UV-enhanced fish predation and the differential migration of zooplankton in response to UV radiation and fish

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Abstract

The intensity and spectral composition of visible light are known to influence fish predation on zooplankton. However, in clear-water systems, ultraviolet (UV) radiation (UVR) may also influence fish predation, directly through UV-enhanced foraging, indirectly through alterations in predator-prey overlap, or in a combination of the two. Here we test the hypothesis that UVR facilitates fish predation on zooplankton in an oligotrophic lake. Experiments were conducted in 2.2-m-long UV-transparent or UV-blocking columns suspended in the epilimnion. Zooplankton consumption by young-of-the-year (YOY) largemouth bass (*Micropterus salmoides*) was compared in the presence and absence of UVR, and the vertical distributions of prey were quantified across light and fish treatments. In addition, a separate experiment was conducted to examine zooplankton vertical responses to UV exposure vs. fish kairomones. Overall, YOY predation on zooplankton was higher in the presence than in the absence of UVR, particularly on diaptomid copepods. This result was only partially explained by zooplankton migratory behaviors, suggesting UV-enhanced searching capabilities in YOY bass. Furthermore, diaptomids displayed a stronger vertical behavioral response to fish kairomones than to UVR whereas *Daphnia* exhibited a stronger response to UVR.

Fish predation on zooplankton is most often assessed in terms of the quantity and spectral distribution of visible light (400–700 nm) present in the water column. Both light intensity and spectral composition influence the reaction distance and predation rate of fish predators. The visible light environment can also alter prey selection by fish, affecting the size distribution and species composition of zooplankton communities (Brooks and Dodson 1965). As a consequence, visible light is recognized as the primary proximate cue that zooplankton use to assess predation risk and initiate diel vertical migrations out of the surface waters during the day (Forward 1988; Lampert 1989). However, in clear, ultraviolet (UV)-transparent systems, UV radiation (UVR) may also enhance fish predation on zooplankton, both directly and indirectly (Leech and Johnsen 2003).

UVR extends deep into the water column of fresh waters with low concentrations of dissolved organic carbon (DOC, $<1-2 \text{ mg } \text{L}^{-1}$). Within the UV spectrum, UV-A radiation (320–400 nm) penetrates to greater depths than UV-B (290–320 nm) (Morris et al. 1995). For example, in small glacial lakes with DOC concentrations less than 1 mg L⁻¹, 320-nm UV-B can reach depths in excess of 10 m and 380nm UV-A can extend to twice these depths (Williamson et al. 1996). Increased exposure to UVR, particularly UV-B, can lead to deleterious effects on growth, reproduction, and survival of many aquatic organisms, including young-ofthe-year (YOY) fish and their zooplankton prey (Leech and Williamson 2000; Olson et al. 2006). Negative phototactic migrations in response to ambient UVR levels have been observed in both zooplankton (Leech and Williamson 2001; Alonso et al. 2004; Boeing et al. 2004) and fish (Kelly and Bothwell 2002; Ylönen et al. 2005; Holtby and Bothwell 2008), suggesting that behavioral avoidance of UVR has the potential to influence interactions between predator and prey in time and space.

In addition, although some wavelengths of UVR are potentially damaging to aquatic organisms, others are potentially beneficial. Numerous species of freshwater and marine fishes as well as invertebrates possess UV photoreceptors (reviewed in Leech and Johnsen 2003). In many freshwater fishes, UV photoreceptors are present only during early life history stages, coinciding with planktivory in the surface waters, and have a peak absorbance in the UV-A range (350-370 nm) (Loew et al. 1993; Leech and Johnsen 2003). Navigation (Hawryshyn 1992) as well as recognition and communication between conspecifics, predators, and prey (Losey et al. 1999; Siebeck 2004) are augmented by UV perception in some species. Studies have also shown that UV vision may enhance prey contrast, increasing the foraging efficiency of YOY fish (Loew et al. 1993; Browman et al. 1994), yet others have detected no beneficial effects of UVR on foraging (Leech and Johnsen 2006; Holtby and Bothwell 2008).

