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# Photoresponses of late instar *Chaoborus punctipennis* larvae to UVR

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**Abstract**

With a few clear exceptions (e.g., *Daphnia*) it is uncertain if most aquatic invertebrates can detect and respond to ultraviolet radiation (UVR). It is known that many aquatic invertebrates are vulnerable to UVR and that anthropogenically-induced increases in surface UVR have occurred in recent decades. We examined the photoresponses of late larval instars of *Chaoborus punctipennis* to different combinations of UVA (320–400 nm), UVB (300–320 nm) and visible light (400–700 nm) to determine whether the larvae can detect and/or avoid UVR. To accomplish this, we exposed late instar *C. punctipennis* larvae to a directional light source of UVR only (peak wavelength at 360 nm), visible light only or visible plus various wavebands of UVR. We examined negative phototaxis for 10 min at a quantum flux of $2.62\times10^{13}$ quanta $s^{-1}$ $cm^{-2}$ (S.D. = $3.63\times10^{12}$ quanta $s^{-1}$ $cm^{-2}$). In the dark, larvae stayed close to the surface of the experimental vessels. Under all treatments containing visible light the larvae exhibited negative phototaxis and occupied the bottom of the vessels. Under UVR only, the larvae occupied the middle of the water column. Our results suggest that late instar *C. punctipennis* larvae are unable to detect and avoid UVB and short UVA wavelengths but they can detect long UVA wavelengths.

## Introduction

The ability to detect and respond to UVR is of vital importance to terrestrial as well as aquatic species as a sustained increase in UVB radiation continues due to stratospheric ozone depletion (Siebeck et al. 1994). In addition to providing an important cue for escaping damage, UV photoreception has also been found to play important roles in foraging behavior, navigation, the control of circadian rhythms and intraspecies communication in vertebrate as well as invertebrate species (Tovée 1995). It is therefore important that we examine the UV photoresponses of aquatic invertebrate species, especially keystone species that have been found to be highly susceptible to UVR damage.

While many studies have shown that terrestrial insects are sensitive to UVR (e.g., Goodman 1981), few studies have examined UV photoresponses in aquatic invertebrates even though the ability to detect UVR has been postulated as a pre-condition to avoid its damaging effects (Beeton 1959; Siebeck et al. 1994). Negative as well as positive phototactic responses have been found in aquatic species. Flamarique et al. (2000) reported that the copepod *Lepeophtheirus salmonis* moved towards a UVA source. Bollens and Frost (1990) found that the marine copepod *Acartia hudsonica* did not move away from UVR. Hessen (1994) and Rhode et al. (2001) demonstrated that, upon exposure to UVR, *Daphnia* species immediately migrated downward. Pennington and Emlet (1986)

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found that larvae of the echinoderm, *Dendraster excentricus,* migrated downwards upon exposure to UVR. Barcelo and Calkins (1980) found that the crustacean, *Cyclops*, moved away from a UVR source to a protected location. Beeton (1959) illustrated that *Mysis relicta* moved away from UVA (395nm) light. Forward and Cronin (1979) found that 2 out of 7 inter-tidal crab species have poor UVR sensitivity.

Many studies have examined the photoresponse of *Chaoborus* larvae to visible light, but little work has been done to examine their photoresponse to UVR. In general, late (third and fourth) instar *Chaoborus* larvae are negatively phototactic to visible wavelengths, whereas young (first and second) instars are positively phototactic (LaRow 1971; Swift and Forward 1980; Swift and Forward 1982). LaRow (1971) found that under UVR young instar *Chaoborus* moved towards UVA (350 nm), while late instars moved away from UVA (365 nm). Like LaRow (1971), Swift and Forward (1980) found that fourth instar *C. punctipennis* larvae moved away from UVA (380 nm).

