

Does UV play a role in changes in predation and zooplankton community structure in acidified lakes?

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Abstract

Changes in both zooplankton community structure and zooplanktivorous predators often accompany the anthropogenic acidification of lakes. While changes in pH can account for many of the observed changes, combined observations from laboratory bioassay and field experiments as well as surveys suggest that these patterns cannot be explained by changes in pH alone. Dissolved organic carbon (DOC) also declines with lake acidification. Because DOC is the primary factor regulating variation in the depth of penetration of ultraviolet radiation (UVR) in lakes, there is also likely to be an increase in UVR levels during acidification. This suggests that changes in UVR may play some role in changes in predator and prey communities during acidification. As a first step toward testing this hypothesis, we examined the UVR tolerance of larvae of two widespread and abundant zooplanktivorous predators. We performed a series of in situ incubation experiments with the sunfish *Lepomis* and the midge *Chaoborus* in a low DOC (high UVR) lake and in a moderate DOC (low UVR) lake. Substantial UVR-induced mortality of both predators was observed in the surface waters of the low DOC lake. The predators differed in their UVR tolerance levels: the sunfish survived for more than a day under high solar radiation conditions in the surface waters of a low DOC lake, while the midge perished in less than a day. These data and past literature are consistent with the hypothesis that UVR may play a role in changes in planktivorous predators and their prey during lake acidification and recovery.

The effect of changing solar ultraviolet radiation (UVR) on aquatic ecosystems has received much attention in recent years due to concerns about stratospheric ozone depletion, as well as changes in other stressors that alter underwater UVR environments (Schindler et al. 1996; Williamson et al. 1996; Yan et al. 1996). Most efforts have focused on understanding the effects of UVR on the primary producers because their exposure to solar UVR is likely to be high due to their requirements for sunlight for photosynthesis, because they are the base of aquatic food webs, and because they play a major role in global biogeochemical cycles. Several recent studies have demonstrated that herbivores in the surface waters of lakes may also be sensitive to natural levels of solar UVR (Siebeck et al. 1994; Williamson et al. 1994). Reductions in grazing pressure of UV-sensitive herbivores increase the complexity of the ecosystem level response and may actually cause an increase rather than a decrease in the standing crop of primary producers under high UVR conditions (Bothwell et al. 1994). Although the potential for such complex responses of aquatic ecosystems to changing UVR is now widely recognized (Vincent and Roy 1993; Williamson 1995), little is known about how UVR may influence higher trophic levels such as predators. This is an important consideration in lakes where both vertebrate and

invertebrate predators play a central role in the structure and function of plankton communities. Invertebrate predators prey heavily on smaller zooplankton, while visually feeding vertebrate predators prey heavily on larger zooplankton. Both types of predators are highly selective even within a size class and may consequently alter zooplankton species composition, size structure, distribution, abundance, and grazing pressures, with profound implications for lake ecosystem structure and function (Carpenter and Kitchell 1993; Kerfoot and Sih 1987; Zaret 1980).

Changes in predation regimes in anthropogenically acidified lakes are of particular interest due to the potential for interaction of multiple stressors. Two major changes in the predation regime of lakes are often observed as they become acidified: vertebrate predation pressures decrease with reductions in fish populations, while predation pressure from predatory insects such as the phantom midge *Chaoborus* increases as they increase in abundance (Eriksson et al. 1980; Fischer and Frost 1997; Yan et al. 1991). Concomitant changes in zooplankton community structure often include an increase in the abundance of certain zooplankton and decreases in the abundance of others (Yan and Strus 1980; Malley and Chang 1986; Brett 1989; Schindler et al. 1991; Brezonik et al. 1993). Non-insect invertebrate predators such as *Asplanchna*, *Mesocyclops*, *Epischura*, and *Mysis* may also decrease in abundance in acidified lakes (Fischer and Frost 1997; Schindler et al. 1985; Sierszen and Frost 1993). Although changes in pH alone are sufficient to explain some observed changes in zooplankton community structure (Havens et al. 1993), in many cases they are inadequate and other indirect effects are often invoked (Brett 1989; Brezonik et al. 1993; Locke 1991).

One potentially important stressor that has not been adequately investigated in acidified lakes is damaging solar UV

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radiation. Dissolved organic carbon (DOC) is the primary factor controlling the attenuation of solar radiation among lakes (Kirk 1994; Scully and Lean 1994; Morris et al. 1995), and there are several studies that provide evidence for a decrease in DOC and consequent increase in UVR with anthropogenic acidification (Yan et al. 1996; Schindler et al. 1996; Williamson et al. 1996). The actual mechanism of DOC reduction during acidification is controversial (for a brief review, see Williamson et al. 1996). Interestingly, fish and zooplankton community structure are at times closely related to DOC in acidified lakes (Brett 1989; Collier et al. 1990; Nelson and Magnuson 1992). In addition, recent evidence indicates that herbivorous zooplankton and fish eggs are vulnerable to damage by natural levels of UVR in the surface waters of lakes (Williamson et al. 1994, 1997). This suggests that some of the changes observed in these planktivorous predators and their zooplankton prey in acid lakes may be influenced by differences in the UVR environment as well as by pH and other stressors.

As a first step toward understanding the potential interactions between damaging UV radiation, predation, and pH in acidified lakes, we examined the effects of solar UVR on two common predators: the larval stages of the phantom midge *Chaoborus punctipennis*, and larvae of two species of sunfish in the genus *Lepomis*. Both *Lepomis* and *Chaoborus* are important zooplanktivorous predators that are widespread and abundant across North America. We incubated these two predators in the surface waters of two lakes, one lake with low DOC (high UVR) and one with moderate DOC (low UVR), to examine the sensitivity of these predators to natural levels of solar UVR. The central question is whether higher trophic levels (i.e., invertebrate predators and fish) are vulnerable to natural levels of UVR, and if so, do they exhibit differences in their UVR tolerance? The implications of these findings for changes in the predation regimes and zooplankton prey communities in acidified lakes are the focus of the discussion.

