Research Article

High-intensity light blocks Bighead Carp in a laboratory flume

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Abstract

There is a critical need to identify and develop behavioral deterrents that impede the spread of invasive Bigheaded Carp (Hypophthalmichthys spp.) through waterways in North America. High-intensity light has significant advantages over other behavior deterrents because it can be relatively inexpensive, easy to deploy and can be used in shallow waterways. Although previous studies have shown that light has the potential to guide and block the passage of fishes, the efficacy of light has also been found to be species- and situation-specific, and no study has yet examined how well light works for Bigheaded Carp. The present laboratory study sought to determine whether high-intensity white light might be effective at blocking Bighead Carp (H. nobilis) while having minimal effects on another model fish species. We measured the response of juvenile Bighead Carp and Largemouth Bass (Micropterus salmoides) to three types of high-intensity white light (constant light [0 Hz] and strobing light [5 Hz or 12 Hz]) in both a dark [1 lux] and a dimly-lit [100 lux] laboratory flume. High-intensity light consistently blocked at least 74% of Bighead Carp in a dark flume, with strobing and constant light having equivalent effects (p > 0.05). In contrast, a constant light (80%) was more effective than a 5 Hz strobing light (33%) in a dimly-lit flume (p < 0.05). While Largemouth Bass were also blocked by constant light (63%) in a dark flume, both a 5 Hz (82%) and 12 Hz (88%) strobing light were more effective (p < 0.05). When tested in a dimly-lit flume, Largemouth Bass were not blocked by either the constant light or a 5 Hz strobing light (p > 0.05). Taken together, our experiments demonstrate that responses to light can be species- and situation-specific, and that high-intensity constant light has particular promise to block Bighead Carp in both dark and dimly-lit environments without strongly blocking bass. Light might be especially useful in shallow, clear waters that cannot be blocked by other means.

Key words: behavior, background lighting, invasive fish, Largemouth Bass, deterrents

Introduction

The Bighead Carp (Hypophthalmichthys nobilis) and its congener the Silver Carp (H. molitrix), together known as Bigheaded Carp, were introduced from Asia to the Mississippi River Basin in the 1970s and are now spreading into the upper reaches of the Mississippi River and toward the Laurentian Great Lakes (Chapman and Hoff 2011; Lubejko et al. 2017). These microphagous fishes are altering this river’s food web (Solomon et al. 2016; Wang et al. 2018). In addition to being voracious feeders, Silver
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Carp jump out of the water when disturbed, reducing the recreational value of the river for public fishing and boating. Although many strategies have been proposed to stop the upstream spread of Bigheaded Carp, the possibility of blocking carp passage through navigation locks using behavior deterrents (i.e., systems that employ sensory cues to alter the behavior of an animal) appears especially promising because they are generally safe, taxon-specific, and can be applied in targeted manners (Noatch and Suski 2012; Dennis et al. 2019). High-intensity light, operationally defined here as light that exceeds background levels (in our case surface river water on a clear day; e.g. > 1000 lux), has advantages over other types of behavioral deterrents (e.g., sound, air curtains, electricity) because it is relatively inexpensive, easy to deploy and can be used in shallow, constricted waterways where other behavioral deterrents such as sound and electricity may not work (Popper and Carlson 1998; Noatch and Suski 2012). High-intensity light has previously been used to guide or deter migrating salmonids but field studies suggest its effects are species- and scenario-specific (Brett and MacKinnon 1953; Nemeth and Anderson 1992; Johnson et al. 2005; Hamel et al. 2008; Hansen et al. 2018). The behavioral responsiveness of Bigheaded Carp to high-intensity light has not yet been examined.