In the present study, we tested the hypothesis that UVR facilitates fish predation in high UV systems using an enclosure approach and examined the potential differences in UVR facilitation of feeding on different zooplankton species. Field experiments were conducted in 2.2-m-long columns that either transmitted or blocked UVR such that increased fish predation might be a consequence of UVR avoidance behaviors, an enhancement in UV-searching capabilities, or a combination of these factors. An

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additional experiment was conducted using fish kairomones to assess whether zooplankton distribution patterns in the columns were in response to UVR and/or fish predation pressures. Experiments were conducted at a depth of 2–4 m in the epilimnion of a UV-transparent lake in northeastern Pennsylvania, USA.

Methods

Study site—Lake Giles is a highly transparent, oligotrophic system located on the Pocono Plateau of northeastern Pennsylvania (41°23'N, 75°06'W). It has a mean summer Secchi depth of 11–15 m, is acidic (pH = 5.5), and has a DOC concentration of approximately 1 mg L⁻¹. The lake is thermally stratified from late April to late October and remains well-oxygenated at all depths throughout the year. Water temperature and dissolved oxygen during the study were 21–22°C and 8.5 mg O₂ L⁻¹ between 0 and 4 m as determined by a YSI Model 57 oxygen meter.

Light measurements—Underwater light profiles were taken close to solar noon (13:00 h) with a profiling UV radiometer (PUV-500, Biospherical Instruments) on 17 June 2001. Attenuation coefficients (K_d) were calculated for 305, 320, 340, and 380 nm by log-linear regression. Over the depth range at which the experimental columns were suspended (2–4 m), 17% of incident surface 320-nm UV-B penetrated to a depth of 2 m and 5% to a depth of 4 m (see fig. 2B in Cooke et al. 2008). Approximately 27% and 21% of incident surface UV-A radiation at 380 nm was present at 2 and 4 m, respectively (see fig. 2B in Cooke et al. 2008).

Ambient solar radiation was measured during the experimental study in an open field at the Lake Lacawac field station (\sim 17 km from Lake Giles) using a global UV imager (GUV-521, Biospherical Instruments) coupled with a Campbell CR-10 data logger (Campbell Scientific). The GUV 521 has an 8–10 nm bandwidth (full width at half maximum) at four UV wavelengths (305, 320, 340, and 380 nm) as well as photosynthetically active radiation (400–700 nm) and averages solar irradiance data over 15-min intervals. Weather conditions during the experiment were clear to partly cloudy (Fig. 1).

Column and experimental design—The design of the experimental columns is described in detail in Boeing et al. (2004) and Cooke et al. (2008). Briefly, columns (8 cm \times 8 cm \times 2.2 m long, total volume = 14 liters) were constructed of two acrylics with sharp long wave pass cutoffs: OP-2, 50% transmittance at 410 nm (UVR–treatment) and OP-4, 50% transmittance at 272 nm (UVR+ treatment) (CYRO Industries). Each column was divided into 6 discrete sections (depths) with trap doors. All sections were 0.5 m in length except the uppermost and lowermost sections, which were 0.1 m in length.

For each experiment, columns were filled with unfiltered lake surface water and hung from a floating rack. Zooplankton densities in oligotrophic Lake Giles were typically less than 15 individuals per liter (Pocono Comparative Lakes Program [PCLP] database unpubl.). Higher densities were added to the columns to provide sufficient numbers for statistical analysis (Table 1). Zooplankton were collected with 1–2 tows from 0 to 15 m depth using a 48- and 202- μ m mesh bongo net at approximately 20:00 h and mixed in a 4-liter container. Aliquots of 100 mL were then added to each column. *Chaoborus* densities in Lake Giles were <1 individual per liter at the time of these experiments (PCLP database unpubl.), and the few *Chaoborus* individuals collected were removed before zooplankton were introduced to the columns in both the fish feeding and fish kairomone experiments.

At the end of each experiment, the trap doors were shut simultaneously, permitting the sampling of organisms from each discrete depth. Zooplankton from each section were preserved in sucrose formalin. Experiments were set up in a 2×2 factorial design in which the presence and absence of YOY fish and UVR (fish feeding experiment) or the presence and absence of fish kairomones and UVR (fish kairomone experiment) were the two factors, with 3 replicates of each treatment combination.

Fish feeding experiment—YOY largemouth bass, Micropterus salmoides, approximately 15 mm in length were collected on the evening before the experiment and kept at lake temperature in a cooler with lake water until the experimental setup. Observations of the fishes' behavior inside the columns confirmed that they could move freely up and down between sections. Columns were lowered just below the lake surface between 15:00 and 16:00 h on 19 June 2001. At 21:00 h, zooplankton were added to the third section from the top of each column at densities presented in Table 1. Seven fish per column were also added to the same section of 3 UVR+ and 3 UVR – columns. Following the addition of animals, columns were suspended vertically at 2–4 m below the lake surface.

