

Zooplankton behavioral responses to solar UV radiation vary within and among lakes

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*Zooplankton taxa exhibit varying tolerances to ultraviolet radiation (UVR), with rotifers and copepods tending to be more UV tolerant than cladocerans, regardless of lake UV transparency. On the basis of these differences, we hypothesized that UV avoidance behavior would be greatest in zooplankton with low UV tolerance, particularly in high-UV systems. Both downward and upward movements of zooplankton were examined in cylindrical acrylic columns that either transmitted full sunlight or blocked UV-B and short wavelength UV-A radiation. Columns were suspended vertically in the surface waters of a high- and low-UV lake at varying times of day and cloud cover. In the high-UV lake, the cladoceran *Daphnia catawba* displayed a distinct avoidance of the surface waters in the UV+ treatment but often showed a preference for the surface in the UV– treatment. Copepods were less responsive to UVR with calanoids displaying a somewhat greater UV avoidance than cyclopoids. In the low-UV lake, no behavioral differences were observed among UV treatments. These results suggest that UVR may influence the vertical distribution and habitat partitioning of certain zooplankton taxa in high-UV lakes while other factors, such as predation and food limitation, may be more important in low-UV lakes.*

INTRODUCTION

In the past few decades, our understanding of effects of ultraviolet radiation (UVR) on aquatic ecosystems has increased, stimulated by concerns about stratospheric ozone depletion and consequent increases of damaging UV-B radiation reaching the earth's surface. UVR is now known to penetrate deeply into the water column of many freshwater and marine systems (Fleischmann, 1989; Scully and Lean, 1994; Morris *et al.*, 1995). In addition, both laboratory and field experiments have demonstrated that increased exposure to UVR leads to a decrease in survival as well as to 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).

Tolerance to UVR varies across zooplankton taxa (Leech and Williamson, 2000). In laboratory experiments,

cladocerans (*Daphnia* spp.) were shown to be less UV-tolerant than copepods or rotifers regardless of the UVR transparency of their source lake. These differences in UVR tolerance among zooplankton taxa are likely attributable to varying levels and mechanisms of UVR defense. Photorepair, photoprotection and behavioral avoidance are three means by which zooplankton can protect themselves from UV damage (Zagarese and Williamson, 1994). The extent to which species use each mechanism differs both within and among taxa (Hairston, 1979; Ringelberg *et al.*, 1984; Zagarese *et al.*, 1997; Grad *et al.*, 2001). While our understanding of zooplankton photorepair and photoprotection capabilities is increasing, less is known about zooplankton behavioral avoidance of UVR in nature.

Laboratory experiments with polychromatic light have clearly demonstrated that wavelength is an

important behavioral cue to zooplankton. Cladocerans, for example, were shown to become more agitated and negatively phototactic in the presence of short-wavelength blue light but remained calm and were positively phototactic to long-wavelength red light (Smith and Baylor, 1953). These ‘color dances’ of Cladocera were hypothesized to cue zooplankton to high concentrations of algal food, but it was also suggested that these ‘dance’ patterns may explain patterns of diurnal migration. UV photoreceptors have been detected in the compound eye of *Daphnia magna* with peak sensitivity at 348 nm (Smith and Macagno, 1990), and more recent studies with monochromatic light have demonstrated that *D. 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).

Copepods have also shown UV avoidance behavior in the laboratory. In small experimental enclosures examining horizontal movements, *Cyclops serrulatus* were found to avoid exposure to UV-B radiation (280–320 nm) (Barcelo and Calkins, 1978). This study also noted that UV tolerance correlated well with behavioral response (i.e. UV sensitive organisms avoid UV-B exposure). In addition, the action spectrum of phototactic responses in copepods has been demonstrated to be dependent upon pigmentation. Within the visible light spectrum, *Diatomus nevadensis* swimming speeds were faster in blue light compared to red light (Hairston, 1976). In addition, less pigmented individuals were more responsive to changes in wavelength than pigmented individuals (Hairston, 1976). Behavioral responses in the field are less well understood. The harpacticoid copepod *Tigriopus californicus*, which lives in shallow tide pools, was found to aggregate into shaded regions of pools at midday but show no preference at dawn and dusk (Martin *et al.*, 2000). These same authors used lab experiments to demonstrate that *T. californicus* responds more to UV-B than to photosynthetically active radiation (PAR) and suggest that they may possess UV photoreceptors. More recently, a nonmanipulative, whole-lake study reported that during periods of high UV, the percentage of the calanoid copepod *Boeckella gracilipes* occupying the surface waters decreased in two UV transparent Patagonian lakes; however, this pattern was not detected in the low-UV lake (Alonso *et al.*, 2004). This species is also noted to have a low UV tolerance (Zagarese *et al.*, 1997).

Daphnia exhibit a strong vertical avoidance to UVR in nature (Leech and Williamson, 2001). In a set of field incubation experiments, *Daphnia pulicaria* rapidly swam out of the surface waters of a high-UV lake in the presence of full solar radiation. However, in the

absence of UV-B and shorter wavelength UV-A radiation, the majority of *D. pulicaria* remained in the surface waters. Thus, a stronger negative phototactic response was detected in the presence of UVR than in the absence of UVR.

In this study, two central questions are examined: (i) do species of zooplankton other than *Daphnia* respond to UVR in nature? and (ii) do their responses differ from those of *Daphnia*? The differential vertical response of several zooplankton species to UVR is tested in a high- and a low-UV lake. On the basis of known differences in zooplankton UV tolerance, we hypothesized that UV avoidance behavior will be greatest in zooplankton with low UV tolerance. More specifically, cladocerans should exhibit a greater UV avoidance of the surface waters compared to copepods. In addition, UV behavioral responses should be greater in a high-UV lake than in a low-UV lake.

METHOD

Study site

This study took place in two lakes located in the Pocono Mountains of Northeastern Pennsylvania, USA. Lake Giles (41.23° N, 75.21° W) is an oligotrophic system with a mean summer Secchi depth of 11–15 m and a mean dissolved organic carbon (DOC) concentration of 1.2 mgC L⁻¹. Lake Lacawac is a mesotrophic system with a mean summer Secchi depth of 3–4 m and a mean DOC concentration of 4.5 mgC l⁻¹. Both lakes are thermally stratified from early May through late September. Lake Giles remains well oxygenated at all depths throughout the year while the hypolimnion of Lake Lacawac becomes increasingly anoxic from May through September. The fish community of each lake includes both planktivorous and piscivorous fish, including *Lepomis macrochirus*, *Lepomis gibbosus*, *Salmo* spp. and *Micropterus salmoides*.