A variety of laboratory and field experiments have examined the possibility that high-intensity light can deter fishes. Although behavioral responses of fish to high-intensity light has been reported to vary greatly (see Supplementary material Table S1), test protocols have also differed (e.g., field or lab; species tested; type of light source; constant or strobing light; light spectrum; background lighting) suggesting that responses are likely both species- and situation-specific. Some studies have suggested promise. For example, juvenile Pacific salmonids (*Oncorhynchus* sp.) displayed a 75% reduction to entrainment within a navigation lock when exposed to a 5 Hz strobing light (Johnson et al. 2005). Similarly, Chinook Salmon smolts (*Oncorhynchus tshawytscha*) were repelled by a strobing red light in a laboratory raceway (Hansen et al. 2018). In addition to salmonids, adult Largemouth Bass (*Micropterus salmoides*) held in a darkened field enclosure were deterred by high-intensity light regardless of its color spectra or strobing rate (Sullivan et al. 2016). Similarly, adult Common Carp (*Cyprinus carpio*) and Brown Bullhead (*Ameiurus nebulosus*) in an illuminated laboratory arena were deterred by a strobing light with randomized pulse frequencies (Kim and Mandrak 2017). While these studies all show promise, none have examined whether fish responses to high-intensity light changes with repeated exposure (i.e., whether fish habituate), a phenomenon which would be very important in lock chambers where fish may repeatedly challenge the deterrent system. Additionally, while most studies show light to be effective, studies of Sea Lamprey (*Petromyzon marinus*), Walleye (*Sander vitreus*), Channel Catfish
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(Ictalurus punctatus), Muskellunge (Esox masquinongy), White Sturgeon (Acipenser transmontanus) and Largemouth Bass show that this is not always the case, suggesting species differences (Flammang et al. 2014; Stewart et al. 2014; Miehls et al. 2017; Kim and Mandrak 2017; Ford et al. 2018). If understood, these differences could potentially be exploited to develop species-specific barriers that stop some invasive fishes while allowing native fishes to pass.

Although several characteristics of light likely determine its ability to block fish passage (e.g., intensity, wavelength, background lighting and exposure time), responsiveness of fishes to different pulse frequencies of light (e.g., constant or strobing) have been the most studied and it has been shown to influence fish behavior. Five studies, three of which employed salmonids, have directly compared the effectiveness of constant and strobing lights to alter fish behavior. For example, early work by Brett and MacKinnon (1953) and Nemeth and Anderson (1992) showed that juvenile salmonids were more deterred by a strobing light than a constant light, although their effectiveness differed between species and was influenced by background lighting. Similarly, Ford et al. (2018) showed that White Sturgeon only avoided a 1 Hz strobing red light and did not respond to constant light. However, recent studies by Sullivan et al. (2016) and Hansen et al. (2018) suggest that strobing lights may not always be more effective than constant light as shown for Largemouth Bass and Chinook Salmon. Species differences in responsiveness to constant and strobing lights could be due to both retinal physiology and swimming behavior. In a study examining the retinal physiology of Bigheaded Carp, Vetter et al. (2018) demonstrated that slower pulse frequencies with longer pulse durations required more time to recover retinal sensitivity suggesting that Bigheaded Carp are more likely to respond to faster pulse frequencies with shorter pulse durations because their retinal sensitivity is less likely to be impaired. However, behavioral studies of Largemouth Bass, Walleye and Rainbow Smelt have all shown that pulse frequency seemingly does not influence the effectiveness of high-intensity light (Hamel et al. 2008; Flammang et al. 2014; Sullivan et al. 2016), perhaps suggesting fish swimming behavior and how they orient to light may be important.

Background light levels and time-of-day have also been shown to impact fish behavior and their responsiveness to light deterrents. Ambient light levels influence many facets of fish behavior including orientation, communication, circadian movements and avoidance from predators (Li and Maaswinkel 2007). Most studies which have examined the effectiveness of high-intensity light have only tested one type of background lighting (Johnson et al. 2005; Kim and Mandrak 2017; Kim et al. 2019). However, four studies that directly compared different background lighting conditions, have all shown that background lighting alters fish responsiveness to high-intensity light (Nemeth and Anderson 1992; Stewart et al. 2014; Ford et al.
2018; Hansen et al. 2018). Nemeth and Anderson (1992) found that strobing lights were only effective at deterring juvenile Coho Salmon during the night. A recent study by Stewart et al. (2014) found that the escape rate of juvenile Muskie within a laboratory raceway was higher during the day compared to night. Background lighting also influenced the response of White Sturgeon and Chinook Salmon to different light spectra, with salmon only being deterred by red light in daylight (Hansen et al. 2018) and sturgeon being more attracted to light during the night than day (Ford et al. 2018). Further study of background lighting (and time-of-day) is needed.