While previous studies have examined *Chaoborus* photoresponses to monochromatic light, the photoresponses of *Chaoborus* to polychromatic light – i.e., the UVR waveband and UVR plus visible light are currently unknown. Therefore, the objectives of this study were to, (a) examine the photoresponses of late instar *C. punctipennis* larvae to different combinations of UVB, UVA and visible wavelengths and (b) determine whether *C. punctipennis* larvae are able to detect and if so, avoid UV wavelengths. To do this, we exposed *C. punctipennis* larvae to a directional light source of UVR only, or visible plus various wavebands of UVR, and examined their phototactic behavior. Phototaxis refers to directional movement of an organism in response to light from a directional source (Diehn et al. 1977). A negative phototactic response consists of movement away from a light source, e.g., descent into the water column away from surface light. Following Swift and Forward (1980), we infer from a negative phototatic behavioral response that the organism can both detect and avoid light of a particular spectral quality and intensity.

It is important that we determine the photoresponses of *C. punctipennis* to UV wavelengths in light of their extreme vulnerability to UVR (Persaud and Yan 2003; Williamson et al. 1999). In addition, short wavelength UVB radiation is increasing as depletion of stratospheric ozone continues with concomitant increases in the UVR:visible light ratio. Furthermore, in north temperate regions, and well within the species distribution range of *C. punctipennis*, there are many lakes with low concentrations of chromophoric dissolved organic matter and hence low UV attenuation (Gunn et al. 2001).

## Methods

*Chaoborus punctipennis* larvae were exposed to a directional light source and negative phototaxis was examined in order to study the responses of *C. punctipennis* larvae to different combinations of UVR and visible wavelengths. Optical cut-off and neutral density filters were used in order to expose the larvae to eight different wavebands of visible (400–700 nm), UVA (320–400 nm) and long UVB wavelengths (300–320 nm) of approximately equal quantum flux. In examining relative photoresponses it is important to maintain approximately equal quantum fluxes so that variations in response to different wavebands reflect spectral composition, not quantum flux (Swift and Forward 1982).

All the behavioral experiments were performed using a directional light stimulus generated by a 300 W Xenon arc lamp (Oriel Instruments, Connecticut) within the "IncUVator" (Figure 1) at the National Water Research Institute (NWRI), Burlington, Ontario, Canada. The IncUVator is a multi-chambered, temperature controlled, UVR exposure system developed by the NWRI (Desrosiers et al. 1994). Xenon arc lamps produce UV-visible light spectra similar to natural sunlight in quality and intensity.

The spectral quality and intensity of the light stimuli were measured with an Ocean Optics SD 1000 spectroradiometer (Ocean Optics Inc., Florida) and verified with an OL-754 Optronics spectroradiometer (Optronics Laboratory, Florida). The Ocean Optics SD 1000 was equipped with an air sensor mounted on a purpose-built in – platform for the IncUVator and operated through a PC via a digital acquisition card. This Ocean Optics spectroradiometer was used to take scans before all experiments. The OL-754 spectroradiometer, equipped with an Optronics – OL 86-T-WP submersible receptor, was used to take scans 5 mm below the water surface to confirm the intensities under different filter combinations and IncUVator settings. Quantum fluxes were calculated using the energy measurements obtained from these scans.