Zooplankton and fish were added to the columns at night in order to have the experiment in place before sunrise, when fish feed more actively (i.e., crepuscular feeding, Keast and Welsh 1968) and the ratio of UV to visible photons is greater (Leech and Johnsen 2003). We assumed that there were few to no zooplankton consumed prior to sunrise given that YOY bass are primarily visual feeders with reduced prey detection in darkness. The experiment was terminated at 10:30 h the next day (20 June 2001), providing the fish with approximately 4.5 h of daylight to forage.

Fish kairomone experiment—A second experiment was conducted on 28 June 2001 in order to assess potential differences in zooplankton behavioral responses to UVR vs. fish kairomone. Zooplankton were collected and introduced to each column as described for the previous experiment. An equal concentration of fish kairomone was established throughout the columns. In 3 UVR+ and 3 UVR- columns, 30% of the volume of each column section was replaced with water taken from a cooler that contained approximately 15-mm-long juvenile bass (approx. 4 individuals L⁻¹) for 5 h. Columns were then suspended vertically between 2 and 4 m below the lake surface for 2.5 h (from 14:15 h to 16:45 h). This duration is



Fig. 1. Ambient ultraviolet (UV) and photosynthetically active radiation (PAR) were measured during the experimental study in an open field at the Lake Lacawac field station (\sim 17 km for Lake Giles) using a global UV imager (GUV 521, Biospherical Instruments) coupled with a Campbell CR-10 data logger (Campbell Scientific) (*see* Methods for details). Shaded regions represent the daylight hours during the fish feeding experiment on 20 June (4:15–10:30 h) as well as the time frame of the fish kairomone experiment on 28 June (14:15–16:30 h).

short enough to ensure that the fish kairomones did not degrade over the course of the experiment (Dodson 1988).

Statistical analyses—Zooplankton from each column section were enumerated under a dissecting microscope in the laboratory. Zooplankton were identified to species with copepods further identified to life history stage and sex. To test for potential differential mortality among zooplankton groups induced by UVR (not expected in these very short experiments), a two-way ANOVA was performed with UVR and zooplankton group (including species, life history stage, or sex) as the two factors and the final number of zooplankton in the columns in the absence of fish as the response variable. To test for the effects of UVR on fish consumption of zooplankton, a separate two-way ANOVA was performed with UVR and zooplankton group as the two factors and the final number of zooplankton in the presence of fish as the response variable. Data for both tests were square root transformed to normalize variance. It was discovered after the experiment was conducted that one of the UV-blocking columns was improperly constructed with one UV-transparent side. Thus, this column had to be eliminated from the analysis (UVR-, no fish treatment), resulting in an unbalanced design.

Table 1. Mean number of zooplankton per liter introduced to the UVR+ and UVR- columns (14 liters total) in the fish feeding experiment (\pm SE, n=6) and the fish kairomone experiment (\pm SE, n=11).

Species	Feeding experiment	Kairomone experiment
Daphnia catawba	41±2	32±2
Leptodiaptomus minutus		
females	23 ± 1	14 ± 1
L. minutus males	13 ± 1	5 ± 0
Calanoid copepodids	99±3	92±6
Cyclops scutifer adults	8 ± 1	8 ± 1
Cyclopoid copepodids	6±1	23±4
Nauplii	9±1	8 ± 1

The effect of UVR and fish on the vertical distribution of zooplankton within the columns was analyzed using a threeway ANOVA for each zooplankton group with interactions. The ANOVAs were conducted using UVR, fish presence, and section depth as factors and zooplankton density in each column section as the response variable. Section depth is the individual depth of each of the six column sections and was classified as a categorical factor. Zooplankton density rather than absolute number in each section was used as the response variable to account for differences in the size of the column sections (i.e., two 0.64-liter sections at the top and bottom of the columns and four 3.2-liter sections in between). Data were square root transformed to normalize variance. Again, these tests were unbalanced because of the removal of the improperly constructed column. A t-test was conducted to compare the mean depth of the YOY bass in the presence and absence of UVR.