Methods

Study sites—The three study lakes are on the Pocono Plateau of northeastern Pennsylvania and form the core lakes of the Pocono Comparative Lakes Program. Lake Giles (41°23'N, 75°06'W) is a highly transparent (summer Secchi depths between 12 and 16 m), low color (midsummer epilimnetic absorbance at 320 nm, $\sim 0.25 \text{ m}^{-1}$) acidic (pH 5.2–5.4), poorly buffered (acid neutralizing capacity, ANC, is usually negative, in the range of -10 to $0 \mu\text{eq liter}^{-1}$) oligotrophic lake (TP = $0.23 \mu\text{M}$) with a low DOC concentration ($\sim 1.1 \text{ mg liter}^{-1}$) and thus high levels of UV radiation in the surface waters. Lake Lacawac (41°23'N, 75°18'W) is a slightly acidic (pH 6.2–6.5), soft-water (ANC 20–40 $\mu\text{eq liter}^{-1}$) mesotrophic lake (TP = $0.46 \mu\text{M}$) with summer Secchi depths in the range of 4–6 m, moderate color (midsummer epilimnetic absorbance at 320 nm, $\sim 7.5 \text{ m}^{-1}$) and moderate DOC concentrations ($\sim 4.8 \text{ mg liter}^{-1}$), and thus low to moderate levels of UVR in the surface waters. Lake Waynewood (41°23'N, 75°21'W) is a circumneutral (pH 6.8–8.6+) better buffered (ANC 250–400 $\mu\text{eq liter}^{-1}$) eutrophic lake

(TP = $0.78 \mu\text{M}$) with summer Secchi depths in the range of 2–4 m, moderate color (midsummer epilimnetic absorbance at 320 nm, $\sim 10 \text{ m}^{-1}$) and moderate DOC concentration ($\sim 5.3 \text{ mg liter}^{-1}$), and thus low to moderate levels of UV radiation in the surface waters. (These, and more extensive data are given by R. E. Moeller et al. in an unpublished summary report on the Limnology of the Pocono Comparative Lakes Program core lakes, 1989–1993, available from Lehigh University Libraries through interlibrary loan; optical data are from Morris and Hargreaves 1997).

Optical measurements—Diffuse attenuation coefficients (K_d , m^{-1}) in the experimental lakes as well as other experimental conditions are summarized in Table 1. Underwater solar radiation was measured with a Biospherical Instruments PUV-501 (Biospherical Instr.). Underwater diffuse attenuation coefficients were measured as the slope of the linear regression relationship between the natural logarithm of downwelling irradiance vs. depth in the surface waters of each lake. Ambient solar radiation data were collected and summed over 15-min time intervals with a Biospherical GUV 521 coupled with a Campbell CR-10 data logger (Campbell Scientific, Inc.) located on a weather station near Lake Lacawac. Both the PUV and the GUV are medium bandwidth instruments (8–10-nm full width at half-maximum response) that measure incident solar radiation at four different UVR wavelengths (305, 320, 340, and 380 nm) as well as photosynthetically active radiation (PAR, 400–700 nm). Although they do not collect complete spectral data, these instruments do compare favorably with some of the higher resolution spectroradiometers (Kirk et al. 1994; Laurion et al. 1997). The ambient irradiance data from the 305-nm band of the GUV and the calculated K_d values for the 305-nm band of the PUV were used to estimate UV radiation doses at depth during each experiment. Because UV-A as well as UV-B may be damaging, UVR doses were also estimated with data from the 320-nm band (the boundary wavelength between UV-B and UV-A), and no differences in the patterns in the results were observed.

For ease of interpretation, doses are expressed in units of 305-nm exposure days. One exposure day can be thought of as the amount of 305-nm (UV-B) radiation received at the water surface on a sunny day in June or July. These 2 months were selected because of their proximity to summer solstice. This was determined by gathering the total irradiance data from the 305-nm band of the GUV for each day in June and July over a 3-yr period from 1994 to 1996. The 3 d with the highest daily 305-nm irradiance each of these 2 months of each year were selected, and the average of these 18 values was calculated. This average ($1.01 \text{ kJ m}^{-2} \text{ nm}^{-1}$) was defined as 1 exposure day. The average column ozone on the 18 reference days ranged from 285 to 315 Dobson units (avg = 306, typical for this region), as estimated from satellite column ozone data from the TOMS instrument on the Meteor 3 satellite for 1994 (available at <http://jwocky.gsfc.nasa.gov>) and from NOAA's Climate Prediction Center for 1995 and 1996 (<http://nic.fb4.noaa.gov/products/stratosphere/tovsto/>). The dose for each experimental duration was then converted from $\text{kJ m}^{-2} \text{ nm}^{-1}$ (at 305 nm) to 305-nm exposure days by dividing by

Table 1. Experimental and optical data for all UV exposure experiments. Experiment codes indicate respectively the source and incubation lakes (prefix, G—Giles, L—Lacawac, W—Waynewood), the test species and experiment number (B—bluegill, P—pumpkinseed, C—*Chaoborus*), and incubation depth (cm). Starting time and experimental duration (Dur.) are given in decimal hours (EDT) and decimal days respectively. Thus, a start time of 16.5 = 1630, not 1650, and a duration of 4.29 d = 4 d, 7 h. PAR levels and UV doses are for the experimental duration at the depth of incubation, with units of mol m⁻² for PAR, and units of exposure days for total UVR exposure. Details given in methods section.