The overarching goal of this study was to determine if there is a specific type of high-intensity light that might be particularly effective at blocking Bighead Carp in both dark [< 1 lux] and dimly-lit [100 lux] environments, while having minimal effects on another species. To accomplish this goal, we asked several questions. First, we asked whether high-intensity light blocks the passage of invasive Bighead Carp, and if so, whether this response might change with repeated exposure (e.g., do fish habituate)? Second, we asked whether the pulse frequency of light (e.g., constant vs strobing light) alters its effectiveness to block Bighead Carp? Third, we asked whether background lighting (e.g., a dark or dimly-lit environment) influences the response of Bighead Carp to high-intensity light? Finally, we asked whether Largemouth Bass, a fish native to the Mississippi River Basin, responds to high-intensity light in the same manner as Bighead Carp? To answer these questions, we tested groups of Bighead Carp and Largemouth Bass in both a dark [1 lux] and dimly-lit [100 lux] laboratory flume and repeatedly exposed these fishes to high-intensity white light with different pulse frequencies.

Materials and methods

Experimental Design and Protocol

We tested the effects of exposing groups of 10 naive Bighead Carp or Largemouth Bass to three types of high-intensity white light (constant light [0 Hz], 5 Hz strobing light, 12 Hz strobing light) in either dark [< 1 lux] or dimly-lit conditions [100 lux]. Our experiment had two steps. First, we exposed groups of either Bighead Carp or Largemouth Bass to 3 types of light (constant light or strobing light [5 Hz or 12 Hz]) in a dark flume [< 1 lux] to determine which pulse frequency of light (if any) was most effective at stopping carp. To visualize the fish, the dark flume was illuminated by infrared light (VT-IR1 and VT-IR2; Vitek; Valencia, CA; 840 nm wavelength), whose frequency range was seemingly out of the visual range of both Bighead Carp (Vetter et al. 2018) and Largemouth Bass (Mitchem et al. 2019). The flume was then dimly-lit by installing overhead white lights (100 lux – similar to the light level of a cloudy day, and also that measured at a depth of 3 m in the Mississippi River), and new fish were tested with either a constant light or a 5 Hz strobing light (the 12 Hz strobing light was not
tested because it was just as effective as the 5 Hz light). A 2 Hz strobing light was also tested in a pilot experiment using Bighead Carp to confirm that this frequency, which is not known to elicit epileptic seizures in humans (Fisher et al. 2005), is also effective.

We conducted a total of 14 experiments. Each experiment was comprised of 10 trials in which a different group of 10 naïve fish of the same species was tested on a randomly chosen stimulus, similar to the protocol used by Dennis et al. (2019). Briefly, each trial started with a 1-h acclimation period, which was followed by 8 sets of exposure periods, each of which started with a 6-min pre-test period (no stimulus), followed by a 6-min test period (stimulus on [or not in the no-treatment control experiments]), and then a 10-min recovery period (no stimulus). Fish were exposed 8 times because that was the average number of times that adult Silver Carp have been noted to challenge a navigational lock in the Mississippi River (Sara Tripp, Missouri Department of Conservation, Cape Girardeau, MO, personal communication). All trials were conducted between 0500 h–2100 h. Fish position was recorded during pre-test and test periods using overhead and underwater low-light cameras and analyzed after trials by quantifying the number of times fish crossed the midline of the flume where the deterrent system was located (i.e., passage rate). Fish orientation within the flume was not discernable.

Fish

Juvenile fish were obtained from a commercial fish farm (Osage Catfisheries; Osage Beach, MO). Largemouth Bass (TL: 162 ± 23 mm; TW: 51 ± 23 g) were held in flow-through circular tanks (300 L; 1 m diameter) and fed 2.5 mm floating pellets (Skretting, Tooele, Utah), while Bighead Carp (TL: 135 ± 23 mm; TW: 25 ± 13 g) were maintained in flow-through circular tanks (1,000 L; 2 m diameter) and fed a diet of *Spirulina* and *Chlorella* algae (Hansen et al. 2014). All tanks were supplied with 18 °C well water, aerated using air stones and relatively quiet (80–100 dB ref. 1 μPa). Holding tanks were dimly illuminated (5 lux; 16 h day: 8 h night) for fish being tested in the dark flume, while fish tested in the dimly-lit flume were held in tanks at 100 lux (16 h day: 8 h night).