During the 2.5-h kairomone experiment, not all of the zooplankton migrated from the section in which they were introduced. Thus, the data were analyzed in terms of the number of zooplankton that migrated up into the top two sections vs. down into the bottom three sections. Log-linear analyses were performed using SAS 9.1 software (SAS Institute) to test for significant movements in response to light, fish kairomone, and their interaction as described in Cooke et al. (2008). Analyses focused on the behaviors of the two most abundant crustacean zooplankton, *Daphnia catawba* and *Leptodiaptomus minutus*.

Results

Fish feeding experiment—Zooplankton abundance in the presence of UVR and fish: In the absence of fish, no significant effect of UVR ($F_{1,6} = 0.07$, p = 0.84) or interaction between UVR and zooplankton group ($F_{1,6} =$ 0.29, p = 0.94) was seen on the final number of zooplankton in the columns, indicating no significant mortality attributable to UVR exposure during the experiment (Fig. 2A). Zooplankton abundance did significantly vary with zooplankton group ($F_{1,6} = 229.09$, p <0.0001), related to differences in the initial zooplankton community structure (Table 1; Fig. 2A).

In the presence of fish, there was a significant effect of UVR on the final number of zooplankton in the columns

($F_{1,6} = 11.05$, p = 0.002), indicating a difference in fish predation in the presence and absence of UVR. Although there was a significant effect of zooplankton group ($F_{1,6} =$ 167.49, p < 0.0001), there was no significant interaction between UVR and zooplankton group ($F_{1,6} = 1.18$, p =0.34). This suggests that there was no difference in fish predation among zooplankton groups in the presence and absence of UVR. Despite this lack of significant interaction, predation intensity appeared higher on diaptomids in the presence of UVR compared to *Daphnia*, cyclopoids, and nauplii (Fig. 2B). Furthermore, if analyzed individually, both *L. minutus* females and copepodids do show a significant difference (Fig. 2B). Overall, fish consumed 15.2% more zooplankton in the presence of UVR compared to its absence (*t*-test = 3.35, df = 4, p = 0.01).

Zooplankton and fish distribution patterns: No significant effect of UVR on zooplankton density was seen across all species and life history stages (Table 2). However, there was a significant effect of fish on zooplankton density for all zooplankton groups (Table 2). Furthermore, the addition of fish to the columns had a significant effect on the depth distribution of all zooplankton, both in the presence and in the absence of UVR (Table 2). Only *Daphnia* and copepod nauplii displayed a significant interaction between depth and UVR (Table 2).

In the absence of fish, L. minutus adults and copepodids were distributed evenly throughout the columns (Fig. 3, data not shown for copepodids) whereas D. catawba were distributed in the deeper column sections in the presence of UVR and in the shallower column sections in the absence of UVR (Fig. 3). In the presence of fish, L. minutus adults and copepodids were located in the deeper column sections in both the presence and the absence of UVR (Fig. 3, data not shown for copepodids), whereas Daphnia were concentrated in the middle sections in the presence of UVR and in the upper sections in the absence of UVR (Fig. 3). Distributions of copepod nauplii in the presence and absence of UVR and fish were similar to those of *Daphnia*, whereas Cyclops scutifer adults and copepodids were concentrated at the bottom of the columns both in the presence and in the absence of UVR and fish (data not shown).

Fish were located primarily in the bottom two sections of the columns at the end of the feeding experiment in both the presence and the absence of UVR. There was one exception in which all seven fish were found within the top three sections of a UVR – column. Mean fish depths (\pm SE) was 3.8 \pm 0.12 m in the UVR+ treatment and 3.55 \pm 0.51 m in the UVR- treatment and were not significantly different (*t*-test = 0.64, df = 2, *p* = 0.29).

Fish kairomone experiment—L. minutus adults responded more strongly to fish kairomones than did Daphnia (Fig. 4A,B). In both the presence and the absence of UVR, L. minutus were distributed deeper in the columns in response to the addition of fish kairomone (Fig. 4B). Furthermore, the vertical response of L. minutus to fish kairomone ($\chi^2 = 189.19$, df = 2, p < 0.001) was stronger than the response to UVR ($\chi^2 = 8.17$, df = 2, p = 0.02).



Fig. 2. The total number of zooplankton in the UVR+ and UVR- columns in the (A) absence and (B) presence of fish at the end of the fish feeding experiment. *L. minutus* are separated in female (F) and male (M) adults. Male adult cyclopoids were rare, so females and male cyclopoid adults were not separated. Nauplii were represented primarily by calanoids. Error bars represent standard errors (n = 2, 3). Asterisks indicate significant differences.