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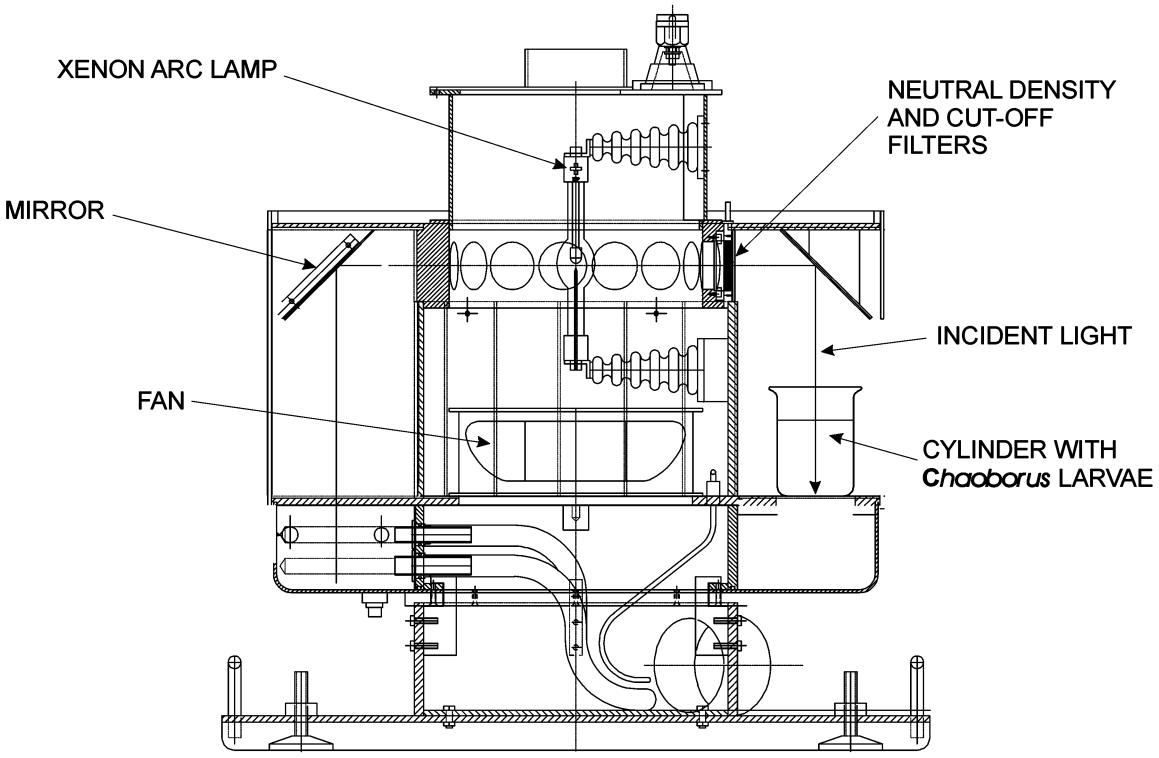


*Figure 1.* Diagram of the Incuvator and the general experimental set-up.

*Experimental cylinders and filters*

Experimental cylinders were made of borosilicate glass. The cylinders were square in cross section (6.5×6.5 cm), 12 cm high, and had 4 mm thick walls. To create a collimated light environment, three sidewalls of the cylinders were covered with black construction paper and a black Acrylite® disc was placed at the bottom of the cylinder to minimize internal reflection. The uncovered sidewall of the cylinder had a mm scale line so that the depths of the larvae could be readily determined.

We used a series of Schott (Mainz, Germany) and Hoya (Lewisville, Texas) cut-off and neutral density filters to obtain different wavebands of light at appropriate intensities. Cut-off filters were used to manipulate the spectral quality of the light. A total of eight cut-off filters were used: WG 305, WG 320, UV 340, UV 360, GG 385, GG 400, GG 420 and U-360 (Figures. 2 a and b). Except for the U-360 filter, all of the cut-off filters were long-pass filters, i.e., they removed shorter wavelengths. Unlike long-pass filters, the U-360 filter transmitted UV and absorbed visible wavelengths (Figure 2b). In contrast to the cut-off filters, the neutral density filters reduced the overall intensity of incident irradiance without affecting the spectral quality of the transmitted light. The NG4 and NG11 filters reduced the intensity by 97% and 38%, respectively.

*Collection of larvae*

Late instar *C. punctipennis* larvae used in the experiments were collected from Plastic Lake, near Dorset, Ontario, and Johnnie Lake, in Killarney Provincial Park, Ontario, Canada. Larvae were collected after dark using a 150 μm mesh net (Yan et al. 1985) hauled vertically through the water column. Larvae were maintained for up to 2 months in the dark at 5 °C. Just prior to initiating an experiment we removed larvae from storage, placed them in Petri dishes, fed them zooplankton, and left them for 2–3 h to warm up to room temperature (20–21 °C) in the dark. Pre-experiment light exposure was always minimized by covering the Petri dishes with black construction paper. After the larvae were acclimated to room temperature they were placed in the experimental cylinders filled with water from Ruth-Roy

