton and their meroplanktonic habits.

tolerance also showed no significant relationship to UVR transparency of the source lake ($P > 0.15$; Fig. 4).

The patterns in the LD_{50} values (UVR tolerance) did vary significantly among taxa ($P < 0.0001$). The UVR tolerances of the smaller rotifers tested (*Gastropus stylifer* and *Keratella* spp.) were consistently high ($\text{LD}_{50} = 82\text{--}100\%$; Table 4, Rotifer section). The larger, more transparent rotifer, *Asplanchna priodonta*, was less UVR tolerant, and showed somewhat greater variability in its response to UVR ($\text{LD}_{50} = 39\text{--}85\%$; Table 4, Rotifer section) compared to the smaller rotifers. The mean LD_{50} for all rotifers combined was 79–86%, depending on whether equal weight was given to genus or to species (Table 5). Cladocerans had the lowest UVR tolerance and the highest variability among species ($\text{LD}_{50} = 25\text{--}100\%$, mean = 52%; Table 4, Cladoceran section; Table 5). *Daphnia pulex* appeared to be more tolerant than *D. catawba* (mean $\text{LD}_{50} = 78\%$ and 44%, respectively; Table 4, Cladoceran section). Adult calanoid and cyclopoid copepods exhibited generally high UVR tolerances ($\text{LD}_{50} = 68\text{--}100\%$, mean = 91%; Table 4, Copepod section, calanoid vs. cyclopoid; Table 5). Copepod nauplii were generally more intermediate in their UVR tolerances ($\text{LD}_{50} = 61\text{--}71\%$; Table 4, Copepod section, nauplii).

There was a significant difference in the tolerance of *Cyclops* adults and nauplii in one experiment ($\text{LD}_{50} = 97\%$ and 63%, respectively; $P < 0.0001$; Table 4,

TABLE 4. Experimental data for all UVR exposure experiments.

Experiment	Date	Species	Lake	Lake UVR level	LD ₅₀	Body length (μm)	Intra-specific pairs
Rotifers							
96Expt2	VI-11-96	<i>Asplanchna priodonta</i>	Wildcreek	high	40	403	
96Expt4	VI-23-96	<i>Asplanchna priodonta</i>	Silver	high	62	411	
96Expt5	VI-26-96	<i>Asplanchna priodonta</i>	Lacawac	low	46	328	
96Expt9	VII-16-96	<i>Asplanchna priodonta</i>	Wildcreek	high	48	370	
97Expt11	IX-15-97	<i>Asplanchna priodonta</i>	Silver	high	85	323	
97Expt3	V-29-97	<i>Gastropus stylifer</i>	Giles	high	82	125	
96Expt10	VII-24-96	<i>Keratella cochlearis</i>	Lacawac	low	86	83	
96Expt11	VII-26-96	<i>Keratella cochlearis</i>	Lacawac	low	100	90	
96Expt15	IX-19-96	<i>Keratella cochlearis</i>	Lacawac	low	81	91	
96Expt6	VII-1-96	<i>Keratella cochlearis</i>	Waynewood	low	100	91	
97Expt10	IX-4-97	<i>Keratella cochlearis</i>	Waynewood	low	100	81	
97Expt1	V-13-97	<i>Keratella crassa</i>	Waynewood	low	100	127	
97Expt2	V-27-97	<i>Keratella crassa</i>	Lacawac	low	100	123	
96Expt1	VI-4-96	<i>Keratella taurocephala</i>	Giles	high	100	100	
96Expt10	VII-24-96	<i>Keratella taurocephala</i>	Lacawac	low	100	105	
96Expt11	VII-26-96	<i>Keratella taurocephala</i>	Lacawac	low	100	104	
96Expt5	VI-26-96	<i>Keratella taurocephala</i>	Lacawac	low	100	187	
96Expt8	VII-11-96	<i>Keratella taurocephala</i>	Lacawac	low	100	78	
96Expt13	VII-13-96	<i>Keratella taurocephala</i>	Silver	high	100	102	
Copepods							
<i>Cyclopoids</i>							
96Expt3	VI-19-96	<i>Cyclops scutifer</i>	Lacawac	low	97	1163	1***
97Expt4	VI-5-97	<i>Cyclops scutifer</i>	Giles	high	68	1037	2
97Expt8	VI-17-97	<i>Cyclops scutifer</i>	Silver	high	77	1117	
96Expt7	VII-9-96	<i>Mesocyclops edax</i>	Paupac	low	100	1321	
<i>Calanoids</i>							
96Expt9	VII-16-96	<i>Diaptomus minutus</i>	Wildcreek	high	69	677	
97Expt9	VI-19-96	<i>Diaptomus minutus</i>	Lacawac	low	100	723	3***
96Expt12	VII-29-96	<i>Diaptomus spatulocrenatus</i>	Giles	high	100	970	
97Expt11	IX-15-97	<i>Diaptomus spatulocrenatus</i>	Giles	high	100	1050	
<i>Nauplii</i>							
96Expt3	VI-19-96	<i>Nauplii</i>	Lacawac	low	63	143	1***
97Expt4	VI-5-97	<i>Nauplii</i>	Giles	high	69	202	2
97Expt7	VI-15-97	<i>Nauplii</i>	Lacawac	low	61	206	
97Expt9	VIII-29-97	<i>Nauplii</i>	Lacawac	low	66	182	3***
Cladocerans							
96Expt15	IX-19-96	<i>Daphnia catawba</i>	Lacawac	low	52	1527	
97Expt2	V-27-97	<i>Daphnia catawba</i>	Lacawac	low	35	1407	
97Expt3	V-29-97	<i>Daphnia catawba</i>	Giles	high	25	1280	
96Expt6	VII-1-96	<i>Daphnia pulicaria</i>	Waynewood	low	100	1606	
97Expt1	V-13-97	<i>Daphnia pulicaria</i>	Waynewood	low	55	1184	
97Expt10	IX-4-97	<i>Daphnia pulicaria</i>	Waynewood	low	47	1357	
Insect larva							
97Expt7	VI-15-97	Early <i>Chaoborus punctipennis</i>	Lacawac	low	47	2257	
96Expt14	VIII-5-96	Early <i>Chaoborus punctipennis</i> (I & II)	Silver	high	59	2900	4***
96Expt14	VIII-5-96	Late <i>Chaoborus punctipennis</i> (III & IV)	Silver	high	100	7500	4***

