Ultraviolet vision and foraging in juvenile bluegill (*Lepomis macrochirus*)

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Abstract: Ultraviolet (UV) photoreceptors have been reported in a wide variety of freshwater and marine organisms, suggesting that UV vision is prominent in aquatic ecosystems. However, its adaptive significance remains speculative. The present study tested whether the foraging of juvenile bluegill (*Lepomis macrochirus*) is enhanced in the presence of UV radiation (UVR). Laboratory feeding trials were conducted in a laminar flow tank in which *L. macrochirus* juveniles between 2.3 and 3.5 cm standard length were fed the cladoceran *Daphnia magna*. Sighting and striking distances, as well as capture success, were measured in the presence and absence of UVR. Mean sighting and striking distances and capture success did not differ significantly between the two light treatments. There were also no significant differences in the frequency distributions of sighting and striking distance. These results suggest that UV vision may not be used to enhance foraging in *L. macrochirus* on *Daphnia* within the size class tested.

Résumé : Les photorécepteurs d'ultraviolet (UV) sont connus chez une grande variété d'organismes d'eau douce et d'organismes marins, ce qui laisse croire que la vision UV est importante dans les écosystèmes aquatiques. Cependant, on ne peut que spéculer sur leur signification adaptative. Notre étude vérifie si la recherche de nourriture chez de jeunes crapets arlequins (*Lepomis macrochirus*) est améliorée en présence de radiation ultraviolette (UVR). Nous avons fait des essais alimentaires en laboratoire dans un aquarium à flux laminaire dans lequel des jeunes *L. macrochirus* de 2,3–3,5 cm de longueur standard ont été nourris de cladocères *Daphnia magna*. Nous avons mesuré les distance de repérage et d'attaque, de même que le succès de capture, en présence et en l'absence de UVR. Il n'y a pas de différence significative dans les distances moyennes de repérage et d'attaque, ni dans les taux moyens de capture, dans les deux régimes lumineux. Il n'y a pas non plus de différences significatives dans les distributions de fréquence des distances de repérage et d'attaque. Ces résultats indiquent que la vision UV ne sert sans doute pas à améliorer la recherche de nourriture chez les *L. macrochirus* sur les *Daphnia* de la classe de taille examinée.

[Traduit par la Rédaction]

Introduction

Ultraviolet (UV) vision is widespread throughout the animal kingdom, including terrestrial and aquatic organisms (Goldsmith and Bernard 1985; Jacobs 1992; Tovee 1995). Among aquatic organisms, most UV photoreceptors have been described in fish species, although UV photosensitivity has also been reported in annelids, cnidarians, and crustaceans (reviewed by Leech and Johnsen 2003). UV sensitivity, in coordination with other photoreceptor channels, allows the visual systems of organisms that contain them to make certain discriminations, such as the electric field vector, or e-vector, distribution of polarized skylight (Hawryshyn 1992; Parkyn and Hawryshyn 1993) and color (Jacobs 1992; Coughlin and Hawryshyn 1994). Recognition and communication between conspecifics and mates at UV wavelengths is suggested in certain species of coral reef fish (Shashar 1994; Losey et al. 1999; Siebeck 2004) and is demonstrated in the guppy, *Poecilia reticulata* (Smith et al. 2002), and the Panuco swordtail, *Xiphophorus nigrensis* (Cummings et al. 2003).

UV vision is also thought to enhance prey contrast (Loew et al. 1993; Browman et al. 1994; Shashar 1994). Relatively transparent planktonic prey, both freshwater and marine, absorb light at UV wavelengths (Loew and McFarland 1990; Johnsen and Widder 2001). Because of this, these zooplankters may appear darker against a bright UV-rich background. In addition, planktonic prey also scatter or reflect UV and thus may appear lighter or darker depending on the direction of illumination (Loew and McFarland 1990). Laboratory experiments have demonstrated that larval fish and salmonid alevins within the genera *Lepomis*, *Perca*, and *Oncorhynchus* catch more prey (Loew et al. 1993) and have longer pursuit distances (Browman et al. 1994) in the presence of UV radiation (UVR). Furthermore, some species can feed under UV-A radiation alone (Loew et al. 1993). Predation rates of African cichlids feeding on *Artemia* spp. were greater for species with UV sensitivity compared with those without (Jordan et al. 2004). However, recent experiments with rainbow trout, *Oncorhynchus mykiss*, suggest that UV vision does not enhance foraging under natural levels of solar radiation (Rocco et al. 2002). Similar results also were found for the guppy feeding on *Daphnia pulex* under artificial illumination (White et al. 2005). Interestingly, although guppy for-

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aging efficiency was not enhanced by UV, a significant UV effect on mate choice has been demonstrated in previous experiments (Smith et al. 2002).

The objective of the present study was to determine if prey detection in juvenile bluegill (*Lepomis macrochirus*) improves in the presence of UVR. We chose bluegill feeding on *Daphnia* as our model system as both are widely distributed in fresh waters across North America and have been the focus of numerous feeding studies in the past. For example, Vineyard and O'Brien (1976) reported a reduction in the reaction distance of bluegill feeding on daphnia as visible illumination decreased and turbidity increased. Luecke and O'Brien (1981) noted that bluegill (5–9 cm in length) are better able to feed when presented daphniid prey in the forward hemisphere, and sighting distances are often greater than striking distances at both low and high light intensities.