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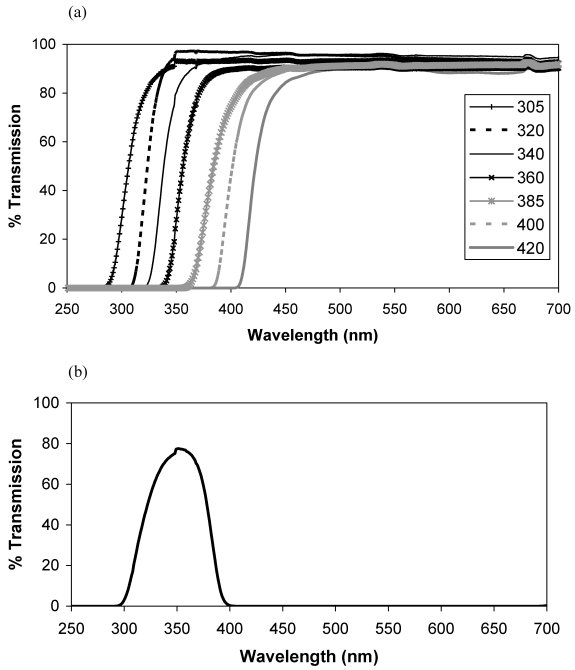


*Figure 2.* The % transmission of the optical cut-off filters – (a) UVR and visible light transmitting filters and (b) UVR only transmitting filter (U-360), used for the spectral sensitivity experiments.

Lake. We used Ruth-Roy Lake water for these experiments because of its low DOC content (0.2 $mg \cdot L^{-1}$; Gunn et al. 2001). All of the water was filtered through 0.5 μm filter paper (Rundfilter: MN GF-2, 10 cm diameter) and stored at 5 °C until required. Cylinders were filled to 10 cm depth with Ruth-Roy Lake water. All experiments were performed at room temperature (20–21 °C).

Some experiments were conducted using larvae that were not stored at 5 °C, instead they were collected from the field and used immediately. The behavior of these animals did not differ significantly from those housed at the lab for more extended periods of time ($p > 0.5$, two-way ANOVA).

*Negative phototaxis and experimental protocol*

Movement away from the light source was used as an indication of negative phototaxis, and the depths (cm) to which the larvae moved away from the light stimulus were used to indicate the degree of sensitivity (ability to detect and avoid), i.e., the further the larvae moved from the source, the greater the inferred sensitivity. The 10 cm height of the cylinders clearly restricted the potential for downward movement of the animals, but it did not compromise our ability to compare phototaxis under UV illumination in the presence and absence of visible light. We observed the larvae individually to avoid interference from light scattering and shading induced by the presence of other larvae. Larvae were used only once.

A standard protocol was followed for all experiments. The larvae were allowed to sit in the dark (experimental cylinders covered with black construction paper and aluminum foil) for 2 min in the IncUVator in Ruth-Roy Lake water. During this 2 min period larvae acclimated to the experimental cylinders and IncUVator environment. Following the acclimation period, larvae were exposed to the light stimulus and their position in the water column was recorded every 15 sec for 10 min. Depths were measured (via visual inspection) from the surface of the water column. Throughout the experiments all laboratory lights were turned off to minimize external light leakage into the IncUVator chamber.

Ten min was chosen as the experimental observation period because preliminary testing indicated that larvae exhibited negative phototactic behavior at overly variable rates within the first 4 to 5 min of exposure. Following the experimental protocol larvae were exposed to different intensities of light transmitted through a 320 nm cut-off filter reduced to the appropriate intensity with a NG4 filter. We recorded the time required for the larvae to detect the light source and respond (by moving to the bottom) and found that at low intensities *C. punctipennis* responded to the light stimulus within 4.25 min. By fixing on a 10 min observation time we were able to observe the stable photoresponses that followed the initial unstable phototactic reactions.

