The effect of ultraviolet radiation on the foraging rate of juvenile bluegill (Lepomis macrochirus)

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Abstract Fish depend on visual cues for orientation, communication, and foraging behavior. Therefore, any trait that would allow fish to have enhanced visibility would be favored by natural selection. Recent ozone depletion has led to ubiquitous ultraviolet radiation (UVR) in aquatic environments. Fish that utilize ultraviolet (UV) vision through UV photoreceptors to may exhibit enhanced foraging. In this study, juvenile bluegill (*Lepomis macrochirus*) were fed *Daphnia* in the presence and absence of ultraviolet-A (UVA) radiation to determine if UV wavelengths enhanced their foraging rates. Results showed that in the presence of UVA, bluegill detect and identify *Daphnia* more quickly than in the absence of UVA. The foraging rates do not differ between the two light conditions. Consequently, bluegill may be utilizing UV photoreceptors for a different function than foraging.

Introduction

Many fish species depend on visual cues for orientation, communication, and foraging behavior (Tovee 1995; Guthrie 1986). The visual environment of an aquatic system, particularly its light intensity and spectral composition, affects the feeding ability, reaction distance, and predation rate of many fish species (Jordan et al. 2004; Leech et al. 2009). In predatory species, the detection and successful capture of prey are essential for growth and survival. This is especially true for larval and juvenile individuals because they require adequate amounts of prey to accelerate growth (Modarressie and Bakker 2007). Studies have shown that with increases in turbidity or dissolved organic carbon (which decrease water clarity) that predatory fish have reduced prey encounter rates and capture success, and often are unable to select preferred prey (Ljunggren and Sandstrom 2007; Horppila and Nurminen 2005; Abrahams and Kattenfeld 1997; Jonsson et al. 2013). This can ultimately affect fish growth, production, population size structure,
and community composition (Estlander et al. 2012; Stasko et al. 2012). Accordingly, any characteristic that would allow for fish species to have enhanced visibility in their environment would be evolutionarily favored. Ultraviolet (UV) light is more abundant in aquatic environments since recent ozone depletion (Mandronich 1994), and the ability to perceive the wavelength of light being transmitted through the water column may be advantageous for aquatic organisms.

A wide range of aquatic and terrestrial organisms, including both invertebrates and vertebrates, have developed UV-sensitive photoreceptors that allow for the detection of ultraviolet light in their environment (Goldsmith and Bernard 1985; Tovee 1995; Jacobs 1995). Fish species are common among organisms that have developed these photoreceptors, and independent of foraging behavior these photoreceptors aid in intraspecific and mate communication, navigation, color detection, and circadian rhythm (Leech and Johnsen 2006, Modarressie and Bakker 2007; Tovee 1995; Coughlin and Hawryshyn 1994). UV vision may be critical for communication between intraspecific individuals because predator and prey of that species may not perceive UV visual cues. Among male northern swordtails (Xiphophorus), UV ornamentation increases attractiveness to females without drawing attention to their major predator (Cummings et al. 2003). Additionally, Novales Flamarique (2000) suggests that because of the arrangement of UV photoreceptors, adult sockeye salmon (Oncorhynchus nerka) use UV vision for navigation during migrations.

There is evidence that UV photoreceptors of many fish species enhance rates of zooplanktivory. Juvenile yellow perch (Perca flavescens), rainbow trout (Oncorhynchus mykiss), and pumpkinseed (Lepomis gibbosus) possess UV photoreceptors that are not present during adulthood, suggesting that juveniles of these species detect and recognize prey items using UV
visual cues (Loew et al. 1993; Browman et al. 1994). Studies done on largemouth bass 
(*Micropterus salmoides*), threespine stickleback (*Gasterosteus aculeatus*), and some species of 
African cichlid show that feeding rates on zooplanktonic prey increase in the presence of 

Zooplanktivorous fish that utilize visually-mediated foraging habits must be able to detect 
a contrast between their prey and the background to forage efficiently (Utne-Palm 2001). As a 
strategy for predator avoidance, many types of zooplankton demonstrate some level of 
transparency as a form of camouflage (Johnsen and Widder 1998; Utne-Palm 2001). However, the 
presence of ultraviolet radiation in aquatic environments complicates the ability of zooplankton to 
remain camouflaged due to their ability to absorb or reflect short wavelengths of light (Johnsen 
and Widder 2001; Loew and McFarland 1990). Zooplankton that absorb ultraviolet radiation, like 
*Daphnia*, appear darker on naturally UV reflecting backgrounds, creating greater contrast (Loew 
and McFarland 1990; Modarressie and Bakker 2007). Some zooplankton also have the ability to 
scatter short wavelengths of light making them appear lighter or darker than their background 
depending on the illumination, shape, and refractive index differences (Leech and Johnsen 2006; 
2003; Loew and McFarland 1990). Therefore, fish species that use visual cues in the UV spectrum 
to forage on zooplankton with UV absorbing or reflecting properties have an advantage.