Significant migratory responses to fish kairomone were also detected in the *Daphnia* ($\chi^2 = 47.07$, df = 2, p < 0.001); however, *Daphnia* displayed a stronger migratory response to UVR ($\chi^2 = 225.44$, df = 2, p < 0.001), with a greater percentage of individuals moving into the deeper column sections in the presence of UVR (Fig. 4A). No significant interactive effect between UVR and fish kairomone was seen on *Daphnia* movements ($\chi^2 = 5.60$, df = 2, p = 0.06) but there was a significant interactive effect in *L. minutus* ($\chi^2 = 6.46$, df = 2, p = 0.04).

Discussion

UV-enhanced fish predation—Results of our field study demonstrate that UVR has the potential to enhance YOY predation on zooplankton in UV-transparent lakes. More zooplankton were consumed by YOY bass in the presence than in the absence of UVR in high-UV Lake Giles. Given our experimental design and lack of knowledge of the vertical distribution of the fish throughout the experiment, we cannot discern the mechanism behind this increase in predation, which may be attributable to zooplankton migratory behaviors in response to variations in UVR, UV-enhanced prey detection, a reduction in escape ability, or a combination of these factors.

Zooplankton vertical distributions may have contributed to the increase in prey consumption in the presence of UVR. For example, *Daphnia* and copepod nauplii, which are known to be less UV-tolerant than *L. minutus* (Leech and Williamson 2000), were more abundant in the deeper column sections in the presence of UVR but were more uniformly distributed in the absence of UVR. Given that fish are often attracted to high densities of prey (Mills et al. 1986), more *Daphnia* and nauplii should be consumed in the presence of UVR as they concentrated in the deeper column sections in UVR avoidance.

Table 2. Results of three-way ANOVAs (p values) examining the effects of ultraviolet radiation (UVR) and fish on zooplankton vertical distribution patterns at the end of the fish feeding experiment. UVR, fish, and section depth were the three factors, and zooplankton density in each column section was the response variable (n=11). Female and male adult copepods had similar distribution patterns and were combined for the analysis.

	Daphnia	L. minutus adults	L. minutus copepodids	Cyclopoid adults	Cyclopoid copepodids	Nauplii
Depth	0.003	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.002
Fish	< 0.0001	< 0.0001	< 0.0001	< 0.0001	< 0.0001	0.004
UVR	0.25	0.48	0.39	0.42	0.99	0.68
Depth×fish	0.008	< 0.0001	0.002	< 0.0001	< 0.0001	0.02
Depth×UVR	< 0.0001	0.94	0.21	0.24	0.05	0.006
Fish×UVR	0.72	0.91	0.58	0.06	0.55	0.37
Depth×Fish×UVR	0.16	0.76	0.84	0.99	0.99	0.31

However, there was no significant difference in the number of *Daphnia* and nauplii eaten in the two light treatments despite their deeper distribution in the presence of UVR. Furthermore, diaptomid adults and copepodids were more abundant at the bottom of columns in both the presence and the absence of UVR in response to fish predators, yet predation was higher in the presence of UVR. The cold stenothermal cyclopoid *C.* scutifer was also concentrated in the bottom of both the UVR+ and UVR- columns but was equally preyed upon in the presence and in the absence of UVR. Together these patterns suggest that factors other than zooplankton distribution alone influenced prey selection and predation intensity.



Fig. 3. Distribution of *D. catawba* and *L. minutus* adults in each experimental treatment with and without UVR and fish in the fish feeding experiment. Error bars represent standard errors (n = 2, 3). Arrows indicate the depths at which the zooplankton and fish were initially introduced.



Fig. 4. Distribution of (A) *D. catawba* and (B) *L. minutus* adults in the presence and absence of UVR and fish kairomones in the fish kairomone experiment. Data are the mean percentage $(\pm SE)$ that swam to either the top two or bottom three sections of the columns.