Exp. code	Start date	Start time	Dur. (d)	Attenuation coef. (K_p , m ⁻¹)					UV dose (kJ m ⁻² nm ⁻¹)					Total			Percent survival		
				305	320	340	380	PAR	305	320	340	380	PAR	UVR	Dark	Mylar	Quartz		
<i>Lepomis</i> experiments																			
LG-P6-5	7 Jul	16.5	4.29	0.35	0.25	0.21	0.13	0.13	3.22	25.52	48.53	68.91	182.30	3.20	92	10	0		
LG-P6-80	7 Jul	16.5	4.29	0.35	0.25	0.21	0.13	0.13	2.48	21.16	41.46	62.51	165.40	2.46	100	78	32		
LG-P7-80	12 Jul	15.5	3.06	0.35	0.25	0.21	0.13	0.13	1.44	12.70	24.94	37.22	98.87	1.43	90	22	45		
LG-P9a-5	18 Jul	17	1.06	0.39	0.31	0.26	0.16	0.13	0.80	6.87	13.18	18.80	50.88	0.80	84	82	32		
LG-P9a-80	18 Jul	17	1.06	0.39	0.31	0.26	0.16	0.13	0.60	5.44	10.85	16.67	46.15	0.59	88	98	90		
LG-P9b-80	18 Jul	17	3.02	0.39	0.31	0.26	0.16	0.13	1.74	15.10	30.00	46.02	126.60	1.73	92	20	4		
LL-P2-5	13 Jun	19	2.63	13.8	11.3	8.6	4.7	0.81	1.04	9.03	19.50	33.40	108.00	1.03	100	85	95		
LL-P2-100	13 Jun	19	2.63	13.8	11.3	8.6	4.7	0.81	0.00	0.00	0.01	0.40	50.20	0.00	100	92	100		
LL-P6-5	7 Jul	13.5	4.33	13.3	10.89	8.47	4.24	0.67	1.84	16.20	34.60	60.40	191.00	1.83	92	86	82		
LL-P6-80	7 Jul	13.5	4.33	13.3	10.89	8.47	4.24	0.67	0.00	0.00	0.06	2.51	116.00	0.00	100	86	86		
LL-P9-5	18 Jul	19.5	2.98	11.2	9.17	7.85	4.14	0.67	1.35	12.20	24.80	42.30	135.00	1.34	96	22	10		
GG-B10-80	22 Jul	11.5	3.27	0.39	0.31	0.26	0.16	0.13	1.64	14.06	27.57	41.80	111.50	1.63	82	89	36		
GG-B11-5	27 Jul	13.5	2.19	0.45	0.38	0.31	0.19	0.19	1.51	11.07	20.43	28.53	72.48	1.49	94	82	84		
GG-B11-80	27 Jul	13.5	2.19	0.45	0.38	0.31	0.19	0.19	1.07	8.33	16.19	24.74	62.85	1.06	84	96	78		
GL-B10-5	22 Jul	14	3.79	11.2	9.17	7.85	4.14	0.67	1.10	10.30	21.10	35.60	111.00	1.09	100	82	56		
GL-B11-5	27 Jul	16	2.13	11.7	9.6	7.09	3.77	0.74	0.77	6.36	13.30	21.90	64.90	0.76	96	88	86		
GL-B11-80	27 Jul	16	2.13	11.7	9.6	7.09	3.77	0.74	0.00	0.00	0.07	1.30	37.20	0.00	93	88	75		
<i>Chaoborus</i> experiments																			
LG-C6a-5	18 Jul	17	1	0.39	0.31	0.26	0.16	0.13	0.78	6.45	12.27	17.50	47.12	0.78	94	8.3	1.7		
LG-C6a-80	18 Jul	17	1	0.39	0.31	0.26	0.16	0.13	0.58	5.11	10.10	15.52	42.75	0.58	96	0	0		
LG-C6c-5	20 Jul	18.5	0.98	0.39	0.31	0.26	0.16	0.13	0.82	6.37	12.07	17.11	45.51	0.82	90	0	0		
LG-C6c-200	20 Jul	18.5	0.98	0.39	0.31	0.26	0.16	0.13	0.39	3.48	7.27	12.53	35.32	0.38	94	13	9		
LL-C6a-5	18 Jul	19	1	11.2	9.17	7.85	4.14	0.67	0.46	4.30	8.78	15.00	48.60	0.46	98	15	0		
LL-C6a-80	18 Jul	19	1	11.2	9.17	7.85	4.14	0.67	0.00	0.00	0.02	0.67	29.40	0.00	98	95	95		
LL-C6b-5	18 Jul	19	3	11.2	9.17	7.85	4.14	0.67	1.35	12.20	24.80	42.30	135.00	1.34	84	0	0		
LL-C6b-80	18 Jul	19	3	11.2	9.17	7.85	4.14	0.67	0.00	0.01	0.07	1.90	81.80	0.00	83	65	82		
LL-C6c-5	20 Jul	18.5	0.98	11.2	9.17	7.85	4.14	0.67	0.48	4.09	8.26	14.00	44.30	0.48	92	14	37		
LL-C6c-40	20 Jul	18.5	0.98	11.2	9.17	7.85	4.14	0.67	0.01	0.17	0.53	3.29	35.00	0.01	98	92	89		
WW-C4a-5	11 Jul	20	0.96	14.2	11.7	8.8	4.5	0.7	0.46	4.16	9.10	16.20	54.10	0.46	90	10	10		
WW-C4a-185	11 Jul	20	0.96	14.2	11.7	8.8	4.5	0.7	0.00	0.00	0.00	0.01	16.30	0.00	89	100	89		
WW-C4b-5	13 Jul	22	1.88	14.2	11.7	8.8	4.5	0.7	0.45	4.30	9.36	16.10	49.60	0.45	100	30	12		
WW-C4b-50	13 Jul	22	1.88	14.2	11.7	8.8	4.5	0.7	0.00	0.02	0.18	2.14	36.80	0.00	89	88	100		

1.01. An exposure day is thus a theoretical maximum dose that would likely be reduced by additional attenuation of UV by atmospheric conditions (e.g., increased clouds, ozone concentrations, aerosols) and attenuation in the water column (estimated from K_d values). In a low DOC lake such as Giles, the attenuation depth (1% of surface irradiance) for 305-nm UV-B radiation may exceed 10 m during midsummer, while in a moderate DOC lake like Lacawac or Waynewood, the attenuation depth for 305 nm UV-B is <0.5 m.