Laboratory Flume

Trials were conducted in a custom-built indoor elliptical fiberglass flume (8 m long × 1 m wide channel × 0.3 m water depth; 1.0 m wall height) (Figure 1), the same flume used by Dennis et al. (2019) except two high-intensity light bars (Fish Guidance Systems Ltd.; Southampton, UK) were placed mid-line, 5 cm away from the unused porous air pipes. Each high-intensity light bar had a single row of light-emitting diodes that was angled at 45° toward the porous pipes. Only high-intensity light bars (i.e. no air...
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Figure 1. Schematic drawing of an overhead view of the elliptical fiberglass flume with a contour map of light levels (lux) produced by the high-intensity light in a dark flume. Two high-intensity light bars were placed 5 cm from the air curtains in both channels – underwater speakers and air curtain were present but not used. Water inflow to the tank is indicated by a black circle and the direction of flow (when on) is marked by the black arrow. Standpipes ensured that water depth was maintained at 0.3 m. A plan view of the light levels (lux) produced by the high-intensity light bars in a dark flume is presented in the right panel. Lux measurements on the east (right) side of the flume receded to background light levels (< 1 lux).

curtains or underwater speakers) were used in this study. Fish movement was monitored using a combination of overhead and underwater cameras and infrared lights. Following established protocols (Dennis et al. 2019), Bighead Carp were tested in slow-flowing water (1.66 cm/s) while Largemouth Bass were tested in still water – conditions designed to encourage fish movement but not interfere with light transmission.

Light Stimuli

Three types of stimuli were tested: constant light [0 Hz], 5 Hz strobing light, and 12 Hz strobing light. Light emitted from the high-intensity light bar was a broad-spectrum white light which contained all wavelengths between 350 and 800 nm. Notably, Vetter et al. (2018) found the retina of Bigheaded Carp to be broadly sensitive to visible (white) light but not deep
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Figure 2. Light levels (lux) measured within 8 m of the high-intensity light bars during 0 Hz constant light exposure in either a dark flume (Panel A) or a dimly-lit flume (Panel B). Reported light measurements were taken at a 0.15 m depth along the midpoint of the flume.

Light intensity measurements (lux) were acquired using a portable meter (MW700, Milwaukee Instruments) with a waterproof probe (peak wavelength: 560 nm; accuracy: ± 6% of reading). This light meter was placed at a depth of 0.15 m and measurements were taken at 0.25 m intervals across the width of the channel. Light measurements were also taken at: 0.00, 0.10, 0.20, 0.30, 0.40, 0.50, 0.60, 0.80, 1.00, 1.20, 1.60, 2.00, 2.40, 3.00, 3.60, 4.20, 5.40, and 6.60 m away from the high-intensity light bars (see Figures 1, 2). Lux measurements near the light source approached 15,000 lux and decreased to background light measurements within 2.4 m (Figures 1, 2).

Statistical Analysis

Generalized linear mixed models (GLMM) were used to analyze passage rate data for each species and background lighting combination, resulting in a total of 4 GLMMs (Tables S2–S5). A custom design matrix, written in R, was entered into each GLMM to allow us to analyze specific comparisons of interest (e.g., to compare particular stimuli with the no-treatment control or determine if passage rates changed with repeated exposure; see Tables S2–S5), rather than examine all possible contrasts, thereby enhancing power and simplifying the overall analysis. This approach, which differs slightly from the statistical design used by Dennis et al. (2019), also allowed us to answer our four questions with much greater power than a three-way ANOVA.
would have permitted. It also allowed us to account for changes in passage rate due to time spent in the flume by comparing the rate of change in the stimulus experiment to the rate of change observed in the no-treatment control experiment. In each GLMM, “fish group number” was entered as a random effect to account for repeated measurements taken from the same group of fish (i.e., each group was exposed to a stimulus eight times and passage rates were taken during each exposure). Passage rate data was transformed to fit a Poisson distribution because it is count data. Assumptions for each GLMM (e.g., residuals are randomly distributed, no over-dispersion; see McCullagh and Nelder 1989) were checked visually using a plot of the deviance residuals versus fitted values to test for random distribution of residuals (McCullagh and Nelder 1989), while over-dispersion was tested by examining the variance of the residuals (McCullagh and Nelder 1989). If the variance of the residuals was greater than 2, we corrected for this hyper-variability by dividing our test statistic by the square root of the dispersion parameter (McCullagh and Nelder 1989) and calculating new p-values for each comparison in that GLMM. Raw passage rate counts for Bighead Carp and Largemouth Bass were used as the response variable for experiments conducted in a dark flume because these fish moved as individuals. For those experiments performed in the dimly-lit flume [100 lux], fish were observed to move in groups (typically as one large group of 10) and raw passage rate data did not fit a Poisson distribution (as determined with the fitted residual plot), so we converted individual passage into group passage rate (i.e., raw passage rate / 10) which resulted in a model that met the assumptions needed for a GLMM. All analyses were performed using R and at an α value of 0.05.