Here laboratory feeding trials were conducted in a laminar flow tank in which sighting and striking distances of bluegill feeding on *Daphnia* prey were measured in the presence and absence of UVR. Placing the fish in laminar flow allows for better control of fish location and orientation and offers a promising technique for testing similar types of behavioral questions. UV and visible spectral reflectance of *Lepomis* and *Daphnia* were also measured.

Materials and methods

Study organism

Bluegill juveniles were collected from a shallow pond in Gainesville, Florida (29.7°N, 82.3°W), on 21 January 2003 (M. Allen, Department of Fisheries and Aquatic Sciences, University of Florida, Gainesville, FL 32611, USA) and were housed in a 50-gallon tank in the laboratory at Duke University, Durham, North Carolina, USA. Fish were kept at 22–23 °C under room illumination and fed fish pellets. All fish were cared for in accordance with established humane protocols (Duke University IACUC Protocol Number A-153-02-05).

Lepomis UV sensitivity test

UV photoreceptors have been detected in pumpkinseed, *Lepomis gibbosus* (Loew et al. 1993), and unusually large beta band absorption has been observed in the red photoreceptor of juvenile bluegill (E. Loew, Program in Physiology, Cornell University, Ithaca, NY 14853, USA, unpublished data). Together, these suggested that bluegill may also have UV sensitivity, via either a UV photopigment or beta band absorption of the red pigment, as is the case for some bats (e.g., *Glossophaga soricina*, Winter et al. 2003). UV sensitivity associated with a beta band would not allow for a chromatic mechanism in the UV, but nevertheless allows for sensitivity to UVR. Preliminary experiments tested for UV sensitivity in the following manner. Ten juvenile bluegill similar in size to those used in the experimental study were adapted to a dim incandescent light and then exposed to flashes of UVR using a UV lamp (UVL-21, UVP, Upland, California, USA) fitted with a Hoya U-330 visible-blocking filter (Edmund Optics, Barrington, New Jersey, USA). The wavelength of peak emission was 366 nm, with a full-width half-maximum of 12 nm (measured using the USB2000 spectroradiometer fitted with a cosine collector; CC3, Ocean Optics Inc., Dunedin, Florida, USA). The integrated irradiance at 5 cm from the lamp was 1.5×10^{15} photons·cm^{-2}·s^{-1}, which is approximately equal to the irradiance in this waveband at noon. No radiation at visible wavelengths could be measured. The low level of fluorescence induced by the UV source was insignificant compared with the adapting illumination and could not be detected. In response to these flashes of UVR, the fish initially exhibited a jerking response and would sometimes swim towards the lamp. These responses do not confirm that the bluegill possess UV-A photoreceptors but do demonstrate UV sensitivity.

Reflectance measurements

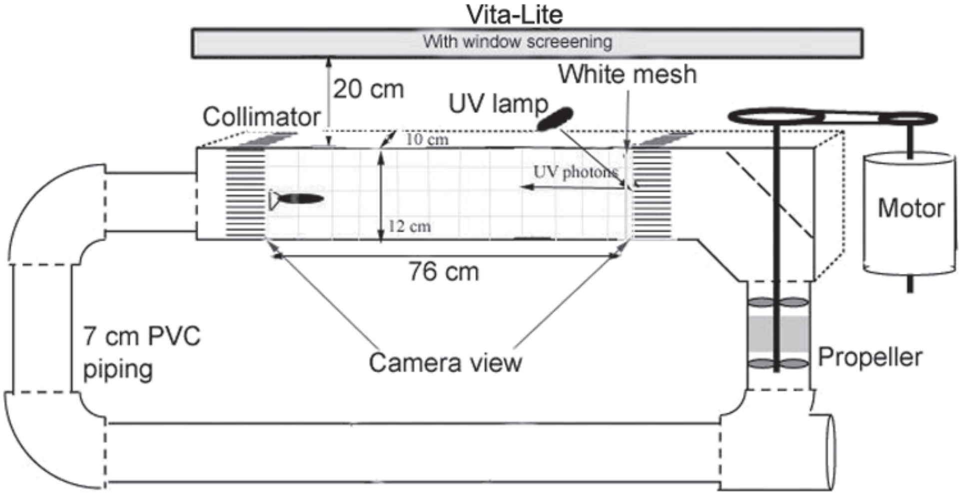
Diffuse reflectance of fish and *Daphnia* were measured using the USB2000 spectroradiometer fitted with a reflectance probe (R400-7, Ocean Optics). The sensor was placed at a 45° angle and calibrated using a white standard (WS-1, Ocean Optics). Fish and *Daphnia* were patted dry, placed on a white background, and measured. UV and visible reflectance was averaged over three to five measurements. For the bluegill, measurements were taken at different locations on the body from the head to the tail, including the abdomen, caudal peduncle, and the caudal fin.

Experimental apparatus and lamp setup

Experiments were conducted in a laminar flow tank designed and built by S. Vogel, Duke University (Fig. 1). The tank consists of a rectilinear working section (76 cm × 10 cm × 12.5 cm), connected at both ends with 7 cm diameter polyvinyl chloride (PVC) tubing. A propeller connected to a variable-speed motor (Master Motor 20000 Series, Minarik Corp., Glendale, California, USA) is housed at one end of the working section. Laminar flow is maintained using honeycombs of hollow tubes (diameter = 5 mm) placed upstream and downstream of the working section. The flow tank was kept in a darkened room and filled with 48 μm filtered, clear water taken from the 50-gallon housing tank. A 1 cm^2 grid was placed along the back wall of the working section of the tank to measure sighting and striking distances of the fish, and a video camera was placed on the opposite side of the rectilinear working section from the grid to record experiments.