The purpose of this study was to determine if the foraging efficiency of juvenile bluegill 
(*Lepomis macrochirus*) is enhanced in the presence of UV light due to the UV photoreception. 
The model system used was juvenile bluegill feeding on *Daphnia spp.* in the presence or absence 
of an ultraviolet-A (UVA; 320-400 nm) light source. Foraging efficiency is defined in this study 
as the rate at which juvenile bluegill consume *Daphnia*. Bluegill inhabiting the littoral zones of 
lakes spend long periods of time hovering above aquatic vegetation in search of a variety of prey
items, including cladocerans like *Daphnia* (Gerry et al. 2012). Since UVA wavelengths penetrate up to 2.5 times deeper than UVB wavelengths (Williamson et al. 1996), littoral fish are subject to experience UVA at persistent rates. Given that some species of fish have shown evidence of enhanced foraging rates on zooplankton in the presence of UV, the ability of zooplankton to absorb or reflect UV light, and the natural history of bluegill, I hypothesize that juvenile bluegill will find and consume *Daphnia* at a faster rate in the presence of a UVA light source than in the absence of a UVA light source.

**Materials and Methods**

This research was conducted at the University of Notre Dame Environmental Research Center (UNDERC) property located in the upper peninsula of Michigan and northern Wisconsin. The juvenile bluegill (40-75cm) used in this study were collected from Bay Lake. Bay Lake has a surface area of 67.3 hectares and a max depth of 13.7 meters. With a Secchi depth of 4.3 meters and a dissolved organic carbon (DOC) concentration of 6.1 mg/L, Bay Lake is considered a relatively clear, low DOC lake (Craig et al. 2015). Bluegill were captured with minnow traps that were placed in the shallow, littoral areas of the lake. Traps were set in the lake for a maximum of 12 hours (checked morning and evening) to reduce predation of the bluegill by species like largemouth bass.

After the bluegill were collected they were taken to the lab and placed in 10-gallon tanks that had been filled with water from Tenderfoot Lake. Spectrophotometry was used to compare the percent transmittance of water from Bay Lake and Tenderfoot Lake to better match fishes’ lab housing and experimental conditions to their natural environment. This was done to control for the chance that bluegill experience seasonal changes in spectral sensitivity that correspond
with seasonal changes in the light environment (Leech and Johnsen 2003; Muntz and Wainwright 1978; Muntz and Mouat 1984). Fish were presented with *Daphnia* for one hour after capture to help accustom them to eating *Daphnia* in a tank. The bluegill were then placed in similar tanks with no *Daphnia* for a 10-12 hour starvation period. One hour prior to the end of the starvation period, the bluegill were placed in individual 25x16x6 cm tanks with 8 cm of water to acclimate before running trials. The sides and bottom of these tanks were covered with UVA-reflecting aluminum foil and the back was covered with white paper to act as contrast for viewing bluegill foraging on *Daphnia*.

The two experimental conditions were bluegill feeding on *Daphnia* with the addition of a UVA light source (UV+) and bluegill feeding on *Daphnia* in the absence of a UVA light source and with ambient lighting (UV0). Nineteen fish (mean length ± SD: 47.05 cm ± 5.6 cm) were tested under UV+ conditions with a CFL spiral light bulb (14 W, Black) suspended 16 cm from the surface of the water and nineteen fish (mean length ± SD: 54.74 cm ± 8.98 cm) were tested under UV0 conditions in the ambient lighting of the lab. Trials were run for a total of seven minutes: three minutes for acclimation and four minutes for feeding. At the end of the third minute, 15-20 live *Daphnia* were introduced into the tank in 50 mL of water. On minutes one and two, 50 mL of water was poured into the tank so that when the *Daphnia* were introduced on the third minute the bluegill would not be shocked. Three measurements were taken per trial: (1) the amount of time in seconds it takes for the fish to eat one *Daphnia* (Time 1), (2) the amount of time in seconds it takes for the fish to eat five *Daphnia* (Time 5), and (3) the time elapsed between the consumption of the first *Daphnia* and the fifth *Daphnia* (ΔT).
Data were analyzed using the RStudio 1.1 statistical software (R Core Team). Two t-tests and a Kruskal-Wallis test were conducted with time 1 and ΔT data and Time 5 data to determine if the mean forging times were different between the UV+ and UV0 treatments.