Each GLMM examined a set of contrasts selected to answer our particular questions (see Tables S2–S5). First, to determine whether a particular stimulus altered passage rates (i.e., did light block fish passage?), log-linear passage rates obtained during the stimulus experiment (for both pre-test [n = 80 observations] and test periods [n = 80 observations]) were compared to log-linear passage rates during the no-treatment control experiment (pre-test and test periods within the GLMM were combined for control [n = 160 observations]). If significance was noted by the model (p < 0.05, Bonferroni-corrected for multiple comparisons [p < 0.0125 under dimly-lit conditions, p < 0.0083 under dark conditions]), we then calculated blockage efficiencies for each stimulus. Blockage efficiencies were calculated by dividing each test passage value by the total mean passage rate during the no-treatment control (average of 160 observations), averaged across all 80 test passage values, and then multiplied by 100. We used blockage efficiencies because they accounted for any changes in basal passage rate. Because we also wanted to address if passage rate changed with repeated exposure (i.e., did Bighead Carp or Largemouth Bass habituate or sensitize
to the stimulus?), we examined temporal variation in passage rate over the course of the eight trial periods by fitting curves (linear, quadratic, etc.) to passage rate data collected during both pre-test (n = 10 trends) and test periods (n = 10 trends) for each stimulus. If any of the trends were significant (p < 0.05, Bonferroni-corrected for multiple comparisons [p < 0.0071]), we then compared this calculated relationship to that of the matching curve for the no-treatment control experiment using a z-test (McCullagh and Nelder 1989). A significant z-test (p < 0.05, Bonferroni-corrected for multiple comparisons [p < 0.0125 under dimly-lit conditions, p < 0.0083 under dark conditions]), was interpreted to mean that passage rate over the 8 trials changed due to repeated exposure to the stimulus. Habituation was operationally defined as a linear increase in test passage rate with repeated exposure to a stimulus (Groves and Thompson 1970; Rankin et al. 2009) that was also significantly different from the linear trend observed in passage rate during the no-treatment control. Sensitization was operationally defined as a decrease in test passage rate due to repeated stimulus exposure (Plappert et al. 1999) that was also significantly different from the trend observed in passage rate during the no-treatment control experiment. To identify trial(s) within particular experiments that witnessed significant responses to light exposure, we compared mean passage rates of their pre-test and test periods (p < 0.05, Bonferroni-corrected for multiple comparisons [p < 0.0063]; n = 10 observations [passage rates] per trial period).

Finally, we used a series of z-tests to compare sets of blockage efficiencies to answer our remaining questions. To answer our second question (i.e., does the pulse frequency of light alter its effectiveness to block fish?), we used a series of Bonferroni-corrected z-tests (p < 0.0083 for each test) that directly compared blockage efficiencies between different pulse frequencies of light when tested in either a dark or dimly-lit flume. To answer our third question (i.e., does background lighting alter the effectiveness of high-intensity light to block fish passage?), we used a series of Bonferroni-corrected z-tests (p < 0.0083) to compare blockage efficiencies of high-intensity light (either constant light [0 Hz] or strobing light [5 Hz]) when tested in both a dark [1 lux] and dimly-lit [100 lux] flume. Finally, to answer whether Largemouth Bass respond to light stimuli in a similar manner as Bighead Carp, we used a series of z-tests (p < 0.05) to compare Largemouth Bass and Bighead Carp blockage efficiencies for each high-intensity light experiment.

For ease of reporting (see below), results were compiled by species and then background lighting (e.g., dark or dimly-lit flume). Because the GLMM is a log-linear model, reported blockage efficiencies (mean ± SD) for each species and experiment were back-transformed to a linear scale to aid comparisons. Figures are presented as box-and-whisker plots (with medians, means and inter-quartile ranges) because these raw data were not normally distributed.
Figure 3. Passage rate (i.e., the number of passages per 6-min pre-test or test period) of Bighead Carp to 7 light stimuli and background lighting combinations across time: A) no-treatment control [1 lux]; B) 0 Hz constant light [1 lux]; C) 5 Hz strobing light [1 lux]; D) 12 Hz strobing light [1 lux]; E) no-treatment control [100 lux]; F) 0 Hz constant light [100 lux]; and G) 5 Hz strobing light [100 lux]. Box-and-whisker plots in each panel show the lower bound, 25th percentile, median (solid line), mean (dotted line), 75th percentile, and upper bound values for passage rate during pre-test periods (white bars) and test periods (gray bars) over the course of eight consecutive periods (i.e., test numbers). Asterisks denote differences between pre-test and test passage rate for that test period (p < 0.05 [corrected for multiple comparison]). Ten trials, each consisting of 10 naïve Bighead Carp, were used to test each light stimulus and background lighting combination (N=160 observations per experiment).