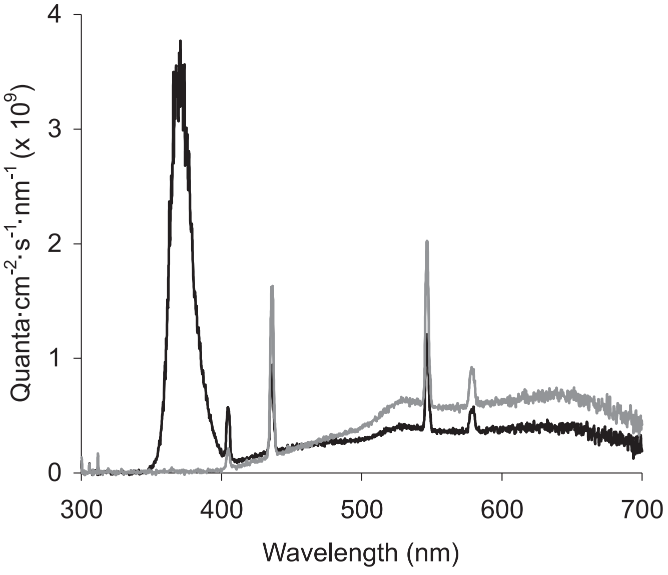
One 1.2 m Vita-Lite (Duro-Test Corporation, Philadelphia, Pennsylvania, USA) was mounted 20 cm directly above the surface of the water. The same UV lamp used in the preliminary studies, but without the visible-blocking filter, was placed directly above the surface of the working section 23 cm downstream from a white Nytex mesh screen. The lamp was angled such that the UVR reflected off the screen upstream of the fish, increasing UV radiance in the horizontal direction. UV irradiance in the flow tank was controlled by placing either UV-transparent (OP-4, Cyro Industries, New Jersey, USA) or UV-opaque (UF3, Polycast Inc., Stamford, Connecticut, USA) acrylic over the working section. The flow tank itself was constructed out of UV-opaque acrylic so that UVR could only enter the tank from above. Preliminary experiments showed that under the full output of the Vita-Lite, the presence or absence of UVR had no effect on the sighting or striking distance of the fish. Therefore, metal window screening was used to reduce the lamp output and replicate twilight conditions. Juvenile bluegills are thought to feed

Fig. 1. Schematic of the experimental laminar flow tank and lamp setup.



more actively at crepuscular periods (Keast and Welsh 1968), and the ratio of UV to visible light is also greater during these times of day (Novales-Flamarique and Hawryshyn 1997; Leech and Johnsen 2003). Downwelling quantal irradiance between 350 and 700 nm was kept constant between UV+ and UV– treatments by moving the tank 5.5 cm closer to the overhead lamp, as well as reducing the amount of window screening in the UV– treatment (Fig. 2).

Fig. 2. Spectra of the ultraviolet plus (UV+) (solid line) and ultraviolet minus (UV–) (shaded line) treatments.



Light measurements

The total number of photons in the fish's field of view was measured using a portable spectroradiometer (USB2000, Ocean Optics Inc., Dunedin, Florida, USA), calibrated using a NIST-traceable UV-visible calibration source (DH-2000-CAL, Ocean Optics). A 1 mm diameter fiber optic cable with an angle of acceptance of 24.8° was fitted to the spectroradiometer. The cable was placed at the position of the fish and directed towards the white Nytex mesh screen. The total number of photons within the field of view was measured from 300 to 700 nm under both UV+ and UV– lighting conditions (Fig. 2). The integrated quanta between the UV+ and UV– treatments were within 9.5% of each other (5.12×10^{11} and 4.65×10^{11} photons·cm^{-2}·s^{-1}, respectively). The light levels approximated those at civil twilight, which is defined as the period when the sun is between 0° and 6° below the horizon.

Experimental design

Fish were starved for 24 h before the start of the experiments. A fish (2.5–3.5 cm total length) was then randomly selected from the housing tank and placed into the flow tank. The lamps were turned on and the fish was allowed to acclimate for 2 h. After acclimation, the flow was incrementally increased to 3 cm·s^{-1}, at which point the fish oriented towards the oncoming current. Fish that did not orient were removed from the study. This flow rate represented the minimum speed at which the fish would orient. Additional speeds were not examined as the focus of our study was on sighting and striking distances in the presence and absence of UVR.

Once oriented, the fish was allowed to acclimate to the flow for an additional 10–15 min before the feeding trial began. Ten *D. magna* (1.3–1.5 mm total length) were introduced to the flow tank one at a time from a pipette placed at the upstream end of the flow tank. Each daphniid could only pass by the fish once, after which a successive daphniid was introduced. Daphnia that were not eaten were trapped behind the white mesh at the upstream end of the flow tank.

Feeding trials were videotaped and measurements of the sighting distance, striking distance, and capture success were measured later. Sighting distance was defined as the distance between the prey and the snout of the fish at the moment that the fish first cued into the prey (denoted by a distinct positioning of the head towards the prey). Typically, fish sighted prey in a forward-looking position (i.e., influenced by flow), between 6 and 23 cm upstream. Daphnia were located closer to the surface of the water at times and near the bottom of the tank at other times. Striking distance was defined as the distance between the snout of the fish and the position of the prey at the moment that the fish lunged after the prey. Daphnia were termed missed if the fish did not see or strike at them or if they were missed during attempted strikes. Eleven fish were tested under UV+ conditions and 13 were tested under UV– conditions.