Light measurements

Ambient solar radiation data were collected in an open field at Lacawac Sanctuary (~17 km from Lake Giles) 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 an 8–10 nm bandwidth (full width at half maximum) at four UV wavelengths (305, 320, 340 and 380 nm) as well as PAR (400–700 nm). This instrument averages solar irradiance data over 15-minute intervals. For each experiment,

Table I: Ambient solar irradiance during experiments

Date	Incubation time (h)	305	320	340	380	PAR	Mean irradiance	
							Giles	Lacawac
14 July 2000	1230–1300	0.034	0.238	0.476	0.662	0.002	659	728
	1545–1615	0.011	0.113	0.234	0.315	0.001	488	403
18 July 2000	1250–1320	0.043	0.246	0.478	0.657	0.002	752	807
	1600–1630	0.022	0.179	0.377	0.541	0.001	517	644
20 July 2000	1250–1320	0.048	0.277	0.540	0.743	0.002	899	849
	1440–1510	0.040	0.247	0.491	0.680	0.002	849	817
2 August 2000	1314–1344	0.033	0.202	0.398	0.548	0.001	694	617
22 August 2000	1205–1235	0.036	0.233	0.470	0.667	0.002	681	841
	1409–1439	0.032	0.215	0.443	0.633	0.002	705	827
25 August 2000	1204–1234	0.035	0.228	0.455	0.632	0.002	814	774
	1410–1440	0.034	0.230	0.470	0.664	0.002	768	907

Average ambient solar irradiance for UV ($W m^{-2} nm^{-1}$) and PAR ($\mu mol m^{-2} s^{-1}$) wavelengths collected during July to August 2000. Data were measured with a Biospherical Global Ultraviolet Imager located at Lacawac Sanctuary in Northeastern, PA. The instrument reported ambient solar irradiance averaged over 15-minute intervals. The last two columns represent mean solar irradiance ($W m^{-2}$, spectral range ~ 300 – 2800 nm) collected with either an Eppley model 8–84 or a LICOR model LI-200SA pyranometer at Lakes Giles and Lacawac. These data were used to estimate cloud cover at each site. Both instruments were mounted on weather stations near the center of each lake and again reported average solar irradiance over 15-minute intervals. For each experiment, light data were averaged over the closest time interval to the incubation period.

irradiance data were averaged over the closest time to the incubation period (Table I).

Total solar irradiance ($W m^{-2}$) was measured with a black and white Model 8–84 pyranometer (Eppley Laboratory, Inc., Newport, Rhode Island, USA) at Lacawac Sanctuary and a LI-COR model LI-200SA pyranometer (LI-COR, Inc., Lincoln, Nebraska, USA) at Lake Giles. Both instruments were mounted on weather stations near the center of each lake and reported average solar irradiance over 15-minute intervals. These data were used to compare variations in irradiance due to cloud cover at each location. On clear days, midday solar irradiance is equal to $\sim 1000 W m^{-2}$ during the summer months. On most dates, overall irradiance was similar at both sites, differing by ~ 2.5 – 10% with an average of 6% (Table I). Therefore, ambient solar radiation data collected with the GUV at Lacawac Sanctuary were assumed to be similar to the exposures at Lake Giles.

Underwater light profiles of UV and PAR were taken with a Biospherical Profiling Ultraviolet Radiometer (PUV) 500 (Biospherical Instruments, San Diego, California, USA). Two profiles were taken, one on 20 July 2000 and the second on 22 August 2000, in Lake Giles while one PUV profile was taken on 21 August 2000 in Lake Lacawac. All PUV profiles were taken at approximately solar noon (1300 h local time). These data were used to calculate extinction coefficients (K_d) for the UV and PAR wavelengths

(calculations described in Morris *et al.*, 1995) as well as for other descriptive optical parameters (Table II).

Experimental design

Acrylic columns were used to examine the vertical swimming response of zooplankton to manipulated solar radiation. Three columns were constructed of a UV-transparent acrylic [UVT, Spartech, Inc. (formerly Townsend/Glasflex), Des Moines, Iowa, USA] that had a 50% transmittance at ~ 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 ~ 300 – 400 nm). Three other columns were constructed of a UV-blocking acrylic ('extruded,' Thermoplastic Processes, Inc., Stirling, NJ, USA) with 50% transmittance at ~ 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, 50% transmittance at 272 nm, CYRO Industries, Mt. Arlington, NJ, USA) or UV-blocking (OP-2, 50% transmittance at 410 nm, CYRO Industries). Previous modeling efforts indicated that the total solar energy (including UVR, visible and infrared radiation) transmitted by the UV-blocking columns was 3–4% less than that of transmitted by the UV-transmitting columns at the water surface (Leech and Williamson, 2001). This percentage decreases exponentially with depth as the lake water and the dissolved and

Table II: Underwater light penetration for Lakes Giles and Lacawac

	Wavelength (nm)				
	305	320	340	380	PAR
Lake Giles					
K_d (20 July 2000)	1.35	1.04	0.80	0.60	0.35
K_d (22 August 2000)	1.77	1.38	1.05	0.59	0.34
$Z_{1\%}$ (m) (20 July 2000)	3.27	4.56	5.71	8.15	13.31
$Z_{1\%}$ (m) (22 August 2000)	2.76	3.57	4.49	8.21	13.75
Irradiance at 1.5 m (20 July 2000)	0.64	5.8	16.15	37.25	0.11
Irradiance at 1.5 m (22 August 2000)	0.28	3.28	9.78	27.23	0.09
Lake Lacawac					
K_d (21 August 2000)	14.57	16.66	12.53	7.47	1.00
$Z_{1\%}$ (m) (21 August 2000)	0.32	0.28	0.37	0.62	4.60
Irradiance at 1.5 m (21 August 2000)	0.00	0.00	0.00	0.00	0.03

Attenuation coefficients (K_d) at wavelengths <400 nm and at 400–700 nm (PAR), 1% attenuation depths ($Z_{1\%}$, depth to which 1% of surface irradiance penetrates), and estimated irradiance ($W\ m^{-2}\ nm^{-1}$) at 1.5 m depth for 305, 320, 340, 380 nm and PAR in Lakes Giles and Lacawac. Attenuation coefficients and 1% attenuation depths were determined from underwater irradiance profiles that were taken with a PUV 500 (Biospherical Instruments, Inc.) on 20 July 2000 and 22 August 2000 in Lake Giles and on 21 August 2000 in Lake Lacawac.

particulate substances in it selectively attenuate the UV portion of the spectrum.