Results

Natural log transformations were performed to obtain parametric data. Data for Time 1 and ΔT were normally distributed under natural log transformation (Shapiro-Wilk, W=0.95087, p=0.09511; W=0.94579, p=0.06473). Data for Time 5 was not made parametric under natural log, log, or square root transformations, so a non-parametric Kruskal-Wallis test was run on Time 5 data.

Juvenile bluegill that were fed Daphnia under UV+ conditions had a lower average Time 1, Time 5, and ΔT (mean ± SE; 31.75 ± 8.84; 84.51 ± 17.86; 54.18 ± 13.21) than bluegill that were fed Daphnia under UV0 conditions (52.42 ± 10.40; 120.72 ± 18.57; 68.28 ± 13.46). The t-test conducted on Time 1 data showed a significant difference in the amount of time it took bluegill to find and consume one Daphnia in the two UV conditions (t=-1.9664; df=35.82; p=0.05; Figure 1). Additionally, the Kruskal-Wallis test showed a significant difference in the amount of time it took for bluegill to consume five Daphnia between the two UV conditions (df=1; p=0.10; Figure 2). There was no significant difference in the time elapsed between the consumption of the first and fifth Daphnia for UV+ and UV0 treatments as shown in the t-test conducted with ΔT data (t=-1.1986; df=35.174; p=0.24; Figure 3).
Discussion

The objective of this study was to determine if the presence of UV photoreceptors in juvenile bluegill (*Lepomis macrochirus*) contributes to their foraging efficiency on *Daphnia* *spp.* In the presence of UVA, bluegill took significantly less time to start feeding on *Daphnia* than bluegill feeding without an additional UVA light source. Similarly, the bluegill with UV+ treatment consumed five *Daphnia* in significantly less time than the UV0 treatment. However, there was no difference in the rate of consumption of *Daphnia* between the treatments. This suggests that ultraviolet light in an aquatic environment may be contributing to the detection and identification of *Daphnia* by juvenile bluegill, but having no effect on foraging rates. Ultraviolet photoreceptors present in many juvenile fish species allow improvement in planktonic prey detection and foraging rates in the presence of ultraviolet light (Loew et al. 1993; Browman et al. 1994; Leech et al. 2009; Modarressie and Bakker 2007). Since *Daphnia* absorb short wavelengths of light to become darker on a UV-reflecting background (Loew and McFarland 1990), if UVA photoreceptors are present in juvenile results should show some enhanced foraging abilities. This does not support my hypothesis that bluegill would see in UVA wavelengths and use this vision to increase foraging rates, but it does suggest that they are perceiving *Daphnia* better in UVA light.

Previous research done on juvenile bluegill has shown that there is no difference in the sighting and striking distance or capture success in the presence or absence of UVR, and it was concluded for the size class tested that ultraviolet vision did not enhance foraging (Leech and Johnsen 2006). However, the size class tested for that study was smaller (23-35 mm) than the bluegill tested during this study (40-75mm). Typically, juvenile fish possess UV photoreceptors and lose them with maturity due to a habitat shift from shallow water to deeper water (Browman
et al. 1994; Loew et al. 1993). The habitat shift is accompanied by a dietary shift from smaller zooplankton to larger zooplankton or fish. However, in some fish species, UV photoreceptors disappear during earlier life history stages and reappear in late juveniles and adults (Novales Flamarique 2000). Cyprinid species and goldfish have UV photoreceptors throughout adulthood because they do not experience habitat or dietary shifts (Leech and Johnsen 2003). Often, bluegill exhibit ontogenetic shifts in food and habitat use that result in bluegill of size 51 to 83 mm shifting from feeding in vegetation to feeding on plankton in the water column above vegetation or in the pelagic zone (Werner and Hall 1988). Bluegill of the size class represented in this study may utilize UV photoreceptors at a more advanced juvenile stage to aid in foraging in open waters.