Statistics

Mean sighting and striking distances, as well as the mean number of missed daphniids, were calculated for each treatment. The mean ratios of sighting to striking distances were also computed. Using SigmaStat (SPSS Inc. 2003), one-way analyses of variance (ANOVA) were performed to test for significant differences between the two light treatments for sighting distance, striking distance, and capture success. A two-group, one-sided power analysis was also performed using SigmaStat to assess the strength of these statistical tests, assuming equal variances and $\alpha = 0.05$. A one-sided test was performed because it was predicted that sighting and striking distances would be greater in the presence of UV.

In addition, the data were analyzed as frequency distributions. The Kolmogorov–Smirnov (K–S) two-sample test was used to detect significant differences between the frequency distributions of the mean sighting and striking distance for each fish in the presence and absence of UVR (after Browman et al. 1994).

Results

Reflectance

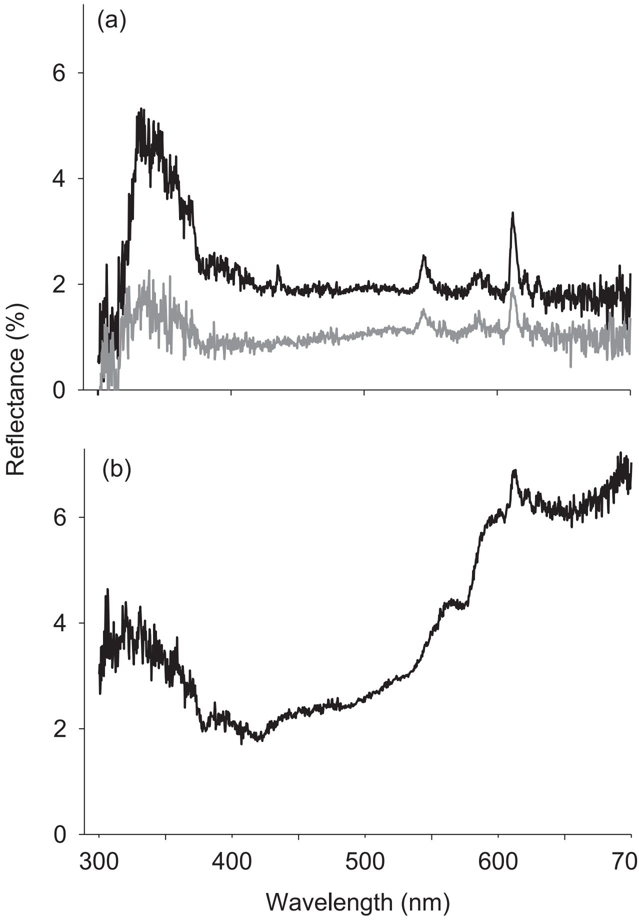
Although overall diffuse reflectance was low (less than 6%), both the bluegills and the Daphnia had increased reflectance at UV wavelengths compared with visible wavelengths (Fig. 3). In bluegill, peak UV reflectance occurred at 335 nm, with similar peak reflectance values across the length of the body, except for the tail. Integrated reflectance in the UV spectrum (300–400 nm) was approximately 33% of that in the visible (400–700 nm). *Daphnia magna* peak reflectance occurred at 320 nm, with an additional broad peak occurring at 610 nm associated with the red coloration of the Daphnia carapace. Integrated reflectance in the UV spectrum was approximately 20% of that in the visible.

Sighting distance, striking distance, and capture success

There was no significant difference in the mean sighting distance ($F_{[1,23]} = 0.669$, $P = 0.42$) or striking distance ($F_{[1,23]} = 0.748$, $P = 0.40$) of the bluegills between the two light treatments (Fig. 4). The frequency distributions of the sighting and striking distances also did not differ significantly between the two light treatments ($P > 0.05$; Fig. 5). The ratio of sighting to striking distance was greater, although not significant, in the presence of UV ($F_{[1,23]} = 3.03$, $P = 0.10$; Fig. 4). An a posteriori power analysis indicated that with our sample size we had an 80% chance of detecting a statistically significant difference between UV+ and UV– treatments if the magnitude of differences between treatments was at least 26% (i.e., 4.1 cm) in sighting distance and at least 49% (i.e., 3.5 cm) in striking distance.

In addition, the number of missed Daphnia per fish did not differ significantly between the two light treatments ($F_{[1,23]} = 0.052$, $P = 0.82$; Fig. 4). On average, bluegill missed 2.5 ± 0.6 standard error (SE) daphnia per fish in both light treatments. The a posteriori power analysis indicated that we had an 80% chance of detecting a statistically significant difference between UV+ and UV– treatments if the difference was 99% or greater.

Fig. 3. Ultraviolet and visible reflectance measurements for (*a*) the bluegill sunfish (*Lepomis macrochirus*) body (solid line) and tail (shaded line) and (*b*) the cladoceran *Daphnia magna*.



Discussion

In high-UV environments, UV sensitivity has been reported in over one-half of the fish species examined, spanning a wide diversity of freshwater and marine families (reviewed in Leech and Johnsen 2003). However, in low-UV environments, the percentage of fish with UV sensitivity decreases dramatically, suggesting that UV vision has some adaptive function (Douglas et al. 1998; Fuller et al. 2004). Although great strides have been made in identifying UV photoreceptors among fish species, our understanding of the roles of UV vision in fish and other aquatic organisms is limited.