Notes: Numbers in the last column indicate early and late life-history stages tested together. Three of these intraspecific pairs showed significant within-pair differences (*** $P < 0.0001$), and one did not ($P > 0.05$).

Copepod section, intraspecific comparison) while in another independent experiment no significant difference was found ($P > 0.05$). Adult calanoid *D. minutus* were more UVR tolerant than nauplii (LD₅₀ = 100% and 66%, respectively; $P < 0.0001$; Table 4, Copepod section, intraspecific comparison). Larval *Chaoborus* were more tolerant in their later instars (LD₅₀ = 100%) than in their earlier instars (LD₅₀ = 59, $P < 0.0001$; Table 4, insect larva section). No consistent differences

in UVR tolerance among months were observed for any of the species tested.

DISCUSSION

Zooplankton UVR tolerance was not related to body size or to lake UVR transparency, but tolerance did show a significant relationship to taxon. Rotifers, copepods, and late instar *Chaoborus* displayed the greatest tolerance to UVR, while cladocerans and early in-

TABLE 5. Mean LD₅₀ ± SE for each taxon calculated by giving equal weight to species or genus.

Taxon	Mean	
	By species	By genus
Rotifers	86 ± 2	79 ± 12
Copepods (primarily adults)	91 ± 5	91 ± 1
Nauplii	...	65 ± 2
Cladocera	52 ± 11	52 ± 11
Insect larva		
Early instars (I and II)	...	53 ± 6
Late instars (III and IV)	...	100 ± 0

Note: Nauplii were not identified taxonomically and may include both cyclopoid and calanoid nauplii.