UV exposure experiments—The two predators used in the experiments included the invertebrate predator *C. punctipennis*, and sunfish in the genus *Lepomis*, including pumpkinseeds (*L. gibbosus*) and bluegill (*L. macrochirus*). Pumpkinseed sunfish and *Chaoborus* were incubated in the surface waters of Lakes Giles (5- and 80-cm depths, for 1 d) and Lacawac (5- and 80-cm depths, for 3 d) in a set of experiments where both predators were simultaneously exposed to the same solar radiation regimes (referred to here as coupled experiments). Predators were exposed to three different light treatments for each given lake and depth, with 10 replicates per treatment. The treatments included fully exposed to solar radiation (quartz), partially shielded from UV-B radiation (Mylar, = 23- μ m-thick Mylar D from E.I. DuPont de Nemours & Co.), and dark controls (wrapped with black polyethylene). Mylar D has a sharp cutoff with 50% transmittance at 316 nm. It thus removes most of the short wavelength UV-B, amounting to about 60% of total solar UV-B radiation (280–320 nm). This estimate for Mylar transmittance was obtained by convoluting (multiplying irradiance by transmittance for each wavelength over a spectral range) a typical solar irradiance spectrum for northeastern Pennsylvania (Kirk 1994) with the transmittance spectrum of Mylar D (B. R. Hargreaves unpubl. data).

Each replicate consisted of five larvae enclosed in a 16-mm-diameter, 40-ml quartz tube (wrapped with the appropriate light filter for treatment) with 202- μ m mesh-covered ends to permit circulation of the surrounding water. These mesh ends were inset with stoppers with holes carved in them so that the test organisms could not approach the very ends of the tubes. The mesh ends in the two light treatments prevented accumulation of any potentially toxic photoproducts, while those in the dark controls verified that any responses observed in the two light treatments were indeed due to damaging solar radiation rather than accumulation of potentially toxic photochemicals in the lake at the depth of incubation. The six coupled experiments included LG-P9a and LG-C6a, each at 5 and 80 cm in Lake Giles, and LL-P9-5 and LL-C6b-5 at 5 cm in Lake Lacawac (see Table 1 for codes). The two predators were also incubated together in Lacawac at 80 cm for 3 d, but *Lepomis* survival was only 72% in the dark controls, so the results were excluded from the combined analysis. The results for the corresponding *Chaoborus* incubation at 80 cm in Lacawac are included in experiment LL-C6b (Table 1).

In addition to the set of six coupled experiments, many other experiments of similar design were performed with *Lepomis* and *Chaoborus* larvae independently during summer 1994. The delicate nature of the fish larvae often led to high mortality rates, particularly in many of the earlier ex-

periments, and only the 25 experiments in which the dark controls were at least 80% are included in this analysis (Table 1). Including the coupled experiments, these totaled 17 experiments with two species of sunfish in the genus *Lepomis* (11 with pumpkinseeds from Lake Lacawac and 6 with bluegill from Lake Giles) and 14 experiments with *Chaoborus* larvae from Lakes Lacawac (10 experiments) and Waynewood (4 experiments) (Table 1). The *Lepomis* larvae were collected in the yolk-sac stage from nests where eggs had recently hatched, while late instar (3 and 4) *Chaoborus* were collected from the middle of the lake with a 202- μ m mesh plankton net after sunset the evening before the experiment started. Experimental results were similar (substantial overlap in points) for the two species of *Lepomis*. Similarly, the source lake made no difference for the *Chaoborus*, so the data are combined within each genus. More than 4,000 animals were used in these experiments. With one exception (experiment LL-P2, with 5 replicates), experiments involved incubation of 10 replicates.

The survivorship data from the coupled experiments were transformed with an arcsine square-root transformation and analyzed with a two-way analysis of variance (ANOVA, species \times filter). A separate ANOVA was carried out for each of the three coupled experiments, where a coupled experiment was defined as one in which both *Lepomis* and *Chaoborus* were incubated in the same lake, at the same depth, for the same time period.

The data from all 31 experiments (coupled and not, Table 1) with dark control survival >80% were pooled and a least-squares linear regression analysis performed on the arcsine square-root transformed means of survival vs. UV-B dose to test for a significant response to damaging solar radiation. Variation in UV-B dose was generated by variation in the incubation lake, depth, and exposure time, and by natural variation in ambient UVR. Only the fully exposed quartz treatments, adjusted for dark control mortality (see below) were used in this analysis. Separate analyses were carried out for *Lepomis* and *Chaoborus*. Student's *t*-statistic was used to test for significant differences between the slopes of the regression lines, which would demonstrate differences in UVR tolerance of the two predators with increasing dose (Zar 1984).

The second type of analysis performed on the combined data from these 31 experiments used the raw percent survival data from the Mylar and quartz treatments to test for a response specifically to shorter wavelength solar UV-B radiation. Mylar blocks most of the shorter UV-B wavelengths which are the critical wavelengths when considering changes in atmospheric ozone concentrations. Quartz transmits all wavelengths of solar radiation. The index used to compare Mylar and quartz treatments to look for a "UV-B response" was adapted from one commonly used to compare multiplicative effects; it also permits the use of zeros (Stewart-Oaten et al. 1986):

$$\text{UV-B response} = \ln[(P_m + 1)/(P_q + 1)]. \quad (1)$$

For this equation as well as those below, single or multiple subscripts are as follows: P_d is percent survival in dark controls, P_m is percent survival in Mylar treatments, P_q percent survival in quartz treatments, P_c is percent survival corrected

for dark controls, and P_t is percent survival in a given treatment. This index is equal to zero if the responses in Mylar and quartz treatments are identical, is positive if survivorship is greater in the UV-B shielded Mylar treatments, and negative if survival is greater in the UV-B transmitting quartz treatments. The null hypothesis that there is no change in this response index with increasing UV-B dose was tested by least-squares linear regression of the response index vs. 305-nm dose.

In all analyses except for the UV-B response, survivorship in the quartz and Mylar treatments was adjusted for dark control mortalities using a modification of Abbott's formula (Newman 1995).

$$P_{tc} = 100 \left[1 - \left(\frac{P_t - P_d}{-P_d} \right) \right]. \quad (2)$$

The response of both predators to UVR was quite variable, making any quantitative modeling efforts tentative at best. On the other hand, the difference between the responses of the two predators was so great, that it did seem useful to generate some estimate for the dose at which 50% of the animals would die (LD_{50}). This was done using least-squares linear regression analysis on the transformed logit survival data after eliminating the extreme values of 0% and 100% survival. The transformed logit function was selected because it behaves almost identically to the commonly used probit transformation, but is particularly suitable for values near 0 and 100% survival (Newman 1995; Sokal and Rohlf 1995):

$$\text{logit} = \ln \left(\frac{P_t}{100 - P_t} \right); \quad (3)$$

$$\text{transformed logit} = (\text{logit}/2) + 5. \quad (4)$$

A transformed logit value of 5 represents 50% survival and can be used to estimate the lethal dose for 50% of the organisms ($=LD_{50}$). Values are not defined for 0 and 100% for the transformed logit function, and these values are of little use in LD_{50} calculations. However, for comparison, a similar analysis was carried out on the entire data set (that is, including 0 and 100% survival values) using the arcsine square-root transformation.