In the present study, average sighting and striking distances, as well as capture success, did not significantly differ in the presence and absence of UVR, suggesting that UVR does not enhance bluegill foraging on *Daphnia* within the size class tested and may be used for other adaptive purposes. Similar results were found in juvenile rainbow trout (Rocco et al. 2002) and guppies (White et al. 2005), i.e., the presence of natural or artificial UV illumination did not enhance the number of prey eaten, prey choice, or sighting distances. However,

Fig. 4. Mean values for (*a*) *Lepomis* sighting and striking distance and (*b*) the ratio between sighting and striking distance and the number of missed *Daphnia* in the presence and absence of ultraviolet (UV) radiation. Solid symbols represent the UV+ treatment, open symbols represent the UV− treatment. Shaded lines denote range; error bars denote standard error.

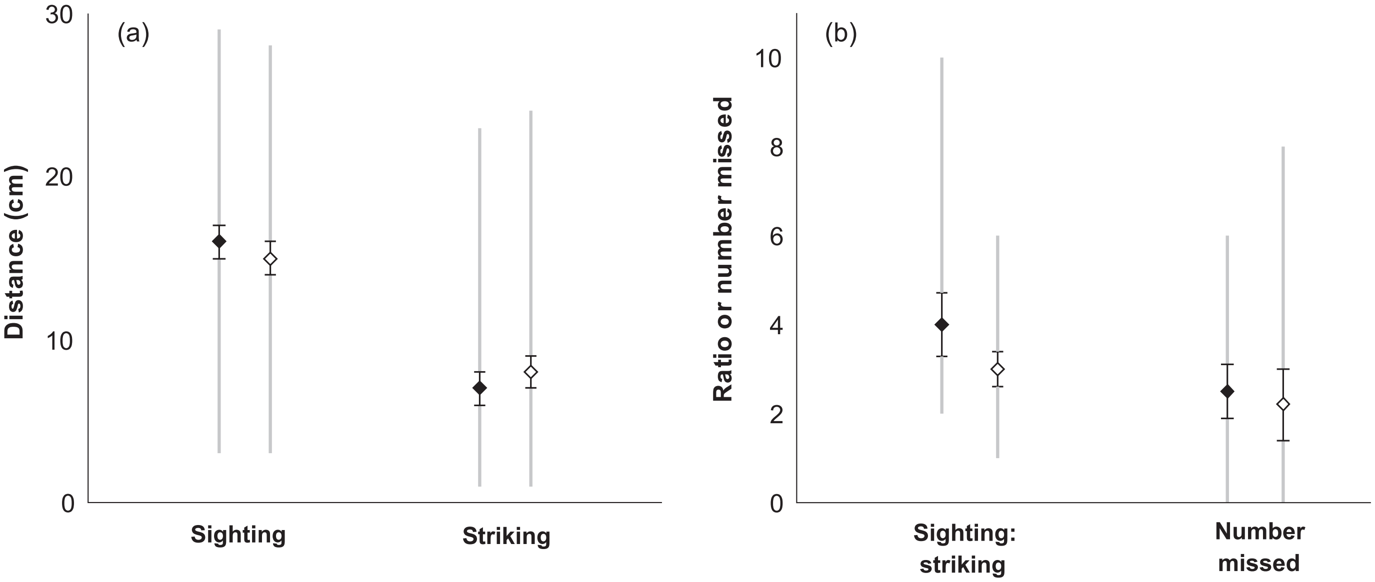
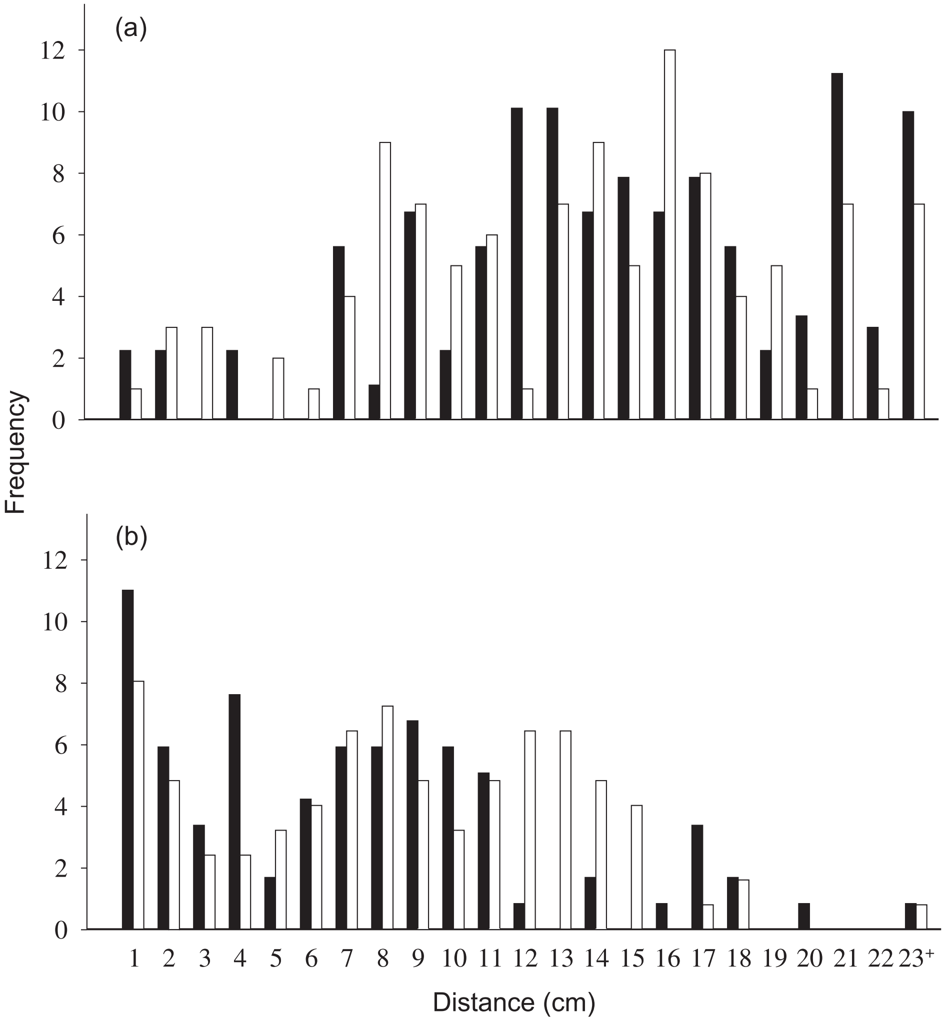