The design of the columns was modified from Leibold and West (Leibold and West, 1993). 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 migration and were constructed of UV-transparent cellulose acetate to avoid UV shading. Columns were assembled by taping together 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.

Zooplankton were collected by towing 48- and 202- μ m mesh plankton nets from 20 m to the surface in Lake Giles and from 10 m to the surface in Lake Lacawac. Organisms were placed in a 4-L polyethylene container that was then placed in a dark cooler until needed. At the beginning of each experiment, the columns were filled with unfiltered lake water by submerging them at the surface. Two types of experiments were performed to allow either upward or downward migrations. This was accomplished by deploying the columns with the small end of the funnels facing either upward or downward for the two types of experiments respectively. We examined migrations in the upwards direction to determine if zooplankton would prefer to be in the shallower surface waters in the absence of UV.

A 300-ml aliquot of zooplankton sample was introduced to each column. In Lake Giles, this provided \sim 200 *Daphnia*, 1500–2000 calanoids and 150 cyclopoids per column. In Lake Lacawac, this provided \sim 30 *Holopedium*, 60–100 calanoids, and 40–60 cyclopoids per column. For downward migration experiments, zooplankton were introduced to the top of each column. For upward migration experiments, zooplankton were introduced to the bottom of each column. UV+ and UV– columns were filled alternately to avoid bias.

Once loaded, the columns were suspended vertically from a floating rack near the center of the lake, \sim 10 cm from the surface. Animals were allowed to migrate for 30 minutes, as determined by prior experiments with *Daphnia* (Leech and Williamson, 2001). At the end of the 30-minute incubation, the contents of each section were immediately emptied into a pre-labeled sample cup through a 1.4-cm opening in each section, which was sealed with a silicon stopper. In experiments testing downward movements, each column was first inverted 180° to prevent further downward migration before the sections were emptied. Samples were preserved in a 4.5% sucrose–formalin solution.

There were a total of fifteen experiments. Four experiments were conducted in Lake Giles to test for differences in vertical swimming responses at midday versus late afternoon. Seven experiments were conducted in Lake Giles and four in Lake Lacawac to compare downward versus upward swimming responses around solar noon (\sim 1300 h local time).

Statistical methods

The total number of individuals of each species in each section of the columns was counted under a dissecting microscope in the laboratory. For all experiments, the percentage of each species or taxonomic group present in each section of each column was calculated for both treatments. The dominant cladoceran in Lake Giles was *Daphnia catawba* and *Holopedium gibberum* in Lake Lacawac. Copepods were divided into calanoids and cyclopoids but were not separated by sex or life history stage (i.e. copepodid versus adult). In both lakes, calanoids were dominated by *Diaptomus minutus* and few *Diaptomus spatulocrenatus*. Cyclopoids were dominated by *Cyclops scutifer* in Lake Giles and *Mesocyclops edax* in Lake Lacawac.

The mean depth of each species or taxonomic group in each column was determined by multiplying the number of individuals 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 each zooplankton species or group in each column. Using MS Excel statistical software, a one-way ANOVA was performed to test for significant differences in the mean depth of each zooplankton species or group in the UV+ and UV– columns. A two-way ANOVA was used to test for significant differences in the mean depths of zooplankton in the UV+ and UV– treatments at midday versus late afternoon.

Linear regression analysis was performed to test for a significant relationship between irradiance and the percentage of zooplankton found in the bottom sections of both the UV+ and UV– columns in Lake Giles. The upward experiment from 20 July 2000 was eliminated from this analysis because during the 30-minute incubation a large cloud passed over for ~10 minutes. This would have been sufficient time for the *Daphnia* to migrate upward in response to lower irradiance (Leech and Williamson, 2001), and because of the conical traps, they would not have been able to swim downward again. Cloud cover was consistent throughout all other experiments.

RESULTS

Lake Giles, high UV

Of all zooplankton species tested, the cladoceran *D. catawba* was most responsive to UVR. In both upward and downward migration experiments, *D. catawba*

displayed a distinct avoidance of the surface waters in the presence of full solar radiation but often showed a preference for the surface in the absence of UV-B and shorter wavelength UV-A radiation (Fig. 1). In 7 out of 11 total experiments, *Daphnia* mean depths were significantly deeper in the UV+ treatment than in the UV– treatment. *Daphnia* mean depths were significantly shallower in the UV+ treatment in one experiment (Table III). Furthermore, differences in mean depths between UV+ and UV– treatments were greatest for *Daphnia* compared to the copepods (Fig. 2).

Copepods were less responsive to UVR. Copepod adults often remained in the column section in which they were introduced (i.e. the 0.5 m section for downward experiments and the >1.5 m section for upward experiments) (Fig. 1). Mean depths of diaptomids in the UV+ and UV– treatments differed significantly in six experiments. In five experiments, diaptomids were significantly deeper in the UV+ treatment and, in one experiment, they were significantly shallower in the UV+ treatment (Table III). Cyclopoids were significantly deeper in the UV+ treatment in three experiments and significantly shallower in one experiment (Table III). Differences in the mean depths between UV+ and UV– treatments for both diaptomids and cyclopoids were less than 0.4 m (Fig. 2).

The responses of *Daphnia* varied among experiments with mean depths becoming increasingly deeper in UV– treatment in late August than in mid-July (Fig. 3). As a result, differences in mean depths between the UV+ and UV– treatments are reduced (Figs 2 and 3). Irradiance appeared to be an important determinant of *Daphnia* depth distributions. As irradiance increased, the percentage of *Daphnia* in the bottom sections of the UV– treatment significantly increased ($R^2 = 0.42$, $P = 0.04$) (Fig. 4). Irradiance did not show a significant relationship with the distributions of copepods. Time of day (i.e., midday versus late afternoon) had no significant effect on the vertical responses of *Daphnia* or copepods (Table III).