The same experimental protocol was followed for dark controls except that the Xenon lamp was not turned on and larval position was recorded at 10 min. If the depth of the larvae was not recorded within 5 sec, the experiment was repeated. Dark controls were performed with and without the IncUVator turned "on" (i.e., computers running and lamp powered, but switched off) to determine whether background "equipment noise" affected larval behavior. No "IncUVator effect" was found. Dark controls that were run with the IncUVator "on" (but light switched off) were not different from those done with the IncUVator "off" ($p = 0.91$, One-way ANOVA).

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*Intensity testing*

Field and experimental observations have shown that downward migration of *C. punctipennis* larvae begins as light intensity exceeds a critical threshold and stops when the light intensity falls below this threshold (Swift and Forward 1980; Swift and Forward 1982). Because of this, the general response pattern is no response at sub-threshold intensities followed by a linear increase in response as intensity increases and then a continuous high level of response at high intensities (response saturation; Forward, pers. comm.). The appropriate light intensity for testing must therefore lie along the linearly increasing portion of the intensity-response curve.

The intensity used in the spectral sensitivity testing was determined through the development of an intensity-response curve. We performed experiments with neutral density and 320 nm cut-off filters. The 320 nm cut-off filter was chosen so that larvae would be exposed to UVR and visible light. We examined responses of 5–8 animals at 8 different intensities plus dark controls. We chose the maximum light intensity ("threshold") within the linear phase of the intensity-response curve for spectral sensitivity testing. This facilitated observation of minute behavioral (positional) responses so that we could more readily determine whether larvae had the ability to detect and avoid specific wavebands.

*Spectral sensitivity*

To test for spectral sensitivity we examined larval responses under 8 different wavebands plus dark controls. Eight optical cut-off filters: WG 305, WG 320, UV 340, UV 360, GG 385, GG 400, GG 420 and U-360 were used. Nine to 20 larvae were observed under the different filter treatments and in the dark.

Light intensity testing indicated that a quantum flux of ~$2.70\times10^{13}$ quanta $s^{-1}$ $cm^{-2}$ produced a detectable response. We employed a NG4 filter with each cut-off filter to achieve this quantum flux. The mean quantum flux actually employed was $2.62\times10^{13}$ quanta $s^{-1}$ $cm^{-2}$ with a standard deviation of $3.63\times10^{12}$ quanta $s^{-1}$ $cm^{-2}$.

*Statistical analyses*

The depth of larvae in the cylinder for each replicate animal was recorded every 15 sec and the average depths ± S.E. (in cm) between 4.25 and 10 min were then calculated for each animal. We used one-way ANOVAs to test for significant differences in this average depth, i.e., photoresponse among the different filter treatments (Table 1). A two-way ANOVA was also used to compare the photoresponses of *C. punctipennis* larvae from Johnnie and Plastic Lakes. We also performed ANOVAs to compare the different photoresponses (i.e., positions at 10 min) of the various filter treatments with dark controls.

*Table 1.* Summary of data for comparison of filter treatments. Average depths and standard error (cm) are calculated for the time period 4.25 to 10 min after initiating the run. Lake indicates the source of animals; all experiments were in Ruth-Roy Lake water. Treaments are indicated as ultraviolet (UV) or visible (VL) radiation.

| Lake | Cut-off filter | Light | Average depth (cm) | S.E. |
|---|---|---|---|---|
| Plastic | 305 | UV + VL | 8.7 | 0.3 |
| Plastic | 320 | UV + VL | 9.1 | 0.2 |
| Plastic | 340 | UV + VL | 8.3 | 0.5 |
| Plastic | 360 | UV + VL | 8.8 | 0.3 |
| Plastic | 385 | UV + VL | 8.9 | 0.3 |
| Plastic | 400 | UV + VL | 8.5 | 0.3 |
| Plastic | 420 | VL only | 8.5 | 0.3 |
| Plastic | U360 | UV only | 5.8 | 0.7 |
| Plastic | Dark | No light | 3.1 | 0.9 |
| Johnnie | 420 | VL only | 4.9 | 1.1 |
| Johnnie | U360 | UV only | 7.5 | 0.8 |

## Results

The photoresponses of late instar *C. punctipennis* larvae varied among filter treatments. Even though there was considerable variation in phototactic behavior amongst individual larvae, a general pattern did emerge. In most cases larvae actively moved towards the cylinder bottom immediately after exposure to the stimulus. Following this initial response, larvae moved up to a stable depth with periodic movements to other depths in the water column (Figure 3). After 10 min in the dark, late instar *C. punctipennis* larvae from Plastic Lake generally stayed near the top of the cylinder at an average depth of 3.1 ± 0.9 cm (n = 20).