Results

Bighead Carp

Dark Flume [1 lux]

Groups of Bighead Carp averaged 14 ± 8 passages (mean ± SD) across the inactive light system during each six-minute period of the no-treatment control experiment [1 lux] (Figure 3A). This passage rate did not change over the course of the experiment (p > 0.05; Table S2). In contrast, when
Table 1. The abilities of different types of high-intensity light (constant-lyit, 5 Hz strobing and 12 Hz strobing) to block Bighead Carp and Largemouth Bass under different background lighting conditions (dark or dimly-lit) in a laboratory flume. This table compares the blockage efficiencies (mean ± SD) of the different types of high-intensity light tested in the same background lighting conditions for each species. The blockage efficiencies of the two species for each of the 5 high-intensity light and background lighting conditions were also compared. Positive blockage efficiencies describe reductions in mean passage rate during exposure to high-intensity light, while negative blockage efficiencies denote increases in mean passage rate during exposure. Within each species, lower case letters identify comparisons between blockage efficiencies for the 3 high-intensity light stimuli [constant light, 5 Hz strobing light, 12 Hz strobing light] when tested in the dark flume [1 lux], while upper case letters compare constant light with 5 Hz strobing light when tested in a dimly-lit flume [100 lux]. Different letters denote differences in blockage efficiency (p < 0.05) with “a or A” identifying the stimulus with the greatest blockage efficiency for that specific background lighting condition and subsequent letters “b or B” identifying stimuli that displayed statistically lower blockage efficiencies. For each experiment, blockage efficiencies of the different species were compared using pairwise z-tests (p < 0.05), with an asterisk (*) identifying the species with the greatest blockage efficiency. Ten trials, each comprised of 10 naïve Bighead Carp or Largemouth Bass, were used to test each light stimulus/background lighting combination (N = 160 observations per experiment).

|                  | Dark Flume (< 1 lux)                  | Dimly-lit Flume (100 lux)                  |
|------------------|--------------------------------------|--------------------------------------------|
|                  | Constant Light [0 Hz]                | Constant Light [0 Hz]                      |
|                  | 5 Hz Strobe Light                    | 5 Hz Strobe Light                         |
|                  | 12 Hz Strobe Light                   |                                            |
| Bighead Carp     | 79% (± 15) a                          | 80% (± 15) a                              |
|                  | 80% (± 15) a                          | 33% (± 15) A                              |
|                  | 74% (± 15) a                          | 88% (± 18) a A                            |
| Largemouth Bass  | 63% (± 16) b                          | −64% (± 10) A                             |
|                  | 82% (± 17) a                          | −23% (± 10) A                             |

Exposed to the constant light, Bighead Carp passage rate declined significantly during exposures #2–#8 (p < 0.05; Figure 3B; Table S2) resulting in an overall average blockage efficiency of 79 ± 15% (mean ± SD) relative to the mean passage rate during the no-treatment control experiment (p < 0.05; Tables 1, S2). While pre-test passage rate did not change (p > 0.05; Table S6), test passage rate decreased by 20% with each subsequent exposure which is symptomatic of sensitization (p < 0.05; Table S6). Similarly, when exposed to the 5 Hz strobing light, Bighead Carp test passage rate dropped significantly compared to the no-treatment control resulting in an overall blockage efficiency of 80 ± 15% (p < 0.05; Tables 1, S2) with significant reductions noted during exposures #2–#8 (p < 0.05; Figure 3C; Table S2). Repeated exposure to the 5 Hz strobing light also resulted in a linear decrease in passage rate (sensitization) during test periods (p < 0.05; Table S6). Finally, when exposed to the 12 Hz strobing light, Bighead Carp passage was significantly blocked at an overall rate of 74 ± 15% (p < 0.05; Table 1, S2) compared to no-treatment control with reductions observed during all 8 exposures (p < 0.05; Figure 3D; Table S2). While pre-test passage rate did not change with repeated exposure to the 12 Hz strobing light (p > 0.05; Table S6), test passage rate decreased, again symptomatic of sensitization (Table S6). Constant light, 5 Hz strobing light and 12 Hz strobing light did not differ in their ability to block carp passage in the dark flume (p > 0.05; Tables 1, S7).