Lake Lacawac, low UV

Overall, there was little response to UV for zooplankton taxa inhabiting Lake Lacawac (Fig. 1; Table IV). The cladoceran *Holopedium* displayed an upward migration while the copepods displayed a downward migration in both the UV+ and UV– treatments. In one experiment (21 August 2000), the mean depth of the cyclopoid copepods was significantly shallower in the UV+ treatment. Mean depths of both the diaptomids and the cyclopoids were deeper in Lake Lacawac compared to that of both the diaptomids and the cyclopoids in Lake Giles (Tables III and IV). Similar to the responses in Lake Giles, nauplii tended to remain in the section in which they were introduced (Table IV).

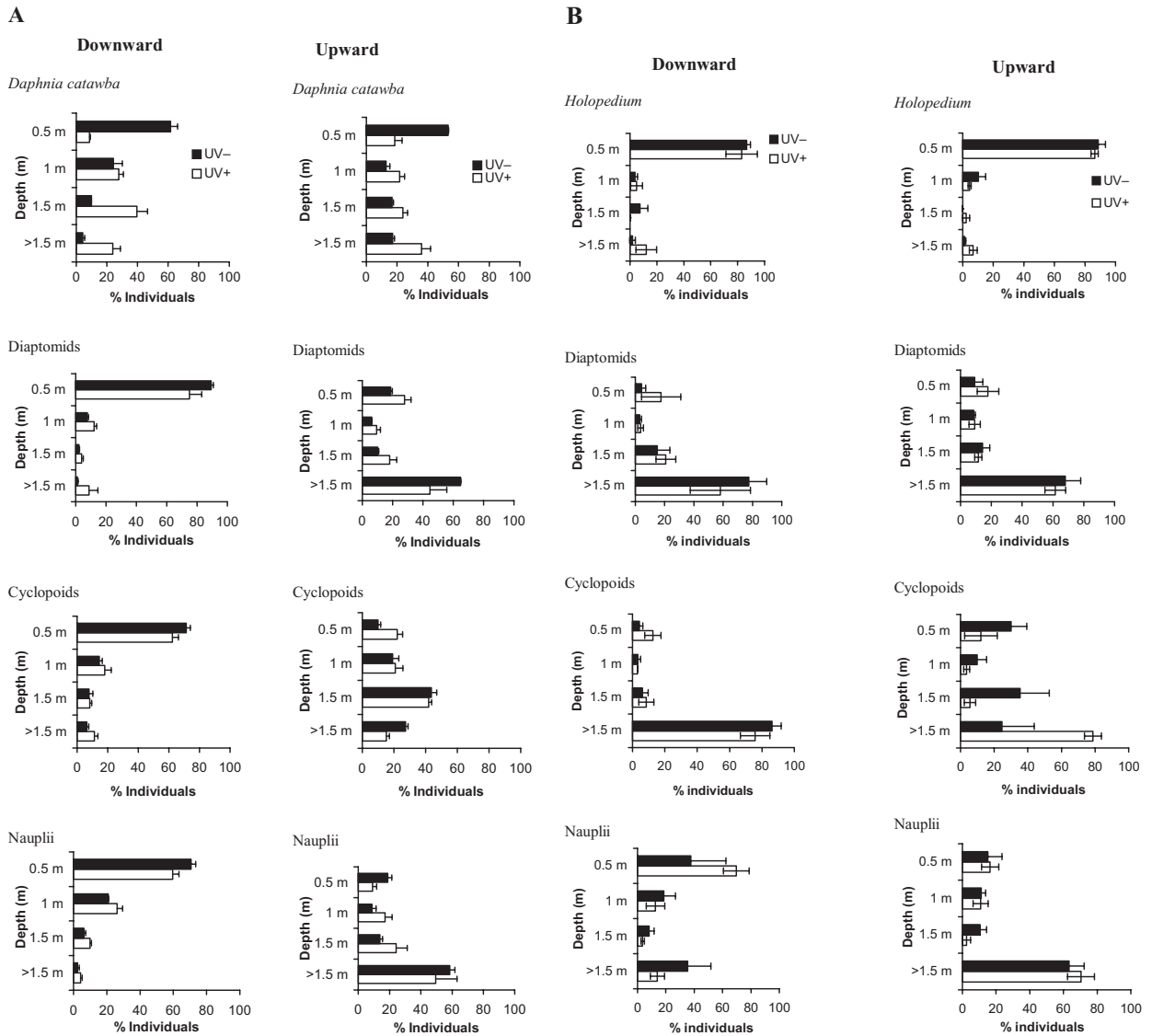


Fig. 1. The vertical distribution of zooplankton in the presence and absence of UVR in Lake Giles, 20 July 2000 (A) and Lake Lacawac, 21 August 2000 (B). Mean percentages in each section of the columns are reported for both downward and upward migration experiments. There were three UV-transmitting columns and three UV-shielding columns. Error bars represent the standard errors.

DISCUSSION

Many factors, both abiotic and biotic, are recognized to induce vertical migrations in zooplankton, and the results of this study suggest that these factors may vary among lakes. Zooplankton with low UVR-tolerance exhibited a greater vertical response to solar UV radiation in the low DOC, high-UV lake compared to that in the high DOC, low-UV lake. The cladoceran *D. catawba* consistently avoided the surface waters of Lake Giles in the presence of UVR but was often abundant in the surface waters in the absence of UVR

(Fig. 1). Furthermore, differences in mean depths between the UV+ and UV- treatments were greatest for *Daphnia* compared to the copepods (Fig. 2). Copepods were less responsive to UVR with calanoids displaying a somewhat greater UV avoidance than cyclopoids (Fig. 1; Table III). In the low-UV lake, no significant response to UV was detected in the cladoceran *Holopedium* or in the copepods. However, the copepods did exhibit a downward movement in both the UV+ and UV- treatments, with overall mean depths greater in Lake Lacawac compared to Lake Giles.