In general *C. punctipennis* larvae exhibited negative phototactic behavior and occupied the bottom of the cylinder when exposed to any of the filter treatments containing visible light (Figure 4). The average photoresponse to the 7 filter treatments containing visible light did not differ ($p = 0.848$, Table 2). These

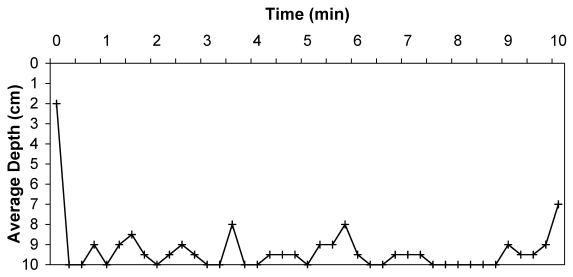


*Figure 3.* Photoresponse of a single late instar *C. punctipennis* larvae to light transmitted by a 305 cut-off filter.

negative phototactic responses were different from the dark control response ($p < 0.001$, Table 2).

Under UVR only, Plastic Lake larvae occupied the middle of the cylinder ($5.8 \pm 0.7$ cm, $n = 14$) after an initial negative phototactic response (Figure 4, Figure 5). This UVR photoresponse was different from that of any filter treatment containing visible light ($p < 0.001$, Table 2). The UVR photoresponse was also different from the behavior in the dark ($p = 0.022$, Table 2).

Johnnie Lake larvae behaved in a manner similar to Plastic Lake larvae when exposed to only visible light or UVR (Table 3). Larvae from Johnnie Lake stayed closer to the surface under UVR only ($4.9 \pm 1.1$ cm, $n = 9$) compared to Plastic Lake larvae (Figure 6); however, the lake effect was not significant ($p = 0.141$, Table 3). Under visible light only, Johnnie Lake larvae generally stayed at the bottom of the cylinders ($7.5 \pm 0.8$ cm, $n = 9$). As with the UVR photoresponse, they stayed higher in the water column compared to Plastic Lake larvae however, the difference in response was not significant ($p = 0.141$). The UVR photoresponses of Johnnie Lake and Plastic Lake larvae were significantly different than those observed under visible light only (Table 3).

## Discussion

The negative phototactic response of late instar *C. punctipennis* larvae that we observed under the visible light only treatment is in agreement with previous studies (Chaston 1969; LaRow 1971; Swift and Forward 1980). Swift and Forward (1980) reported that fourth instar *C. punctipennis* larvae have a peak sensitivity in the violet (400 nm). In the presence of UVR plus visible light, *C. punctipennis* responded as they would to visible light alone.

The intermediate response observed under UVR alone likely indicates *C. punctipennis*' ability to detect long UVA wavelengths and an inability to detect and avoid UVB and short UVA wavelengths. LaRow (1971) and Swift and Forward (1980) reported that late instar *C. punctipennis* larvae moved away from long UVA wavelengths (365 nm, 380 nm, and 390 nm), but peak sensitivity was in the visible light range (400 nm). While the U-360 filter transmitted most UV wavelengths, peak transmittance was at 360 nm with a rapid decrease towards 300 and 400 nm (Figure 2b). *Chaoborus punctipennis* were therefore exposed to only a small flux of the long UVA wavelengths to which they are reportedly sensitive. At the same time they were exposed to a comparatively higher flux of short UVA and long UVB wavelengths to which no sensitivity was previously demonstrated in the literature. If the larvae were as sensitive to these shorter UV wavelengths as they are to longer UVA and visible wavelengths, they would have stayed at the bottom of the cylinder during exposure under the U-360. They did not. Furthermore, the small flux of long UVA wavelengths might have been responsible for movement down the water column to the intermediate position. We therefore postulate that these late instar *C. punctipennis* larvae are unable to detect and avoid short UVA and long UVB wavelengths, but they can detect long UVA wavelengths.