star *Chaoborus* showed generally lower tolerances. While these results were obtained with an artificial UVR source in the laboratory, they are consistent with tolerance patterns found in the field. Incubations done in the surface waters of Lake Giles (high UV system) revealed that *Keratella taurocephala* show little response to UVR in terms of mortality, while *Diaptomus minutus* and *Daphnia catawba* show a moderate to high response, respectively (Williamson et al. 1994). Mortality rates determined with the UV lamp (12-h constant UV) are also similar to those obtained after 1–2 d exposure in the lake. For example, 50% of *Chaoborus punctipennis* die after ~0.5 d exposure to natural sunlight at levels found at the surface of Lake Giles during the period surrounding summer solstice (Williamson et al. 1999). In the current study, the LD₅₀ (exposure level at which 50% mortality occurs after 12-h exposure) for *C. punctipennis* was between 47% and 59% of the full strength of the UV lamp for early instars, while late instars survived the full strength of the lamp. Similar arguments can be made based on the high mortality rates of *Daphnia* after only 2 d of in situ exposure in Lake Giles (Zagarese et al. 1994), compared to the mean 12-h LD₅₀ of 52% found in the current study.

Differences in UVR tolerance among taxa are likely attributable to varying mechanisms of UVR defense. Photoprotection and photorepair (PER) are important physiological responses while vertical migration may be one of the most effective behavioral responses. Here we defined UVR tolerance as the sum of photoprotection and PER. Behavioral avoidance was not examined in this study; however, it is known that both cladocerans and copepods are highly motile and exhibit diel vertical migration (DVM) in lakes with fish. In the laboratory, *Daphnia magna* was found to be negatively phototactic to monochromatic UV wavelengths (260–380 nm) and positively phototactic to visible light (420–600 nm) (Storz and Paul 1998). Copepods have also shown UV avoidance behavior in the laboratory (Barcelo and Calkins 1978). Most rotifers are less motile and do not experience extensive vertical migrations, making behavioral avoidance less likely. Analysis of our zooplankton database revealed that highly UVR sensitive *D. catawba* spends the least time in the epilimnion of

Lake Giles, especially during summer solstice when UVR is high (Fig. 1). While these data do not demonstrate a causal relationship for UV in nature, they are consistent with a UV behavioral avoidance hypothesis. The data are also consistent with behavioral avoidance of visual predators, and experimental manipulations are necessary to demonstrate causality.

Cladocerans and copepods differ in the extent to which they use photoprotection and PER. Cladocerans inhabiting fishless lakes often contain high concentrations of photoprotective pigments such as melanin (Herbert and Emery 1990, Hessen 1993). Copepods, on the other hand, often contain high concentrations of carotenoids (Hairston 1976, 1979, Ringelburg et al. 1984) as well as mycosporine-amino acids (R. Moeller, unpublished data). Interestingly, in both cladocerans and copepods, nonpigmented and pigmented populations of the same species have been observed (Hairston 1979, Hessen 1996). Although no strong correlation has been found between presence of pigmentation and the UV environment, pigmented morphs are generally more tolerant to potentially damaging radiation. Prior data indicate that *Daphnia pulicaria*, *D. pulex*, and *D. galeata* are capable of PER, while *Diaptomus oregonensis* and *Acanthodiaptomus denticornis* depend more on photoprotection (Ringelburg et al. 1984, Siebeck and Bohm 1991). In the southern hemisphere, three species of calanoid copepod from the same genus, *Boeckella*, vary in the extent to which they utilize photoprotection versus PER (Zagarese et al. 1997). Little is known about photoprotection and PER in rotifers.

Our goal in the current experiments was to compare the relative UVR tolerance of zooplankton in relation to their body size and taxon with a constant UV source, rather than to estimate absolute tolerance to solar UV radiation in nature. Although our UV lamps do not simulate natural solar UV radiation, prior experiments show that patterns of tolerance to these lamps are similar to tolerance of natural solar radiation at or near the lakes' surface (Williamson et al. 1999, Zagarese et al. 1994). In order to do a more quantitative comparison with strict dose calculations, biological weighting functions are needed for each species from each lake (Cullen and Neale 1997). Thus far, these weighting functions have not been determined and were not the focus of this study. In our experiments, great emphasis was placed on creating an unbiased experimental approach to test the working hypothesis that UVR tolerance is related to body size. In general, two species, including one large and one small, from the same lake, were exposed together under standard conditions and their UVR tolerances were compared.