Table III: Mean depths of Lake Giles zooplankton in the presence and absence of UV

Date	Time of day	Direction of funnels	Group	Mean Depth (m) ± SE		Significance
				UV+	UV-	
17 July 2000	Midday	Down	<i>Daphnia</i>	1.08 ± 0.02	0.52 ± 0.03	$P < 0.001$
			Late afternoon	1.11 ± 0.04	0.60 ± 0.01	$P < 0.001$
	Midday		Diaptomids	0.88 ± 0.09	0.53 ± 0.04	$P < 0.05$
			Late afternoon	0.79 ± 0.05	0.51 ± 0.02	$P < 0.01$
	Midday		Cyclopoids	0.58 ± 0.04	0.43 ± 0.03	$P < 0.05$
			Late Afternoon	0.58 ± 0.01	0.44 ± 0.01	$P < 0.01$
	Midday		Nauplii	1.09 ± 0.05	0.96 ± 0.11	
			Late afternoon	0.60 ± 0.04	0.53 ± 0.02	
18 July 2000	Midday	Down	<i>Daphnia</i>	1.16 ± 0.03	0.55 ± 0.08	$P < 0.01$
			Late afternoon	1.10 ± 0.03	0.54 ± 0.02	$P < 0.001$
	Midday		Diaptomids	0.80 ± 0.08	0.47 ± 0.02	$P < 0.05$
			Late afternoon	0.63 ± 0.10	0.36 ± 0.01	$P < 0.05$
	Midday		Cyclopoids	0.70 ± 0.10	0.49 ± 0.07	
			Late afternoon	0.54 ± 0.04	0.43 ± 0.03	
	Midday		Nauplii	1.03 ± 0.09	0.93 ± 0.03	
			Late afternoon	0.60 ± 0.01	0.56 ± 0.02	
20 July 2000	Midday	Down	<i>Daphnia</i>	1.30 ± 0.04	0.90 ± 0.02	$P < 0.001$
		Up	1.03 ± 0.04	0.55 ± 0.02	$P < 0.001$	
	Down		Diaptomids	0.54 ± 0.02	0.39 ± 0.03	$P < 0.05$
			Up	0.81 ± 0.04	0.82 ± 0.05	
	Down		Cyclopoids	0.57 ± 0.03	0.48 ± 0.02	
			Up	1.00 ± 0.04	0.95 ± 0.10	
	Down		Nauplii	1.00 ± 0.04	0.86 ± 0.15	
			Up	1.05 ± 0.02	1.02 ± 0.16	
2 August 2000	Midday	Up	<i>Daphnia</i>	1.04 ± 0.05	0.69 ± 0.01	$P < 0.01$
			Diaptomids	0.87 ± 0.09	0.88 ± 0.03	
			Cyclopoids	0.96 ± 0.04	1.09 ± 0.03	
			Nauplii	1.21 ± 0.02	1.35 ± 0.02	$P < 0.01$
22 August 2000	Midday	Down	<i>Daphnia</i>	0.98 ± 0.02	0.82 ± 0.10	
		Up	1.09 ± 0.02	0.97 ± 0.06		
	Down		Diaptomids	0.46 ± 0.09	0.32 ± 0.01	
			Up	1.04 ± 0.08	1.19 ± 0.01	
	Down		Cyclopoids	1.00 ± 0.02	0.69 ± 0.04	$P < 0.01$
			Up	1.00 ± 0.03	1.19 ± 0.04	$P < 0.05$
	Down		Nauplii	0.53 ± 0.02	0.45 ± 0.03	
			Up	1.32 ± 0.12	1.31 ± 0.03	
25 August 2000	Midday	Down	<i>Daphnia</i>	1.07 ± 0.03	1.25 ± 0.01	$P < 0.01$
		Up	1.12 ± 0.04	1.02 ± 0.08		
	Down		Diaptomids	0.35 ± 0.01	0.48 ± 0.00	$P < 0.001$
			Up	1.09 ± 0.05	1.10 ± 0.02	
	Down		Cyclopoids	0.78 ± 0.07	1.00 ± 0.06	
			Up	1.18 ± 0.05	1.22 ± 0.02	
	Down		Nauplii	0.44 ± 0.04	0.72 ± 0.02	$P < 0.01$
			Up	1.45 ± 0.06	1.48 ± 0.03	

The mean depths and standard errors for the different zooplankton groups in each experiment conducted in Lake Giles. Direction of funnels indicates whether column funnels were pointed downward or upward during an experiment. Depths and standard errors are based on data collected from three replicate columns per treatment. Significant differences in the mean depths of organisms in the UV+ and UV- treatments are analysed using a two-way ANOVA.

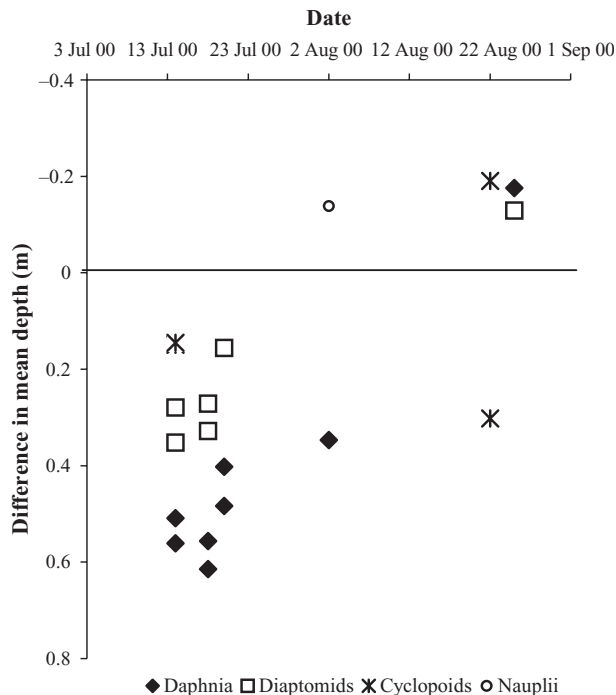


Fig. 2. The difference in mean depth (m) between UV+ and UV- treatments for experiments in which the distribution of each Lake Giles zooplankton group significantly differed between the two light treatments. Data points located above the line indicated mean depths shallower in the presence of UVR while points below the line indicate mean depths deeper in the presence of UVR. *Daphnia catawba* generally exhibited the greatest difference in mean depth between the two light treatments compared to copepods.