An explanation for the insignificant difference found in foraging rates of bluegill in different ultraviolet conditions may be the density of the prey available during trials. The prey densities for this study were relatively low (12.5-16.6 prey items•L⁻¹) compared to other studies on the effectiveness of fish foraging with UVR. A previous study done by on juvenile rainbow trout (Oncorhynchus mykiss) and pumpkinseed (Lepomis gibbosus) found that prey pursuit distances and angles were larger under full-spectrum illumination with very high prey densities (100 prey items•L⁻¹) (Browman et al. 1994). Leech et al. (2009) found that ultraviolet light enhanced predation of young-of-the-year largemouth bass (Micropterus salmoides) on zooplankton. More zooplankton were consumed by bass in the presence of UVR. However, the increase in predation of the bass may be attributed to zooplankton diel vertical migration. Zooplankton aggregate in deeper water in the presence of UVR and fish are often attracted to high densities of prey (Leech et al. 2009). Further experimentation is needed to say if the
presence of UVA wavelengths at high prey densities would enhance the foraging rate of juvenile bluegill.

Bluegill behavior in the presence of a predator, such as an observing researcher, may also lend explanation as to why foraging rates didn’t increase. Per Morgan (1988), the foraging rates of fish decrease in the presence of a predator because of increased vigilance. Foraging movements make an individual more noticeable to a predator, so the risk of attack would increase (Morgan 1988). Bluegill have also shown that they do not maximize energy intake per unit time in the presence of a predator (Gotceitas 1990), and a trade-off exists between predator-avoidance and foraging efficiency (Werner and Hall 1988). The presence of a predator can cause fish to move to either protective habitats where they are less likely to capture advantageous amounts of prey or habitats with a lower density of prey so they are more capable of detecting a predator (Milinski and Heller 1978; Werner and Hall 1988). These types of predator-avoidance trade-offs can be explained by adaptive behavior since foraging can be delayed, but predator avoidance is a priority (Morgan 1988). However, if bluegill that are exposed to UV wavelengths truly have no advantage in terms of foraging rate, they may still benefit from their ability to detect and identify an item as prey. Growth rates and survival of juvenile fish, which ultimately affects population recruitment, are dependent on their ability to find a food source.

For bluegill, the use of UV photoreceptors may be critical, independent of their role in foraging. In lakes with a low DOC concentration and a high UV environment, bluegill embryos show higher levels of mortality than in lakes with a high DOC concentration and a low UV environment (Gutierrez-Rodriguez and Williamson 1999). As an adaptive response, adult bluegill build their nests deeper in high UV lakes than in low UV lakes. Subsequently, UV photoreceptors in bluegill could help adults to avoid depths that result in less recruitment.
Additionally, with the increase in stratospheric ozone depletion, there is ultraviolet light present at considerable depths in many freshwater ecosystems (Leech and Johnsen 2003; Kerr and McElroy 1993). As a tradeoff, aquatic organisms capable of UV vision that are subjected to high levels of UV may need to find a balance between avoiding depths in which UV is damaging and seeking depths with beneficial wavelengths for UV vision. More research needs to be done in order to understand how stratospheric ozone depletion leads to increased levels of ultraviolet radiation in aquatic systems and the effects that this has on aquatic organisms.

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Figure 1. Average time it takes bluegill to eat one *Daphnia* with UV$_+$ treatment (mean ± SE; 31.75 ± 8.84) and UV$_0$ treatment (52.42 ± 10.40). There is a significant difference in average Time 1 between UV treatments (t=-1.9664; df=35.82; p=0.057).
Figure 2. Average time it takes bluegill to eat five *Daphnia* with UV₆ treatment (mean ± SE; 84.51 ± 17.86) and UV₀ treatment (120.72 ± 18.57). There is a significant difference in average Time 5 between UV treatments (df=1; p=0.10).
Figure 3. Average time it takes bluegill to from one to eat five *Daphnia* with UV+ treatment (mean ± SE; 54.18 ± 13.21) and UV₀ treatment (68.28 ± 13.46). There is not a significant difference in average ΔT values between UV treatments (t=-1.1986; df=35.174; p=0.24).