Fig. 5. Frequency distributions of (*a*) sighting distance and (*b*) striking distance for bluegill sunfish (*Lepomis macrochirus*) foraging in the presence (solid bars) and absence (open bars) of ultraviolet radiation.



these results are in contrast to those reported by others in which pursuit distances in rainbow trout and number of prey eaten in pumpkinseed increased in the presence of UVR (Loew et al. 1993; Browman et al. 1994). Furthermore, laboratory experiments demonstrated that yellow perch (*Perca flavescens*) feed better under UV-A radiation alone compared with visible light, even when the quantal flux was less than that at longer wavelengths (Loew et al. 1993).

One possible explanation for the lack of enhanced UV foraging is that the addition of UVR did not sufficiently increase daphniid visibility. Although others have demonstrated that Daphnia scatter UVR (reviewed in Leech and Johnsen 2003), measured diffuse reflectance in the present study was low. UV reflectance was 20% less than visible reflectance, although the integrated visible range was three times larger (400–700 nm) than the UV (300–400 nm). In addition, daphniids typically do not absorb UVR because of a lack of UV-absorbing pigments in the cuticle. Copepods, however, are often highly UV absorptive, and thus using copepods instead of daphniids may have yielded a greater positive effect in UV foraging.

In the present study, as well as in others (Rocco et al. 2002; Jordan et al. 2004), it is important to note the size of the fish examined. Different populations of fish lose their UV photoreceptors at different sizes and (or) ages, thus using length and (or) weight as the sole criteria for presence or absence of UV photoreception is equivocal. It is possible that the bluegill used in our study did not possess UV-A photoreceptors even though UV sensitivity was demonstrated in the preliminary experiments. The presence of a UV-A photoreceptor could have yielded a greater UV effect on foraging than UV sensitivity associated with a beta band (e.g., increased chromatic contrast; Loew et al. 1993).

Experimental lighting conditions are also important to note. To maintain the same total quanta in the UV+ and UV– treatments, the tank was moved closer to the Vita-Lite in the UV– treatment, resulting in 33% more quanta in the visible spectrum of the UV– treatment compared with the UV+ treatment. If the fish were relying solely on visible light for foraging, one might expect an increase in sighting distance with increased visible light. However, based on theoretical modeling of visual summation under dim lighting conditions, the effect on contrast threshold is likely to be small (approximately 23% as calculated by the inverse square root of the photon flux; Theobald et al. 2006). In addition, the use of the white mesh created a bright UV-rich background upon which the daphniids were viewed in the horizontal direction, and a darker background may have provided different results. We chose to use the white mesh to more closely replicate natural conditions. In clear surface waters, the number of UV-A photons often approaches 40% of the total photons seen in the horizontal and downward directions (Losey et al. 1999). Finally, increased blue light relative to shorter wavelength UV can override or shut down the UV channel in some species (Hawryshyn 1991).

We recognize that a larger sample size would have increased the power of our study and may have revealed a significant difference in foraging between the two light treatments. We were able to detect significant UV effects on sighting distance with a difference of approximately 25% or greater with 80% power. It is possible that smaller effects on sighting distance may be present that were not detected. To detect a 10% (i.e., 1.55 cm) or greater difference in sighting distance, a sample size of 158 fish would be needed. Because of the high variability in striking distance, only a 49% or greater difference in this parameter could be detected with 80% power, and at least 215 fish would be needed to detect a 10% (i.e., 0.72 cm) or greater difference. This is even truer in the case of missed strikes. These differences in distance may seem small. However, foraging models generally consider foraging efficiency to be proportional to the sighting distance squared (Aksnes and Giske 1993). Predators are assumed to make tubes of observed territory as they travel, and the radius of the tube is equal to the sighting distance. Thus, a 10% increase in sighting distance leads to a 21% increase in foraging. A 20% increase leads to a 44% increase. Nevertheless, bluegill sighting and striking distances in the present study are within the same range reported by others (Vineyard and O'Brien 1976; Luecke and O'Brien 1981).