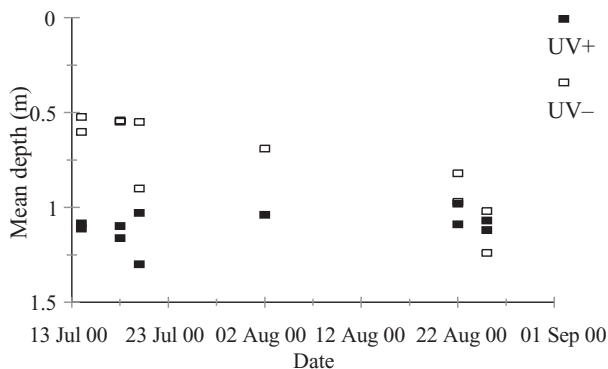


Fig. 3. Mean depths (m) of *Daphnia catawba* in ambient and reduced UV radiation treatments in Lake Giles. Mean depths were consistently deeper in the UV+ treatment in July. However, in the UV- treatment, mean depths decreased from mid-July through late August. Thus, there is a greater difference in mean depth between the UV+ and UV- treatment in mid-July than in late August.

Light intensity and Lake Giles *Daphnia*

Although *Daphnia* in Lake Giles often displayed a preference for the surface waters in the UV-blocking

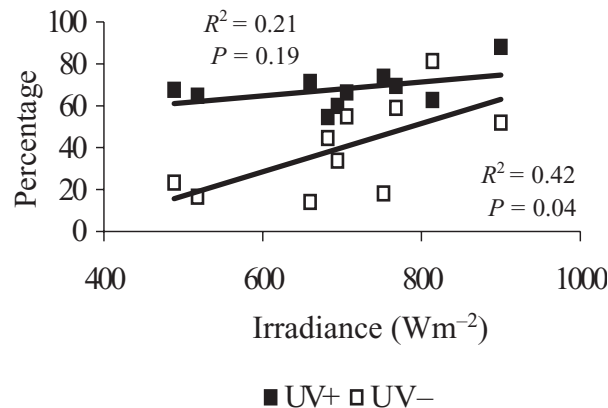


Fig. 4. Linear regression analysis of *Daphnia catawba* depth distributions from all experiments in Lake Giles versus irradiance ($W m^{-2}$, measured with a LICOR pyranometer). A greater percentage of *Daphnia* were found in the bottom sections of the UV- treatment (open squares) as light intensity increased. *Daphnia* were consistently found at greater frequencies in the bottom sections of the UV+ treatment (shaded squares).

treatment, the response was variable, with mean depths increasing in the UV- treatment from mid-July to late August (Fig. 3). The reason for this variability is unknown. It is possible that there is a seasonal variation in the avoidance response of *Daphnia* to UV exposure. Irradiance differed among experiments. Although the experiments in this study were not designed to specifically test zooplankton responses to irradiance, *Daphnia* did exhibit stronger negative phototaxis at higher irradiance values (Fig. 4). No statistically significant responses to irradiance were detected in the copepods.

Laboratory studies have demonstrated that increased brightness initiates negative phototaxis in *Daphnia* as well as other freshwater invertebrates (Hairston, 1976; Swift and Forward, 1988), but less is known of zooplankton responses to increased irradiance in nature under full spectrum solar radiation. In addition to visible light, the UV- columns used in this study also transmitted longer wavelength UV-A light. Zooplankton may therefore be responding to increases in either UV-A or visible light. Prior observations made by Smith and Baylor (Smith and Baylor, 1953) noted that *Daphnia* do detect and respond to blue light with negative phototaxis.

Fish predation or kairomones

Fish predation or increasing kairomone concentrations may also explain the variability in the distributions of Lake Giles *D. catawba* among experiments as well as the difference in the response of the copepods between Lakes Lacawac and Giles. Multiple studies have demonstrated that increased predation induces downward daytime

Table IV: Mean depths of Lake Lacawac zooplankton in the presence and absence of UV

Date	Time of day	Genus/species	Direction of Funnels	Mean depth (m) ± SE		Significance
				UV+	UV-	
21 August 2000	Midday	<i>Holopedium</i>	Down	0.44 ± 0.12	0.37 ± 0.03	<i>P</i> < 0.05
			Up	0.38 ± 0.02	0.30 ± 0.03	
		Diaptomids	Down	1.20 ± 0.19	1.39 ± 0.06	
			Up	1.18 ± 0.08	1.29 ± 0.08	
		Cyclopoids	Down	1.30 ± 0.07	1.49 ± 0.11	
			Up	1.50 ± 0.11	1.02 ± 0.16	
24 August 2000	Midday	<i>Holopedium</i>	Down	0.52 ± 0.13	0.39 ± 0.09	
			Up	0.44 ± 0.02	0.64 ± 0.08	
		Diaptomids	Down	1.38 ± 0.02	1.36 ± 0.05	
			Up	1.15 ± 0.22	1.41 ± 0.00	
		Cyclopoids	Down	1.42 ± 0.01	1.47 ± 0.03	
			Up	1.53 ± 0.11	1.72 ± 0.01	
Nauplii	Down	0.84 ± 0.14	0.83 ± 0.09			
	Up	1.56 ± 0.06	1.59 ± 0.00			

The mean depths and standard errors for the different zooplankton groups in each experiment conducted in Lake Lacawac. Direction of funnels indicates whether the column funnels were pointed downward or upward during an experiment. Depths and standard errors are based on data collected from three replicate columns per treatment. Significant differences in the mean depths of organisms in the UV+ and UV- treatments are analysed using a two-way ANOVA.

migrations in zooplankton (Stich and Lampert, 1981; Gliwicz, 1986; Tjossen, 1990). Neither predator abundance nor kairomone concentrations were monitored during this study, but other studies have noted seasonal increases in predation rates by juvenile fish feeding in the pelagic zone (Hairston, 1988; Boersma *et al.*, 1996). The increase in the percentage of *Daphnia* located in the bottom of both the UV-transparent and UV-blocking columns in Lake Giles on the 22nd and 25th of August 2000 (Fig. 3; Table III) may therefore have been the result of an increase in kairomone concentrations in the lake water used to fill the columns because of a seasonal increase in juvenile fish feeding on zooplankton.