Results

The coupled experiments in which both *Chaoborus* and *Lepomis* were incubated together clearly show a greater UV tolerance in the fish than in the midge predators (Fig. 1). The results of the two-way ANOVA showed significant effects of both species and light treatment in all three experiments (all $P < 0.001$), with significant interaction effects in both of the Lake Giles experiments ($P < 0.001$), but not in Lacawac ($P = 0.466$). During the 1-d exposure in Lake Giles at the 80- and 5-cm depths, predators were exposed to 0.6 and 0.8 exposure days of UVR respectively, while the 3-d exposure at a depth of 5 cm in Lacawac corresponded to 1.3 exposure days of UVR (Table 1, exp. LG-P9a, LG-C6a, LL-P9, and LL-C6b). The significant interaction effects suggest that the patterns of response of the two predators to dam-

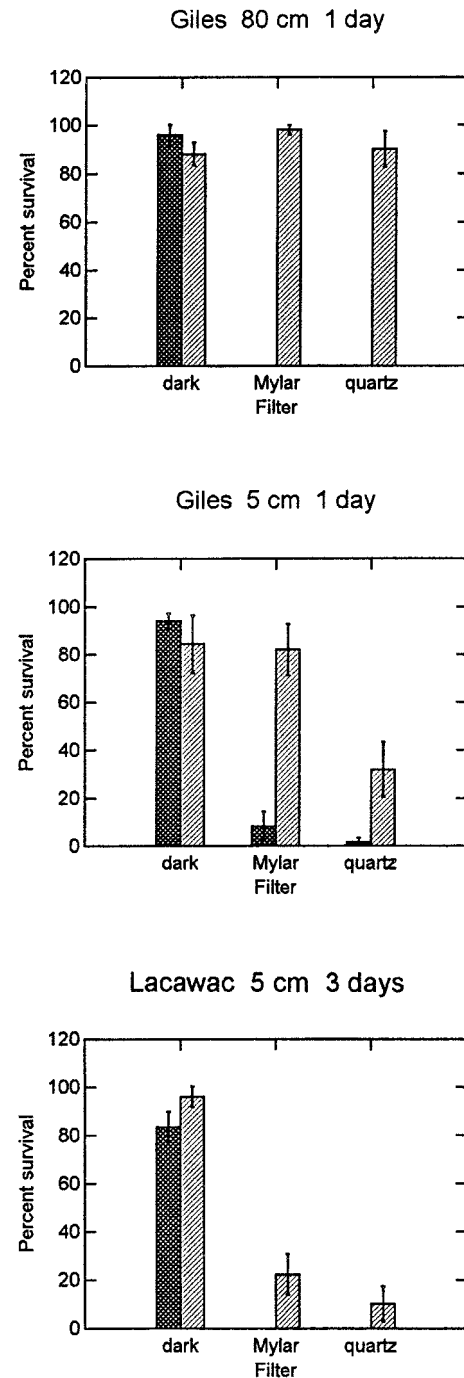


Fig. 1. Percent survival (means and standard errors, $N = 10$) of finfish (*Lepomis*, hatched) and phantom midge (*Chaoborus*, cross-hatched) larvae from Lake Lacawac incubated simultaneously in the surface waters of low UV Lake Lacawac (5-cm depth) for 3 d (305-nm UV dose = 1.3 exposure days), and in high UV Lake Giles (5- and 80-cm depths) for 1 d (305-nm UV dose = 0.8 and 0.6 exposure days respectively). The filter treatments include quartz (full solar radiation), Mylar (removes shorter wavelength UV-B), and black polyethylene (dark controls). Significant differences between species and among filters were observed in all three experiments ($P < 0.001$). Data are from experiments LG-P9a, LG-C6a, LL-P9, and LL-C6b; see Table 1). Lack of bars for *Chaoborus* Mylar and quartz treatments in Giles 80 cm 1-d and Lacawac 5 cm 3-d panels are due to 100% mortality in all replicates.

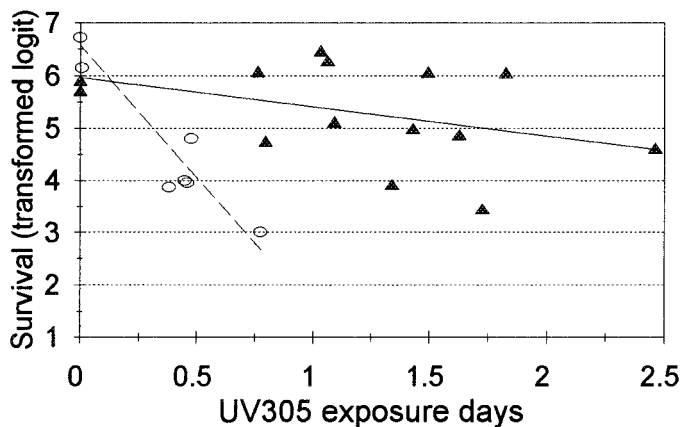


Fig. 2. Survival of *Lepomis* (▲) and *Chaoborus* (○) larvae vs. UV dose in multiple experiments. Only data used to estimate the LD_{50} values and corresponding regression lines are included here. Each point represents the mean survival of a separate experiment for the quartz treatment, adjusted for mortality in the dark controls, and expressed as a transformed logit. For reference, a transformed logit value of 5 represents 50% survival and can be used to estimate the corresponding LD_{50} . Transformed logit values of 3 and 7 represent 2 and 98% survival respectively. LD_{50} values were 0.31 exposure days for *Chaoborus* and 1.75 exposure days for *Lepomis*. One exposure day is defined as equivalent to the amount of 305-nm solar radiation received at the surface of the lake during a sunny day in June or July (avg column ozone = 306 Dobson units). One exposure day = $1.01 \text{ kJ m}^{-2} \text{ nm}^{-1}$ at 305 nm.

aging solar radiation differ in Lake Giles. The lack of significant interaction effects in the Lacawac experiment suggest similar response patterns but differences in the magnitude of the response of the two predators to the higher dose over a longer period of time in Lacawac. The low survival in the Mylar treatments suggests that longer wavelength UV-B and even UV-A radiation is potentially damaging to both predators, but particularly to the midge larvae.