This is the first time that UV foraging has been tested in flowing waters. Conducting the experiments in the laminar flow tank allowed for better control of the positioning and orientation of the fish versus the appearance of the prey. The length of the working section of the flow tank (76 cm) also allowed us to measure longer sighting and striking distances than previously reported. Bluegills typically inhabit both moving and non-moving waters. However, it is possible that UV foraging in bluegill may be more efficient in lakes than in streams and rivers because of the lack of current influencing the prey's position and reduced variability in background contrast upon which the prey are viewed. Recently, Mussi et al. (2004) conducted experiments in a flow tank of similar design and observed that the feeding reaction of shiner perch (*Cymatogaster aggregata*) occurred at longer distances when fed semitransparent artemia (i.e., natural) compared with artemia injected with black ink. The authors suggest that the semitransparent artemia were visible at greater distances because of their increased scattering or diffuse reflectance, making them appear brighter against a dark background. In the present study, daphniids displayed low diffuse reflectance and possessed dark gut contents. These factors are likely to make them appear darker against a brighter background in both light treatments.

Many species of larval and juvenile fish feed more actively during crepuscular periods (i.e., dawn and dusk) (Keast and Welsh 1968). At these times of day, the ratio of UVR to visible light is greater because the light field is mostly composed of skylight, which contains a higher proportion of scattered shorter-wavelength radiation than direct sunlight (Novales-Flamarique and Hawryshyn 1997; Leech and Johnsen 2003). We simulated this in our experiments, with respect to irradiance only, by decreasing visible light intensity using window screening. However, it is possible that there was still sufficient visible light in both treatments to facilitate foraging, and even dimmer conditions with increased relative UVR may have resulted in a stronger UV response. In addition, the fish used in this study were collected from a productive, shallow pond, receiving less UVR than those living in less productive systems. Typically, organisms inhabiting low-UV environments have little to no expression of UV photoreception (Cronin et al. 2002; Fuller et al. 2004).

Future studies comparing animals collected from populations inhabiting both high- and low-UV environments may therefore be of interest.

If bluegill are not using UV vision in foraging, then it may play an important role in communication and recognition between conspecifics and (or) predators. The advantage of signaling at UV wavelengths is that it cannot be detected by predators or prey without UV vision (Losey et al. 1999; Cummings et al. 2003). In the present study, bluegill were shown to be UV reflective, excluding the tail. Another possibility is that the fish are using UV vision to avoid depths at which levels of solar UVR could be potentially damaging. Increased mutation and mortality rates have been noted in both fish eggs and larvae resulting from increased UV exposure (Williamson et al. 1994; Browman et al. 2000), and adult *Lepomis* construct their nests for rearing young deeper in high-UV lakes compared with low-UV lakes (Gutierrez-Rodriguez and Williamson 1999). These early life history stages are particularly susceptible to UV damage because of their often transparent, dermal tissue. Certain species of fish possess photoprotective compounds and DNA repair mechanisms to help protect or alleviate some of the damage associated with UV exposure, whereas others are able to actively avoid high-UV environments. For example, shade-seeking behavior and UV avoidance were observed in larval coho salmon (*Oncorhynchus kisutch*) in outdoor enclosures that provided fish with a choice of light environment (Kelly and Bothwell 2002). Although *O. kisutch* has not been examined for UV photoreceptors, other species within this genus are known to have UV vision (Browman et al. 1994). Negative phototactic responses of *Lepomis* larvae to UVR, as well as intense visible light, have been observed in the field (D. Leech, personal observation); however, UVR avoidance has not been directly tested in bluegill.

Acknowledgements

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References

Aksnes, D.L., and Giske, J. 1993. A theoretical model of aquatic visual feeding. Ecol. Model. **67**: 233–250.

Browman, H.I., Novales-Flamarique, I., and Hawryshyn, C.W. 1994. Ultraviolet photoreception contributes to prey search behavior in two species of zooplanktivorous fishes. J. Exp. Biol. **186**: 187–198.

Browman, H.I., Rodriguez, C.A., Beland, F., Cullen, J.J., Davis, R.F., Kouwenberg, J.H.M., Kuhn, P.S., McArthur, B., Runge, J.A., St-Pierre, J.F., and Vetter, R.D. 2000. Impact of ultraviolet radiation on marine crustacean zooplankton and ichthyoplankton: a synthesis of results from the estuary and Gulf of St. Lawrence, Canada. Mar. Ecol. Prog. Ser. **199**: 293–311.

Coughlin, D., and Hawryshyn, C.W. 1994. The contribution of ultraviolet and short-wavelength sensitive cone mechanisms to color vision in rainbow trout. Brain Behav. Evol. **43**: 219–232.

Cronin, T.W., Caldwell, R.L., and Erdmann, M.V. 2002. Tuning of photoreceptor function in mantis shrimp species occupying a range of depths. I. Visual pigments. J. Comp. Physiol. A, **188**: 179–186.

Cummings, M.E., Rosenthal, G.G., and Ryan, M.J. 2003. A private ultraviolet channel in visual communication. Proc. R. Soc. Lond. B, **270**: 897–904.

Douglas, R.H., Partridge, J.C., and Marshall, N.J. 1998. The eyes of deep-sea fish. I: Lens pigmentation, tapeta and visual pigments. Prog. Retin. Eye Res. **17**: 597–636.

Fuller, R.C., Carleton, K.L., Fadool, J.M., Spady, T.C., and Travis, J. 2004. Population variation in opsin expression in the bluefin killifish, *Lucania goodie*: a real-time PCR study. J. Comp. Physiol. A, **190**: 147–154.

Goldsmith, T.H., and Bernard, G.D. 1985. Visual pigments in invertebrates. Photochem. Photobiol. **42**: 805–809.

Gutierrez-Rodriguez, C., and Williamson, C.E. 1999. Influence of solar ultraviolet radiation on early life-history stages of the bluegill sunfish, *Lepomis macrochirus*. Environ. Biol. Fishes, **55**: 307–319.