In Lake Lacawac, the copepods were consistently found in the bottom of the columns in the presence and absence of UVR, while in Lake Giles, the copepods were distributed throughout the columns if not in the section in which they were introduced (Tables III and IV). Lake Lacawac is a mesotrophic lake and supports a greater biomass of planktivorous fish than Lake Giles. For example, during 1990 fish trapping efforts over several days in the two lakes using twelve 12-h gills yielded 42 planktivorous fish in Lake Giles and 76 in Lacawac (Moeller *et al.*, 1995). Zooplankton may therefore be more responsive to fish predation than UV in Lake Lacawac.

Food limitation

In addition, food availability and/or quality may have influenced the depth distributions of *Daphnia* in Lake Giles, but this appears less plausible. Both laboratory and field experiments have demonstrated that *Daphnia* distributions can vary with the quality and quantity of algal food (Leibold, 1990; Williamson *et al.*, 1996). During this study, no major changes in chlorophyll concentrations were observed in the epilimnion of Lake Giles (0.52–0.68 $\mu\text{g L}^{-1}$) (R. Moeller, unpublished results). However, this does not account for possible shifts in phytoplankton or protozoan species composition, which were not examined. Previous studies have indicated that *Daphnia* remain in the surface waters when food is limiting, regardless of the risk of predation (Johnsen and Jakobsen, 1987). Thus, in this study, *Daphnia* should remain in the surface waters of both UV treatments if food were limiting. This was not so in our experiments, as the majority of *Daphnia* were found in the lower sections of the columns of both light treatments in late August.

The studies that previously reported this behavior were conducted in humic systems. Consequently, UVR as well as visible light would have been attenuated more rapidly. It may be that in high-UV systems, risk of exposure to damaging solar radiation is greater than predation, such that

Daphnia migrate out of the surface waters even when food availability is low.

UV behavioral responses and natural distribution patterns

In general, differences in behavioral responses to UVR appear to be related to UV tolerance and reflect typical migration patterns seen in zooplankton inhabiting Lakes Giles. Diaptomid copepods are both highly epilimnetic throughout the summer months (May to September) and possess high UVR tolerances (Leech and Williamson, 2000). It is therefore not surprising that they display similar distributions in both the presence and absence of UVR. Conditions may have been optimal for diaptomids at both the top and bottom of the columns since they were suspended only within the top of the epilimnion. This may explain why they tended to remain in the section in which they were introduced. Another possibility is that the incubation period was too short for all the calanoids to leave the section of introduction. On average, there were 1500–2000 calanoids introduced to the columns in Lake Giles. Of these an average of 50–60% swam from the section in which they were introduced.

Cyclopoid distributions were also similar in both UV treatments with most individuals remaining in the section in which they were introduced. The reason for this is not clear since the dominant cyclopoid, *C. scutifer*, is typically hypolimnetic in Lake Giles and does not exhibit diel vertical migration (DVM) (Leech *et al.*, 2005). However, they do have moderate to high UVR tolerances (Leech and Williamson, 2000). It is unlikely that they did not have enough time to migrate to the opposite end of the column from which they were introduced because they are strong and fast swimmers (Strickler *et al.*, 1975). In some experiments, approximately 20% of the cyclopoids were found in the opposite end of the column, suggesting that such migrations are possible even for the nauplii (Fig. 1). In addition, cyclopoids appeared to be moving upward in some upward migration experiments (Table III).

Daphnia possess low UV tolerance and display a distinct vertical migration out of the surface waters of Lake Giles during the day from May until late August (Leech and Williamson, 2000). In this study, however, *Daphnia* often exhibited a preference for the surface waters in the absence of UVR (Fig. 1; Table III). *Daphnia pulicaria* from Dutch Springs Reservoir, a high-UV lake in Bethlehem, PA, USA, exhibited a similar preference for the surface in the absence of UVR in the same UV+ and UV– columns used in this study (Leech and Williamson, 2001). Interestingly, *D. pulicaria* in Dutch Springs also typically undergo DVM during the summer months. Fish are present in both systems and are likely to be a

driving force in inducing migrations; yet, in both studies, *Daphnia* spp. were often present in the surface waters in the absence of UVR despite the probable presence of fish kairomones.

Ultimate causes of zooplankton vertical migration

These data suggest that ultimate causes of zooplankton vertical migration may vary among lakes and are supported by recent whole lake observations of zooplankton vertical distribution in lakes of varying UV transparency (Alonso *et al.*, 2004). In high DOC, low-UV lakes with fish, predation may be the ultimate factor driving zooplankton migrations out of the surface waters during the day. However, in low DOC, high-UV systems with or without fish, UV avoidance may be the ultimate cause of zooplankton vertical migration. Future studies are necessary to explore this hypothesis more directly in a wider variety of lakes.

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REFERENCES

- Alonso, C., Rocco, V., Barriga, J. P. *et al.* (2004) Surface avoidance by freshwater zooplankton: field evidence on the role of ultraviolet radiation. *Limnol. Oceanogr.*, **49**, 225–232.
- Barcelo, J. A. and Calkins, J. (1978) Positioning of aquatic microorganisms in response to visible light and simulated solar UV-B irradiation. *Photochem. Photobiol.*, **29**, 75–83.
- Boersma, M., Van Tongeren, O. F. R. and Mooij, W. M. (1996) Seasonal patterns in the mortality of *Daphnia* species in a shallow lake. *Can. J. Fish. Aquat. Sci.*, **53**, 18–28.
- Fleischmann, E. M. (1989) The measurement and penetration of ultraviolet radiation into tropical marine water. *Limnol. Oceanogr.*, **34**, 1623–1629.
- Gliwicz, M. Z. (1986) Predation and the evolution of vertical migration in zooplankton. *Nature*, **320**, 746–748.
- Grad, G., Williamson, C. E. and Karapelou, D. M. (2001) Zooplankton survival and reproduction responses to damaging UV radiation: a test of reciprocity and photoenzymatic repair. *Limnol. Oceanogr.*, **46**, 584–591.
- Hairston, N. G. Jr. (1976) Photoprotection by carotenoid pigments in the copepod *Diaptomus nevadensis*. *Proc. Natl. Acad. Sci. U. S. A.*, **73**, 971–974.