UV photoreceptors have been detected in a diversity of freshwater fishes, particularly during early life history stages (reviewed in Leech and Johnsen 2003). To our knowledge, *M. salmoides* has not been examined for UV photoreceptors; however, UV photoreceptors have been detected in other teleost species such as *Lepomis*, *Perca*, *Salmo*, and *Oncorhynchus* (Loew et al. 1993; Browman et al. 1994; Leech and Johnsen 2003). Though not directly tested, UVR may be contributing to the enhancement of prey detection in our experimental columns, particularly on species with photoprotective compounds such as copepods (Moeller et al. 2005; Persaud et al. 2007).

Although protected from damaging wavelengths of sunlight, zooplankton containing UV-absorbing mycosporine-like amino acids (MAAs) and short-wavelength blue-absorbing carotenoids are more conspicuous to visual predators (Hairston 1979; Hansson 2004). Moreover, copepods often contain higher concentrations of photoprotective compounds compared to cladocerans (Tartarotti et al. 2001; Hansson et al. 2007; Persaud et al. 2007). In Lake Giles, copepod MAA concentrations increase from spring through summer, whereas carotenoid concentrations decrease (Moeller et al. 2005; Persaud et al. 2007). Copepods with high MAA concentrations may appear particularly dark against a UV-rich background and thus more susceptible to predators with UV vision (Loew and McFarland 1990; Leech and Johnsen 2003). Consequently, the daytime downward migration of *L. minutus* is likely an evolutionary response to their visibility to predators, including those with UV vision. *Daphnia* have also been shown to display differences in UV reflectance and absorbance (Loew and McFarland 1990; Leech and Johnsen 2003). However, within the confinement of the columns, their large size may have made them more visible to predators under visible light alone, so the presence of UVR was not a major factor. This may also have been true for *C. scutifer*. In addition to visual foraging, YOY bass may have used mechanoreception and/or chemoreception to locate and capture zooplankton, particularly given the substantial overlap between predator and prey in the bottom sections of the columns.

Fish were located at the bottom of most columns at the end of the feeding experiment, except for one UVRcolumn in which fish were located between 2.0 and 3.1 m. Although the distributions of uneaten prey in the upper to middle column sections tend to suggest greater consumption in the bottom sections, fish likely fed throughout the columns during the experiment with changes in light levels. In nature, many species of larval and juvenile fish avoid the surface waters of lakes and distribute themselves deeper in the water column during the day for various reasons, including piscivore avoidance (Scheuerell and Schindler 2003), UV avoidance (Ylönen et al. 2005), and thermal regulation of metabolism (Wurtsbaugh and Neverman 1988). In addition, deeper distributions are often more pronounced with increased water clarity (Taylor et al. 2000; Mous et al. 2004). This could potentially influence predator-prev overlap, as seen by Alonso et al. (2004) in UV-transparent lakes in Patagonia, where both the dominant planktivore (i.e., early stages of coldwater galaxiid fishes) and zooplankton prey occupied the deeper pelagic waters during the day. Although they did not quantify it, the authors postulated an increase in predation pressures during periods of increased UV intensity. Based on our results, this may be particularly true at depths where UV-A radiation enhances prey visibility.

Differential zooplankton response to fish kairomones and UVR-Although D. catawba and L. minutus displayed a significant behavioral response to both fish kairomones and UVR, the response intensity varied between the two species. Diaptomids were more responsive to fish predators than to UVR exposure, whereas *Daphnia* showed the opposite pattern. In both the presence and the absence of UVR, L. minutus migrated to the lower sections of the columns with the addition of fish kairomone. D. catawba, however, displayed a stronger response to UVR exposure than to fish kairomone, migrating to deeper column sections in UVR avoidance. Thus, factors regulating daytime zooplankton migrations out of the surface waters appear to differ among zooplankton taxa. Nevertheless, surface avoidance in both Daphnia and L. minutus may ultimately still be related to UVR because of vulnerability to either UV damage or UV-foraging predators.

Lake Giles D. catawba are substantially less pigmented than L. minutus (Persaud et al. 2007). Although decreasing their visibility to visual predators, this lack of pigmentation increases susceptibility to damaging solar radiation, which can evoke downward daytime migrations (Leech and Williamson 2001; Boeing et al. 2004; Cooke et al. 2008). Lake Giles D. catawba are known to be more sensitive to UVR compared to the rotifers and copepods (Leech and Williamson 2000) and are typically least abundant in the epilimnion during the day (i.e., <25% of the population, PCLP database unpubl.). It is therefore not surprising that Daphnia exhibited a stronger response to UVR compared to pigmented L. minutus. Similar differential responses to UVR have been shown in *Daphnia* and copepod populations inhabiting Siberian and Swedish lakes, with cladocerans predominantly displaying behavioral escape mechanisms and copepods relying on the accumulation of photoprotective compounds (Hansson et al. 2007).