Hawryshyn, C.W. 1991. Light adaptation properties of the ultraviolet sensitive cone mechanism in comparison to the other receptor mechanisms of goldfish. Vis. Neurosci. **6**: 293–301.

Hawryshyn, C.W. 1992. Polarization vision in fish. Am. Sci. **80**: 164–175.

Jacobs, G.H. 1992. Ultraviolet vision in vertebrates. Am. Zool. **32**: 544–554.

Johnsen, S., and Widder, E.A. 2001. Ultraviolet absorption in transparent zooplankton and its implications for depth distribution and visual predation. Mar. Biol. **138**: 717–730.

Jordan, R., Howe, D., Juanes, F., Stauffer, J., Jr., and Loew, E. 2004. Ultraviolet radiation enhances zooplanktivory rate in ultraviolet sensitive cichlids. Afr. J. Ecol. **42**: 228–231.

Keast, A., and Welsh, L. 1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. J. Fish. Res. Board Can. **25**: 1133–1144.

Kelly, D.J., and Bothwell, M.L. 2002. Avoidance of solar ultraviolet radiation by juvenile coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. **59**: 474–482.

Leech, D.M., and Johnsen, S. 2003. Behavioral responses: UV avoidance and vision. *In* UV effects in aquatic organisms and ecosystems. *Edited by* W. Helbling and H. Zagarese. The Royal Society of Chemistry, Cambridge. pp. 455–481.

Loew, E.R., and McFarland, W.N. 1990. The underwater visual environment. *In* The visual system of fish. *Edited by* R.H. Douglas and M.B.A. Djamgoz. Chapman and Hall Press, London. pp. 1–44.

Loew, E.H., McFarland, W.N., Mills, E.L., and Hunter, D. 1993. A chromatic action spectrum for planktonic predation by juvenile yellow perch, *Perca flavescens*. Can. J. Zool. **71**: 384–386.

Losey, G.S., Cronin, T.W., Goldsmith, T.H., Hyde, D., Marshall, N.J., and McFarland, W.N. 1999. The UV visual world of fishes: a review. J. Fish Biol. **54**: 921–943.

Luecke, C., and O'Brien, W.J. 1981. Prey location volume of a planktivorous fish — a new measure of prey vulnerability. Can. J. Fish. Aquat. Sci. **38**: 1264–1270.

Mussi, M., McFarland, W.N., and Domenici, P. 2004. Visual cues eliciting the feeding reaction of a planktovorous fish swimming in a current. J. Exp. Biol. **208**: 831–842.

Novales-Flamarique, I., and Hawryshyn, C.W. 1997. Is the use of underwater polarized light by fish restricted to crepuscular periods? Vis. Res. **37**: 975–989.

Parkyn, D.C., and Hawryshyn, C.W. 1993. Polarized light sensitivity in the rainbow trout (*Oncorhynchus mykiss*): characterization from multiunit responses in the optic nerve. J. Comp. Physiol. **172**: 493–500.

Rocco, V., Barriga, J.P., Zagarese, H., and Lozada, M. 2002. How much does ultraviolet radiation contribute to the feeding performance of rainbow trout, *Oncorhynchus mykiss*, juveniles under natural illumination? Environ. Biol. Fishes, **63**: 223–228.

Shashar, N. 1994. UV vision by marine animals: mainly questions. *In* Ultraviolet radiation and coral reefs. *Edited by* D. Gulko and P.L. Jokiel. Hawaiian Institute of Marine Biology (HIMB) Tech. Rep. No. 41. University of Hawaii UNIHI-Sea Grant-CR-95-03.

Siebeck, U.E. 2004. Communication in coral reef fish: the role of ultraviolet colour patterns in damselfish territorial behaviour. Anim. Behav. **68**: 273–282.

Smith, E.J., Partridge, J.C., Parsons, K.N., White, E.M., Cuthill, I.C., Bennett, A.T.D., and Church, S.C. 2002. Ultraviolet vision and mate choice in the guppy (*Poecilia reticulata*). Behav. Ecol. **13**: 11–19.

SPSS Inc. 2003. SigmaStat [computer software]. Version 3.0.1. SPSS Inc., Chicago, Illinois.

Theobald, J.C., Greiner, B., Weislo, W.T., and Warrant, E.J. 2006. Visual summation in night-flying sweat bees: a theoretical study. Vis. Res. **46**: 2298–2309.

Tovee, M.J. 1995. Ultra-violet photoreceptors in the animal kingdom: their distribution and function. Trends Ecol. Evol. **10**: 455–459.

Vineyard, G.L., and O'Brien, W.J. 1976. Effects of light and turbidity on reactive distance of bluegill (*Lepomis macrochirus*). J. Fish. Res. Board Can. **32**: 2845–2849.

White, E.M., Church, S.C., Willoughby, L.J., Hudson, S.J., and Partridge, J.C. 2005. Spectral irradiance and foraging efficiency in the guppy, *Poecilia reticulate*. Anim. Behav. **69**: 519–527.

Williamson, C.E., Zagarese, H.E., Schulze, P.C., Hargreaves, B.R., and Seva, J. 1994. The impact of short-term exposure to UV-B radiation on zooplankton communities in north temperate lakes. J. Plankton Res. **16**: 205–218.

Winter, Y., Lopez, J., and von Helversen, O. 2003. Ultraviolet vision in a bat. Nature (London), **425**: 612–614.