- Hairston, N. G. Jr. (1979) The adaptive significance of color polymorphism in two species of *Diaptomus* (Copepoda). *Limnol. Oceanogr.*, **24**, 15–37.
- Hairston, N. G. Jr. (1988) Interannual variation in seasonal predation: its origin and ecological importance. *Limnol. Oceanogr.*, **33**, 1245–1253.
- Johnsen, G. H. and Jakobsen, P. J. (1987) The effect of food limitation on vertical migration in *Daphnia longispina*. *Limnol. Oceanogr.*, **32**, 873–880.
- Karanas, J. J., van Dyke, H. and Worrest, R. C. (1979) Midultraviolet (UV-B) sensitivity of *Acartia clausii* Giesbrecht (Copepoda). *Limnol. Oceanogr.*, **24**, 1104–1116.
- Leech, D. M. and Williamson, C. E. (2000) Is tolerance to UV radiation in zooplankton related to body size, taxon, or lake transparency? *Ecol. Appl.*, **10**, 1530–1540.
- Leech, D. M. and Williamson, C. E. (2001) *In situ* exposure to solar UV radiation alters the depth distribution of *Daphnia*. *Limnol. Oceanogr.*, **46**, 416–420.
- Leech, D. M., Williamson, C. E., Moeller R. E. et al. (2005) UV radiation and zooplankton vertical distribution and abundance: testing for UV behavioral avoidance. *Arch. Fur Hydrobiol.*, **162**, 445–464.
- Leibold, M. A. and West, C. T. (1993) Experimental methods for measuring the effect of light acclimation on vertical migration by *Daphnia* in the field. *Limnol. Oceanogr.*, **38**, 638–643.
- Leibold, M. A. (1990) Resources and predators can affect the vertical distributions of zooplankton. *Limnol. Oceanogr.*, **35**, 938–944.
- Martin, G. G., Speckmann, C. and Beidler, S. (2000) Photobehavior of the harpacticoid copepod *Tigriopus californicus* and the fine structure of its nauplius eye. *Invertebr. Biol.* **119**, 110–124.
- Moeller, R. E., Williamson, C. E., Hargreaves, B. R. and Morris, D. P. (1995) *Limnology of Lakes Lacawac, Giles, and Waynewood 1989–93: An Introduction to the Core Lakes of the Pocono Comparative Lakes Program*. Department of Earth and Environmental Sciences, Lehigh University, Bethlehem, PA.
- Morris, D. P., Zagarese, H., Williamson, C. E. et al. (1995) The attenuation of solar UV radiation in lakes and the role of dissolved organic carbon. *Limnol. Oceanogr.*, **40**, 1381–1391.
- Ringelberg, J., Keyser, A. L. and Flik, B. J. G. (1984) The mortality effect of ultraviolet radiation in a red morph of *Acanthodiatomus denticornis* (Crustacea: Copepoda) and its possible ecological relevance. *Hydrobiologia*, **112**, 217–222.
- Scully, N. M. and Lean, D. R. S. (1994) The attenuation of ultraviolet radiation in temperate lakes. *Arch. Fur Hydrobiol. Beih. Ergebn. Limnol.*, **43**, 135–144.
- Siebeck, O., Vail, T., Williamson, C. E. et al. (1994) Impact of UV-B radiation on zooplankton and fish in pelagic freshwater ecosystems. *Arch. Fur Hydrobiol. Beih. Ergebn. Limnol.*, **43**, 101–114.
- Smith, F. E. and Baylor, E. R. (1953) Color responses in the cladocera and their ecological significance. *Am. Nat.*, **87**, 49–55.
- Smith, K. C. and Macagno, E. R. (1990) UV photoreceptors in the compound eye of *Daphnia magna* (Crustacea, Branchiopoda). A fourth spectral class in single ommatidia. *J. Comp. Physiol., A*, **166**, 597–606.
- Stich, H. B. and Lampert, W. (1981) Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature*, **293**, 396–398.
- Storz, U. C. and Paul, R. J. (1998) Phototaxis in water fleas (*Daphnia magna*) is differently influenced by visible and UV light. *J. Comp. Physiol., A*, **183**, 709–717.
- Strickler, J. R. (1975) Swimming of planktonic *Cyclops* species (Copepoda, Crustacea): pattern, movements, and their control. In Wu, T. Y. T., Brokaw, C. J. and Brennan, C. (eds), *Swimming and Flying in Nature*, Vol. 2, Plenum Press, NY, pp. 599–613.
- Swift, M. C. and Forward, R. B. (1988) Absolute light intensity vs. rate of relative change in intensity: the role of light in the vertical migration of *Chaoborus punctipennis* larvae. *Bull. Mar. Sci.*, **43**, 604–619.
- Tjossen, S. F. (1990) Effects of fish chemical cues on vertical migration behavior of *Chaoborus*. *Limnol. Oceanogr.*, **35**, 1456–1468.
- Williamson, C. E., Zagarese, H. E., Schulze, P. C. et al. (1994). The impact of short-term exposure to UV-B radiation on zooplankton communities in north temperate lakes. *J. Plankton Res.*, **16**, 205–218.
- Williamson, C. E., Sanders, R. W., Moeller, R. E. et al. (1996) Utilization of subsurface food resources for zooplankton reproduction: implications for diel vertical migration theory. *Limnol. Oceanogr.*, **41**, 224–233.
- Zagarese, H. E., Feldman, M. and Williamson, C. E. (1997) UV-B induced damage and photoreactivation in three species of *Boeckella* (Copepoda, Calanoida). *J. Plankton Res.*, **19**, 357–367.
- Zagarese, H. E. and Williamson, C. E. (1994) Modeling the impacts of UV-B radiation on ecological interactions in freshwater and marine ecosystems. In Biggs, R. H. and Joyner, M. B. E. (eds), *Stratospheric Ozone Depletion/UV-B Radiation in the Biosphere*. Springer-Verlag, New York, pp. 315–328.
- Zagarese, H. E., Williamson, C. E., Mislavets, M. et al. (1994) The vulnerability of *Daphnia* to UV radiation in the Northeastern United States. *Arch. Fur Hydrobiol. Beih. Ergebn. Limnol.*, **43**, 207–216.