The coupled experiment at 80 cm in Lake Lacawac for 3 d was not included in these analyses because survival in the fish larvae was <80%. Because UV is attenuated very rapidly in Lake Lacawac, the predators in this experiment were exposed to < 0.01 exposure days of UVR (see Table 1, exp. LL-C6b at 80 cm in Lacawac). The survival of both predators was moderately high in all treatments, and there were no statistically significant light treatment effects (one-way ANOVA across all six treatments, $P = 0.134$). *Chaoborus* exhibited 83, 65, and 82% survival (Table 1, exp. LL-C6b at 80 cm), and *Lepomis* exhibited 72, 84, and 93% survival in the dark, Mylar, and quartz treatments respectively.

The regression analyses performed on the arcsine square-root transformed mean survival data of all of the experiments for each predator type also demonstrate a higher UV tolerance in *Lepomis* than in *Chaoborus*. Statistically significant regression relationships were obtained for both *Chaoborus* ($Y = -80.11X + 70.16$, $r^2 = 0.72$, $P < 0.01$) and *Lepomis* ($Y = -18.45X + 76.99$, $r^2 = 0.30$, $P = 0.028$). The slopes of the regression lines for the two predators were significantly different ($P < 0.001$). The lower r^2 values for *Lepomis* and greater scatter in the plots (Fig. 2) indicate that

the response to UVR of *Lepomis* was also much more variable than that of *Chaoborus*.

When the regressions were repeated on the transformed logit survival data (which excluded the 0% and 100% survival data), the LD_{50} for *Lepomis* was 1.75 exposure days, while the LD_{50} for *Chaoborus* was 0.31 exposure days (Fig. 2). The regression on the transformed logit data for *Lepomis* ($Y = -0.55X + 5.96$, $r^2 = 0.16$, $P = 0.15$) was not as strong as for the arcsine transformed data, while for *Chaoborus* it was stronger ($Y = -5.03X + 6.58$, $r^2 = 0.89$, $P < 0.01$). The lack of statistical significance for the *Lepomis* regression makes estimation of an LD_{50} from these data tentative at best, a caveat that is reinforced by the broad scatter that can be seen in the *Lepomis* data (Fig. 2). When the statistically significant regressions on the arcsine square-root transformed full data set were used to estimate an LD_{50} for comparison, the LD_{50} for *Lepomis* was very similar to that obtained with the transformed logit data (1.73 vs. 1.75 exposure days), while the LD_{50} for *Chaoborus* was identical (0.31 exposure days). But again, the broad scatter in the *Lepomis* data suggest that these modeling estimates are very crude at best, at least for *Lepomis*.

We analyzed the frequency of high UV 305 dose periods (15-min periods) during each of the higher dose *Lepomis* experiments to see whether variation among experiments in the number of 15-min periods with unusually high irradiance might account for the scatter. We found that for doses >0.75 exposure days, the frequency of high UV 305 periods was no different for the experiments with >60% survival than for those with <40% survival. This indicates that the high variation observed in the *Lepomis* survival at higher doses is more likely due to endogenous variability (physiologic or genetic variation in photoprotection or photorepair) than to variation in frequency of periods of unusually high UV dose among experiments.

Chaoborus was less responsive to the removal of the shorter wavelength UV-B than was *Lepomis*. When the Mylar treatments were compared to the quartz by regressing the UV-B response index on 305-nm UV-B dose, there was a significant increase in the index with increasing dose for *Lepomis* ($P < 0.01$) but not for *Chaoborus* ($P = 0.63$, Fig. 3). If the data from the three *Chaoborus* experiments with 0% survival in both Mylar and quartz treatments are removed (based on the argument that the doses were so high that they prevented differentiation of the two treatments), the regression relationship is still not significant ($P = 0.61$).

Discussion

Both the invertebrate predator *Chaoborus* and the vertebrate predator *Lepomis* were found to be vulnerable to damage by natural levels of solar UVR found in the surface waters of lakes. The fish larvae were much more tolerant to UVR than were the midge larvae, and their response was also much more variable. One possible explanation for this variability may be related to the ability of *Lepomis* to photorepair. Fish larvae are known to photorepair, or use longer wavelength UV-A and visible light to repair DNA photodamage (Kaupp and Hunter 1981; Regan et al. 1982; Ahmed

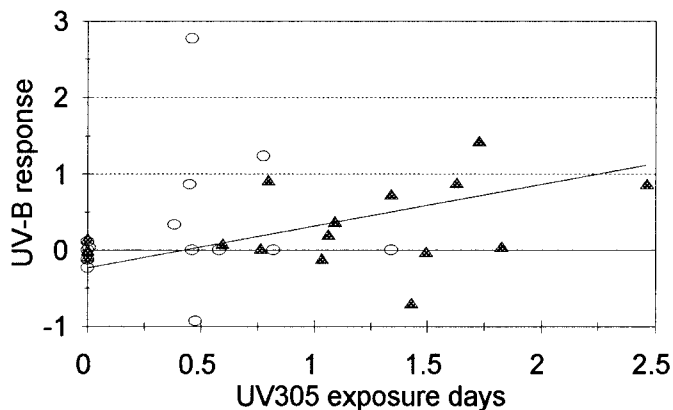


Fig. 3. Response to shorter wavelength solar UV-B radiation by *Lepomis* (\blacktriangle) and *Chaoborus* (\circ) larvae vs. UV-B dose (expressed in 305-nm exposure days) in all experiments. The index used for UV-B response compares the percent survival in Mylar (removes shorter wavelength UV-B) vs. quartz (transmits all UV and longer wavelengths). Positive response values represent a UV-B effect, and this response is expected to increase with increasing UV-B dose. The least-squares regression for *Lepomis* ($Y = 0.55X - 0.23$, $r^2 = 0.42$) is significant ($P < 0.01$), suggesting a sensitivity to shorter wavelength UV-B, while that for *Chaoborus* ($Y = 0.31X + 0.16$, $r^2 = 0.02$) is not ($P = 0.63$, thus no line is drawn in figure). One exposure day = $1.01 \text{ kJ m}^{-2} \text{ nm}^{-1}$ at 305 nm. Details given in Fig. 2 legend and methods.