Late instar *C. punctipennis* larvae are generally benthic during daylight hours when UVR levels are high. Their inability to detect and avoid short UVA and UVB wavelengths is therefore in agreement with their occurrence in "typical" lakes of the northern temperate zone where ambient DOC concentrations (in the range of 2 to 4 mg $L^{-1}$, McQueen et al. 2001) would protect the larvae from UVR; because of rapid attenuation of UVR with depth (Scully and Lean 1994). This inability to detect and avoid UVB is consistent with the "sensitivity hypothesis". According to this hypothesis the spectral sensitivity of zooplankters should match the spectral distribution of light in their environment if photoreceptors are to be of use in controlling vertical migration (Munz 1958; Forward and Cronin 1979). Zooplankters should therefore be most sensitive to the most prevalent wavelengths in the underwater environment. Hence, *C. punctipennis* are highly sensitive to visible light whose energy is less rapidly attenuated with depth compared to UVR.

Visible light is primarily responsible for the migratory behavior of late instar *C. punctipennis* larvae observed in nature, and it certainly elicited the largest

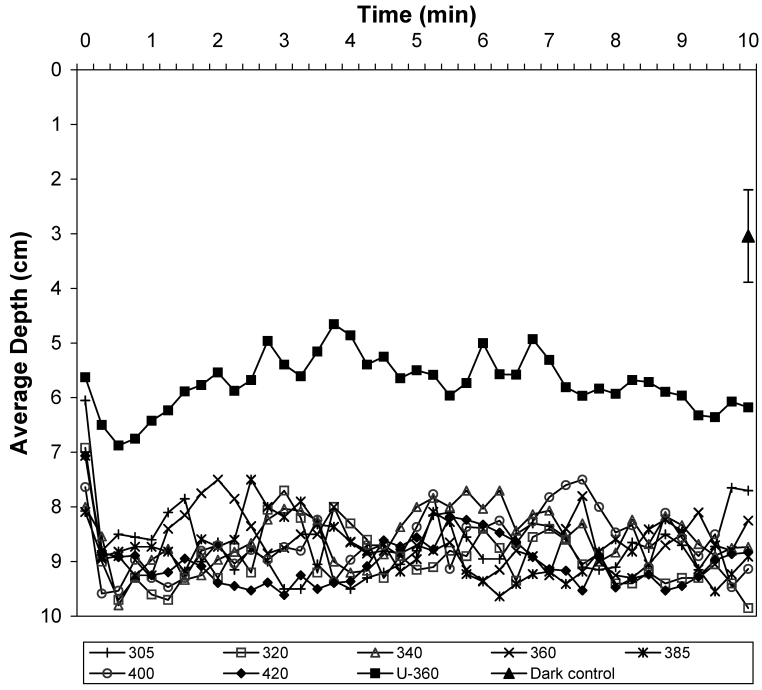


*Figure 4.* The photoresponses of late instar *C. punctipennis* larvae collected from Plastic Lake, Ontario, in the dark and to different wavebands of UVR and visible light. Points represent the average depth among 9 to 20 replicates. For clarity the standard error is only shown for the dark control.

*Table 2.* One-way ANOVA results for the comparison of Plastic Lake *C. punctipennis* photoresponses under the different light treatments and dark controls (VL – visible light).