Dimly-lit Flume [100 lux]

Bighead Carp tended to swim as one large group and averaged 23 ± 17 passages across the inactive light system during each six-minute period of the no-treatment control [100 lux] (Figure 3E). Passage rate did not change over the course of this experiment (p > 0.05; Table S4). When exposed to the constant light, Bighead Carp passage was significantly blocked at an overall rate of 80 ± 23% relative to the no-treatment control (p < 0.05;
Table 2. The abilities of different types of high-intensity light (constantly-lit and 5 Hz strobing) to block Bighead Carp and Largemouth Bass under dark or dimly-lit background lighting in a laboratory flume. This table compares blockage efficiencies (mean ± SD) for each species and high-intensity light type under different background lighting conditions using the same data shown in Table 1. For each species and stimulus combination, different superscript numbers denote differences (p < 0.05) in blockage efficiency with “1” identifying the background lighting condition that resulted in the greater blockage efficiency.

| Stimulus                                | Blockage Efficiency |
|-----------------------------------------|---------------------|
| **Bighead Carp: Constant Light [0 Hz]** |                     |
| Dark Flume                              | 79% (± 15)\(^1\)    |
| Dimly-lit Flume                         | 80% (± 23)\(^1\)    |
| **Bighead Carp: 5 Hz Strobe Light**     |                     |
| Dark Flume                              | 80% (± 15)\(^1\)    |
| Dimly-lit Flume                         | 33% (± 15)\(^2\)    |
| **Largemouth Bass: Constant Light [0 Hz]** |                  |
| Dark Flume                              | 63% (± 16)\(^1\)    |
| Dimly-lit Flume                         | ~64% (± 10)\(^2\)   |
| **Largemouth Bass: 5 Hz Strobe Light**  |                     |
| Dark Flume                              | 82% (± 17)\(^1\)    |
| Dimly-lit Flume                         | ~23% (± 10)\(^2\)   |

Tables 1, S4). Significant decreases in test passage rate, relative to their matched pre-test values, were noted during all 8 exposures to constant light (p < 0.05; Figure 3F; Table S4). Both pre-test and test passage rate did not change with repeated exposure to the constant light (p > 0.05; Table S6). In contrast, Bighead Carp passage rate was only reduced during the first exposure to the 5 Hz strobing light (p < 0.05; Figure 3G; Table S4) resulting in an overall average blockage efficiency of 33 ± 15% (p < 0.05; Tables 1, S4).

While pre-test passage rate did not change with repeated exposure (p > 0.05; Table S6), test passage rate increased by 15% after each exposure to the 5 Hz strobing light which is symptomatic of habituation (p < 0.05; Table S6). Overall, the 5 Hz strobing light was less effective than the constant light at blocking Bighead Carp passages in a dimly-lit flume (p < 0.05; Tables 1, S7). We also found that constant light was equally effective at blocking Bighead Carp passages in both a dimly-lit and a dark flume (p > 0.05; Tables 2, S7), while carp were slightly more likely to pass a 5 Hz strobing light under dimly-lit conditions than in the dark flume (p < 0.05; Tables 2, S7).