and Setlow 1993), and we have done experiments in our laboratory that confirm the ability of *Lepomis* to photorepair. Because photorepair involves the reversal of damage, one would not expect the principle of reciprocity to hold. Reciprocity means that the effect of the total UVR exposure is independent of the time over which the exposure occurs. If reciprocity does not hold, then small variations in the spectral composition of radiation to which organisms are exposed (such as changes with depth, time of day or year, cloud cover, ozone, UV-absorbing aerosols, etc.) will lead to greater variability in the biological response to UVR (Cullen and Neale 1997).

In these experiments the water from two lakes that differed in their DOC concentrations was used as an external filter to vary the UVR levels in the experiments. In low DOC lakes where solar UVR is not attenuated rapidly in the water column, *Lepomis* may experience substantial mortality in only a few sunny days if they remain in the surface waters. *Chaoborus* will likely experience high mortality in less than a day of bright sunlight in the surface waters of a low DOC lake. This suggests that damaging UV radiation alone has the potential to exclude these predators from utilizing the surface waters of low DOC lakes continuously during the day. In lakes with higher DOC concentrations on the other hand, these predators will be protected from UVR damage, and they are thus able to remain in surface waters during the day.

Some simple calculations with the K_d values in Table 1 demonstrate the differences in the 305-nm UVR dose to which an organism would be exposed in lakes with different DOC concentrations. Note that the effect is magnified exponentially with depth. For example, the 305-nm dose at a

depth of 0.1 m in Lake Giles would be 3.7 times greater than at the same depth in Lacawac, while at 0.5 m the dose in Giles would be 646 times greater in Giles than in Lacawac, and at 1 m the difference in 305-nm dose between the two lakes would be over 400,000 times.

What are the implications of these observations for the predation regime in acidified lakes? In lakes with fish, *Chaoborus* is unlikely to be exposed to much UVR, as visible light penetrates much deeper than UVR, and *Chaoborus* larvae must avoid depths with any visible light due to their large size and high vulnerability to visual predators. As lakes become acidified, however, fish populations disappear and the threat of visual predation is no longer a factor for *Chaoborus*. At the same time, DOC may decrease, and thus UVR increase with acidification. A close examination of the literature reveals patterns that are consistent with the hypothesis that UVR plays a role in the observed changes in predation regimes and zooplankton community structure observed in acidified lakes.

A wide range of evidence from field surveys of acidified and nonacidified lakes, whole-lake manipulations, and laboratory bioassay studies has demonstrated that anthropogenic acidification of lakes has led to the loss of many fish species, to the extent that thousands of lakes have been rendered fishless in both North America and Scandinavia (Eaton et al. 1992; Magnuson et al. 1984; Mills et al. 1987). Recruitment failure due to the disruption of spawning behavior and mortality of eggs and larvae are cited as the major factors leading to loss of these fish populations. Although low pH certainly plays a role in this recruitment failure and the loss of fish from acidified lakes (Wright et al. 1976; Gunn and Belzile 1994), it does not seem to explain many of the observed patterns. Schofield and Driscoll (1987 p. 64) state this explicitly:

Observations of fish species occurrence or disappearance at particular lake pH levels are often misconstrued as species specific dose-response functions or uncritically taken as measures of relative species tolerance to acidification. Attempts to verify these field derived relationships by laboratory bioassay have not been entirely satisfactory and conflicting observations appear to have been the rule, rather than the exception ...

A possible clue to these conflicting observations may be related to changes in DOC in acidified lakes. Several investigators have documented decreases in DOC concentrations during lake acidification (Bukaveckas and Driscoll 1991; Schindler et al. 1991). These changes in DOC with acidification appear to have important implications for fish. For example, fish seem to be more tolerant of acid conditions in colored lakes where DOC concentrations are high (Collier et al. 1990; Nelson and Magnuson 1992). One of the mechanisms proposed to explain the increased survival of fish at high DOC concentrations is the ability of organic ligands to bind with aluminum and thus reduce Al toxicity in acid environments (Driscoll et al. 1980). However, at very low pH levels (4.2–4.8) Al may actually enhance the survival of fish eggs (Magnuson et al. 1984; Gunn and Belzile 1994).

A second possible mechanism to explain the mitigating effects of DOC on acidity for fish in acid lakes is the ability

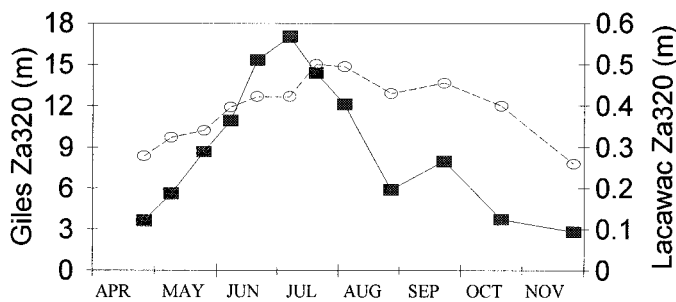


Fig. 4. Seasonal changes in the depth of penetration of UV radiation (320-nm band of PUV) in Lake Lacawac (○) and Lake Giles (■) during 1994. The attenuation depths (1% of surface irradiance) are calculated from the K_d data of Morris and Hargreaves (1997). Note the rapid increase in the depth of UV penetration during spring, especially in low DOC, more acidic Lake Giles. UVR at 320 nm generally penetrates on the order of 1.2–1.3 times as deep as 305-nm radiation.