The differential response to fish kairomones between L. minutus and D. catawba is more surprising, because both copepods and daphnids often initiate downward migrations in the presence of fish infochemicals (Dodson 1988). As discussed above, L. minutus is likely more conspicuous to visual fish predators in the transparent waters of Lake Giles because of high concentrations of photoprotective compounds, including carotenoids and MAAs. Studies have demonstrated that pigmented copepods are more susceptible to fish predation than are unpigmented copepods (Hairston 1979; Byron 1982), increasing predation pressures to migrate downward during daylight. Thus, a trade-off exists between protection from damaging solar radiation and increased visibility to fish predators (Hansson 2004; Hansson et al. 2007). Lake Giles L. minutus, especially copepodid stages, typically occupy depths greater than 5–7 m during the day, with approximately 60-80% of the population in the metalimnion and hypolimnion from mid- to late June (PCLP database unpubl.). Based on the results of the kairomone experiment, it appears that L. minutus is avoiding potential fish predators in the surface waters more than it is avoiding UVR.

Daphnia's response to the fish kairomones could have been confounded or overridden by the presence of Chaoborus kairomones in the columns. Chaoborus typically evoke an upward migration in Daphnia (Dodson 1988; Boeing et al. 2004), and in the presence of both fish and Chaoborus kairomones, Daphnia demonstrate signs of stress, reducing swimming behaviors overall (Weber and van Noordwijk 2002). However, during the present study, Chaoborus were absent from the surface waters at the time the columns were filled, suggesting that Chaoborus kairomone levels were below detection. It is also possible that D. catawba would have displayed a stronger response to the fish kairomone if the experiment was run longer than 2.5 h. In laboratory experiments, the behavioral response of Daphnia magna to fish kairomones significantly increased with increased exposure time, particularly after 2 h (De Meester and Cousyn 1997). Some studies suggest that not all fish kairomones are perceived as an equal threat (Weber 2003), so repeating the experiment with kairomones from other fish species may elicit a different response. Additionally, some *Daphnia* clones either lack a behavioral response (Boeing et al. 2004) or swim upwards (Spaak and Boersma 2001; Boeing et al. 2006) in the presence of fish kairomones. Recent studies indicate that both predation and UVR risk assessment in *Daphnia* varies with body size, such that small daphnids (<0.9 mm) remain in the surface waters whereas larger daphnids (>0.9 mm) migrate to deeper depths (Hansson and Hylander 2009). We did not measure individual body size in the present study. However, it is possible that a larger proportion of the population in the columns was comprised of smaller-bodied individuals, reducing the overall observed response of *Daphnia* to fish kairomones.

Behavior in columns vs. nature—The use of enclosures creates an artificial environment, confining animals to a narrow space and depth range and intensifying predation pressures. In nature, zooplankton would be permitted to migrate deeper than the depths to which the columns were suspended in order to avoid both UVR and fish predators. Thus, consumption related to predator–prey overlap has likely been overestimated in our experiments.

In addition, zooplankton and fish distributions as well as prey consumption would likely differ if the experiments were terminated earlier or later in the day. For example, crepuscular periods (i.e., dawn and dusk) are typically active foraging times for fish (Keast and Welsh 1968), and the proportion of UVR to visible radiation is also greater during these times of day (Leech and Johnsen 2003). This may have resulted in proportionately more zooplankton consumed in the UVR+ enclosures because of UVenhanced foraging alone. On the other hand, the fact that significant differences in UV-induced consumption rates were observed here over a very short time period (<1 d) suggests that UV foraging may be important on a wholelake basis over longer time periods.

Planktivorous fish have long been recognized to have a profound effect on lake structure and function through their effects on zooplankton species diversity and vertical distribution (Brooks and Dodson 1965; Lampert 1989). The results of our study suggest that UVR, in addition to visible light, may interact with fish predation pressure on zooplankton, and that daphnids and copepods have developed alternative strategies to cope with UVR, predation, and their interaction. There is a need for further experimental work that disentangles the different mechanisms by which zooplankton groups cope with these two stressors in transparent lakes and how the costs and benefits of different strategies shape the population and community structure of zooplankton.

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