Different responses to UVR among taxa may be an important factor influencing food web structure and function. In stream communities, UV-B radiation has been demonstrated to affect the balance between primary producers and consumers (Bothwell et al. 1994). In ecosystems where communities are regulated from

the top down by consumers, UVR damage to higher trophic levels may also have a great impact on community and ecosystem processes at lower trophic levels (solar cascade, Williamson 1995). In this study, *Daphnia* exhibited some of the lowest levels of UVR tolerance. Analysis of the zooplankton database revealed that, at times, as much as 40% of the *Daphnia* population may be found in the surface waters of a high UVR lake during the latter portion of the summer or early autumn (Fig. 1). This is important because *Daphnia* play a critical role in aquatic ecosystems as an important link in the cycling of energy resources among trophic levels (Pace 1984, Carpenter et al. 1991). The greater sensitivity of *Daphnia* vs. copepods to UVR suggests that zooplankton community structure, as well as ecosystem structure and function, may be altered by changes in UVR environments related to ozone depletion or changing levels of dissolved organic carbon (DOC) (Schindler et al. 1996, Williamson et al. 1996, Yan et al. 1996).

The UVR tolerance of *Chaoborus* and planktivorous fish, such as the sunfish *Lepomis*, are of interest because they are the two predators that are most likely to induce diel vertical migrations of zooplankton in the study lakes. These predators differ in their predatory tactics. *Chaoborus* larvae are primarily tactile predators and feed on smaller zooplankton at night, while *Lepomis* larvae are visual predators that feed on zooplankton during the daylight hours in the shallow surface waters. *Lepomis* are thus much more likely to be exposed to high UVR than are *Chaoborus*. Prior data on the in situ exposure of *Chaoborus* and two species of *Lepomis* (*gibbosus* and *macrochirus*) to ambient solar radiation in the surface waters of Lakes Giles and Lacawac indicate that late instar *Chaoborus* are much less UVR-tolerant than are larvae of *Lepomis* (Williamson et al. 1999). However, the variability in UVR tolerance in *Lepomis* larvae is somewhat greater than *Chaoborus*, and this variability is greatest at higher UVR exposures.

Here we found that late instars of *Chaoborus* had a greater UVR tolerance than early instars. Unpublished field experiments exposing both early and late *Chaoborus* instars to ambient solar radiation show similar results (S. L. Metzgar, unpublished data). Comparisons of the different life history stages of copepods revealed that *Cyclops scutifer* was no more tolerant than were nauplii, while adult *Diaptomus minutus* were more tolerant than were nauplii. The greater UVR tolerance of later life history stages is consistent with prior studies that have shown a greater tolerance of adult versus larval marine copepods (Karanas et al. 1979).

Although no consistent differences in UVR tolerance across months were observed in this study, a previous study examining the copepod *Diaptomus minutus* from Lakes Giles and Lacawac did report seasonal patterns in UVR tolerance (Stutzman 1996). Organisms were collected from the two lakes and exposed to the same type of UV lamp source used in this study. *Diaptomus*

minutus collected from Giles were more tolerant from late June through September and into October. Lacawac animals were least tolerant in September and showed greatest tolerance in December. This pattern was observed in two consecutive years. The greater tolerance observed in December may be a reflection, at least in part, of the temperature dependence of an organism's tolerance to photodamage (Hairton 1979). It is difficult to say whether seasonal changes in zooplankton UVR tolerance may be due to changes in solar radiation since, as seen in the present study, solar irradiance shows relatively little variation throughout the summer months (Table 2). It is interesting that rotifers and copepods display the greatest tolerance and also are found in greater numbers in the surface waters during the day throughout most of the summer while cladocerans display the least tolerance and are in smaller numbers in the surface waters until the latter portion of the summer (Fig. 1). These patterns are currently the subject of a more in depth analysis (D. Leech, unpublished manuscript).

The present study examines UVR as an acute stressor; however, it is possible that longer term sublethal effects may also be important at even lower UVR levels. Furthermore, UVR is only one of many potential stressors acting on zooplankton communities. Other stressors include pH, temperature, competition, predation, and food limitation. UVR is likely to interact with these stressors through a variety of mechanisms. For example, high UVR levels in the surface waters of low DOC lakes may force zooplankton into deeper waters where habitats are suboptimal due to lower temperatures or greater risk of predation by tactile invertebrate predators. Establishing the UVR tolerances of zooplankton, as we have done here, is the first step in understanding the direct effects of UVR and provides the foundation for investigating more complex interactions with other ecological stressors.

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