of DOC to attenuate UV radiation. As DOC concentrations decline in acidified lakes, the level of UVR in the water column increases (Schindler et al. 1996; Williamson et al. 1996; Yan et al. 1996). Our results in the current study demonstrate the sensitivity of larval fish to natural levels of UVR in the surface waters of a low DOC lake. Previous studies of a similar design demonstrated high UVR-induced mortality in eggs of yellow perch, *Perca flavescens* (Williamson et al. 1997). In addition, it has been noted that spring pulses of acidity with snowmelt may cause particularly high damage in lake biota (Brett 1989; Magnuson et al. 1984; Schofield 1976). These rapid drops in pH would also tend to cause rapid decreases in DOC. Combined with the potentially low DOC content of the snow, snowmelt has the potential to lead to seasonal increases in UV transparency. We have observed pronounced springtime increases in the depth to which UVR penetrates in Lakes Lacawac and Giles (Fig. 4). While photooxidation of DOC is adequate to account for a major portion of these seasonal changes in UV transparency (Morris and Hargreaves 1997), interannual variation in the timing of snowmelt and severity of acid inputs may accelerate these springtime increases in UV radiation and hence threaten fish spawning success in acid lakes.

The generality of UVR damage in fish is not known, but it seems likely given the fact that many freshwater and marine fish produce highly translucent larvae that often reside in shallow surface waters and even the neuston (Crowder and Crawford 1984; Forney 1980; Hunter et al. 1979). In addition, the larvae of some species such as yellow perch are positively phototactic (Thorpe 1977). Fish eggs are known to contain a variety of photoprotective compounds (Chioccare et al. 1980; Grant et al. 1980; Plack et al. 1981), and eggs and larvae have the ability to repair photodamage (Kaupp and Hunter 1981; Malloy et al. 1997), providing evidence that damaging solar radiation has been an important environmental stressor in the early life history stages of fish for some time. Collectively these observations support the hypothesis that UVR damage may explain some of the variability in recruitment success of fish in acidified lakes.

In acidified lakes where fish have been eliminated, large predatory insects such as *Chaoborus* often increase in abun-

dance (Eriksson et al. 1980; Fischer and Frost 1997; Yan et al. 1991). One proposed mechanism for this increase is a decrease in fish predation (Eriksson et al. 1980). While one cannot attribute an increase in *Chaoborus* to corresponding increases in UV radiation during acidification, there are some signals that UVR plays a role in which species of *Chaoborus* are present. In regions where acidification is a problem but fish are present in a lake, *C. punctipennis* is frequently the most widespread and abundant species (Yan et al. 1985). This species is relatively small, highly transparent, and exhibits a strong diel migration pattern into the sediments during the day to avoid fish predation. In acidified lakes with no fish, *Chaoborus* is able to persist due to its high tolerance of acid conditions, but changes in abundance with acidification are not consistent across lakes (Brett 1989). For example, while *C. punctipennis* increased in experimentally acidified Little Rock Lake (Fischer and Frost 1997), a survey of 33 lakes ranging in pH from 4.5 to 7.2 showed no apparent relationship between the abundance of this species and either pH or the presence or absence of fish (Yan et al. 1985). These same investigators did, however, observe a positive relationship between color (a close correlate of DOC) and *Chaoborus* abundance in the more acidic group of lakes that they studied (pH 4.5–6.6).

In fishless acidified lakes other species of *Chaoborus* often dominate, including *C. obscuripes* in Europe, and *C. americanus* in North America (Bendell and McNicol 1987; Brett 1989; Nyman et al. 1985). These two latter species tend to remain in the water column during the day, do not exhibit strong vertical migrations, and are thus potentially exposed to high UVR levels in acidified lakes. Interestingly, they are both also highly pigmented (Brett 1989), and thus likely to be resistant to damaging solar UVR. The increased abundance of pigmented *Chaoborus* in the absence of fish predation is reminiscent of similar trade-offs in selective pressures noted for zooplankton in earlier studies (Hairston 1976; Luecke and O'Brien 1981).

The response of zooplankton communities to acidification is complex, but a few reasonably consistent patterns exist. For example, diversity may decline (Confer et al. 1983), and non-insect invertebrate predators including *Asplanchna priodonta*, *Leptodora kindtii*, *Epischura lacustris*, *Mesocyclops edax*, and *Mysis relicta* generally decline (Brezonik et al. 1993; Schindler et al. 1991; Sierszen and Frost 1993). One of the most consistent patterns of change in zooplankton communities with acidification is a pattern of increasing abundance of *Keratella taurocephala*, often accompanied by declines in *Keratella cochlearis* (Gonzalez and Frost 1994; Siegfried et al. 1989; Yan and Geiling 1985). However, laboratory bioassay studies provide evidence that these changes are not due to low pH (Gonzalez and Frost 1994), and these changes are attributed to changes in food availability or invertebrate predation with acidification, or other yet unknown indirect effects (Gonzalez and Frost 1994). In an in situ set of incubation experiments we found *K. taurocephala* to be the most UVR tolerant zooplankton species, while the species that we found was most sensitive to UVR (*Daphnia catawba*) declines in acidified lakes at a pH of <5.1 (Williamson et al. 1994). It is below a pH of about 5.0 that the greatest increase in UVR is expected in acidified lakes due

to a rapid decline in DOC (Williamson et al. 1996). There are also several studies that show a relationship between DOC (or some co-correlate such as color) and zooplankton community structure in lakes (Brett 1989; Siegfried et al. 1989; Olson et al. 1995). However, many factors other than UVR are influenced by DOC (Williamson et al. 1999) and many factors other than pH and DOC change with lake acidification (Frost et al. 1999); hence changes in zooplankton community structure with DOC or acidification cannot be attributed to UVR without experimental verification.

We have demonstrated that two important predators in freshwater ecosystems, the invertebrate predator *Chaoborus* and the vertebrate predator *Lepomis*, are vulnerable to natural levels of UVR in lakes and that these two predators differ in their tolerance of damaging solar UVR. The (limited) existing information on the relationships between DOC, UVR, and the relative abundance of predators and their zooplankton prey suggests that UVR may interact with other stressors in important ways during lake acidification and recovery.

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