| Treatments | F | df | p |
|---|---|---|---|
| All VL | 0.444 | 6 | 0.848 |
| VL vs. Dark | 79.992 | 1 | $< 0.001$ |
| UVR only vs. All VL | 37.329 | 1 | $< 0.001$ |
| UVR only vs. Dark | 5.787 | 1 | 0.022 |

response in our treatments. Because of the depth of our cylinders, we could not distinguish any visible light spectral responses, but because of the strong negative phototactic response in the visible light only and combination treatments (UV plus visible radiation) late instar *C. punctipennis* do escape the lethal effects of UV wavelengths in lakes with typical DOC concentrations. In such lakes 1% UVR depths lie within 1 m of the lake surface (Schindler et al. 1996). This negative phototatic response to visible light should continue to protect late instar larval *Chaoborus* in most lakes in the future, even if UVB continues to increase due to stratospheric ozone depletion and climate-driven declines in DOC levels in lakes (Schindler et al. 1996; Yan et al. 1996). However, there are limits. If DOC levels fall below 2 mg $L^{-1}$ UVR penetration increases dramatically hence, in shallow lakes, late instar larvae may not be fully protected unless they burrow into lake sediments during the day.

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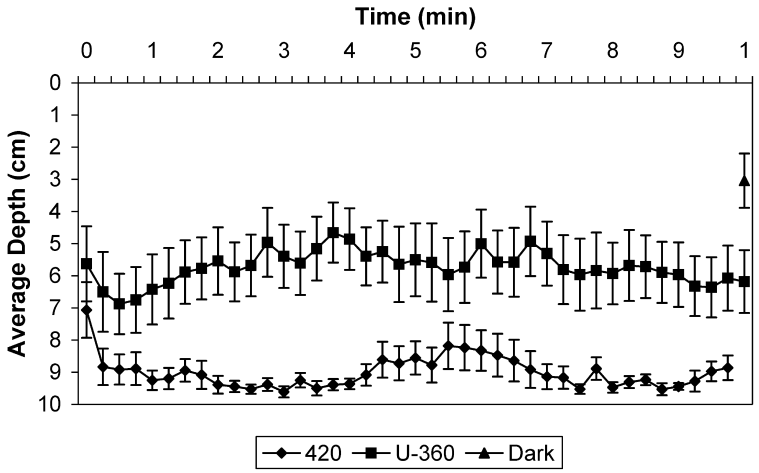


*Figure 5.* The photoresponses of late instar *C. punctipennis* larvae collected from Plastic Lake to UVR only (U-360 filter) and visible light only (420 filter), and in the dark. Points represent the average depth ± S.E. (cm) every 15 sec.

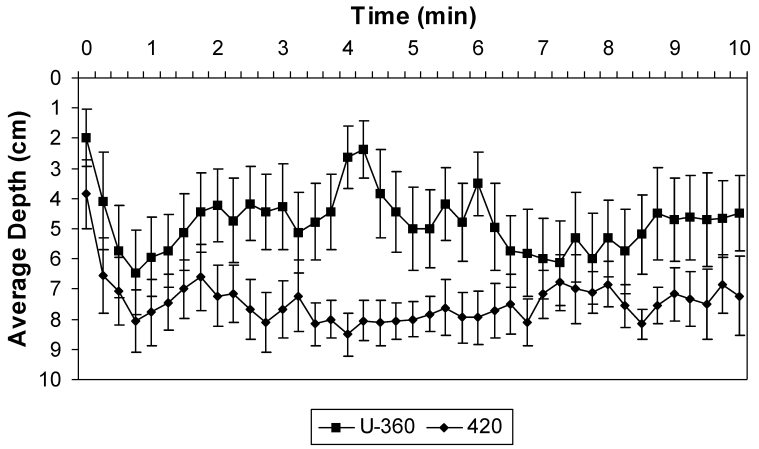


*Figure 6.* The photoresponses of late instar *C. punctipennis* larvae collected from Johnnie Lake to UVR only (U-360 filter) and visible light only (420 filter). Points represent the average depth ± S.E. (cm) every 15 sec.

*Table 3.* Two-way ANOVA results for the comparison of photoresponses under UVR and visible light only treatments among late instar *C. punctipennis* larvae from Plastic Lake and Johnnie Lake

| | F | df | p |
|---|---|---|---|
| Lake | 2.247 | 1 | 0.141 |
| Treatment | 14.233 | 1 | $< 0.001$ |
| Lake * Treatment | 0.131 | 1 | 0.719 |

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