**Largemouth Bass**

**Dark Flume [1 lux]**

Groups of Largemouth Bass averaged 15 ± 8 passages across the inactive light system during each 6-min periods of the no-treatment control experiment [1 lux] (Figure 4A). This passage rate decreased significantly over time (p < 0.05; Table S3). When exposed to the constant light, Largemouth Bass passage was significantly blocked at an overall rate of 63 ± 16% (Table 1) compared to the no-treatment control experiment (p < 0.05; Table S3) with significant reductions observed during 5 of 8 exposures (Figure 4B; Table S3). While pre-test passage rate did not change with repeated exposure (p > 0.05; Table S6), test passage rate increased in a quadratic fashion which is
Figure 4. Passage rate (i.e., the number of passages per 6-min pre-test or test period) of Largemouth Bass to 7 light stimuli and background lighting combinations across time: A) no-treatment control [1 lux]; B) 0 Hz constant light [1 lux]; C) 5 Hz strobing light [1 lux]; D) 12 Hz strobing light [1 lux]; E) no-treatment control [100 lux]; F) 0 Hz constant light [100 lux]; and G) 5 Hz strobing light [100 lux]. Box-and-whisker plots in each panel show the lower bound, 25th percentile, median (solid line), mean (dotted line), 75th percentile, and upper bound values for passage rate during pre-test periods (white bars) and test periods (gray bars) over the course of eight consecutive periods (i.e., test numbers). Asterisks denote differences between pre-test and test passage rate for that specific test number (p < 0.05; corrected for multiple comparison). Ten trials, each consisting of 10 naïve Largemouth Bass, were used to test each light stimulus and background lighting combination (N = 160 observations per experiment).

Symptomatic of habituation (p < 0.05; Table S6). When exposed to the 5 Hz strobing light, bass passage was blocked by 82 ± 17% compared to the no-treatment control experiment (p < 0.05; Tables 1, S4) with significant reductions noted for 7 of the 8 exposures (p < 0.05; Figure 4C; Table S3). Both pre-test and test passage rate declined with repeated exposure to the 5 Hz strobing light (p < 0.05; Table S3); however, this rate did not differ from the decline in passage rate noted during the no-treatment control...
experiment (p > 0.05; Table S6). Similarly, Largemouth Bass significantly reduced their passage across the light deterrent during all 8 exposures to the 12 Hz strobing light (p < 0.05; Figure 4D; Table S3) resulting in an overall blockage efficiency of 88 ± 18% (Table 1) when compared with passage rate in the no-treatment control experiment (p < 0.05; Table S3). Both pre-test and test passage rate significantly declined with repeated exposure to the 12 Hz strobing light (p < 0.05; Table S3); however, this rate did not differ from the decline in passage rate noted during the no-treatment control experiment (p > 0.05; Table S6). Overall, constant light was less effective at blocking Largemouth Bass than both types of strobing light (5 Hz and 12 Hz) (p < 0.05; Tables 1, S7). Comparing these results for Largemouth Bass with Bighead Carp, we found that constant light was more effective at blocking Bighead Carp than Largemouth Bass (p < 0.05; Tables 1, S8). In contrast, Largemouth Bass were blocked to a greater extent than Bighead Carp by the 12Hz strobing light (p < 0.05; Tables 1, S8), while no difference in blockage efficiency was observed between these species for the 5 Hz strobing light (p > 0.05; Tables 1, S8).

**Dimly-lit Flume [100 lux]**

Largemouth Bass averaged 30 ± 15 passages during the no-treatment control experiment [100 lux] (Figure 4E) and this passage rate did not change over time (p > 0.05; Table S5). When exposed to the constant light, Largemouth Bass passage rate increased significantly resulting in a −64 ± 10% blockage efficiency (i.e., they increased passage over the high-intensity light) compared to the no-treatment control (p < 0.05; Tables 1, S5) with no significant differences between any matched pre-test and test period (p > 0.05; Figure 4F; Table S5). Passage rate did not change with repeated exposure to the constant light (p > 0.05; Table S6). Similarly, Largemouth Bass increased their passage rate during exposure to the 5 Hz strobing light resulting in a blockage efficiency of −23 ± 10% (Table 1), although this passage rate was not significantly different than the passage rate observed during the no-treatment control (p > 0.05; Table S5), and no differences were detected among matched pre-test and test periods (p > 0.05; Figure 4G; Table S5). Passage rate did not change with repeated exposure to the 5 Hz strobing light (p > 0.05; Table S6). Overall, no difference between the constant light and 5 Hz strobing light was measured in their ability to block Largemouth Bass passages in a dimly-lit flume (p > 0.05; Tables 1, S7). However, both types of high-intensity lights were more effective at blocking bass when tested in a dark flume than in the dimly-lit flume (p < 0.05; Tables 2, S7). Comparing these species, we found that Bighead Carp were blocked to a greater extent than Largemouth Bass by both the constant light and 5 Hz strobing light in the dimly-lit flume (p < 0.05; Tables 1, S8).
Discussion

This study establishes that high-intensity white light is extremely effective at blocking Bighead Carp movement in the laboratory and can block 80% of Bighead Carp in both a dimly-lit and dark flume, with constant light being the better stimulus in dimly-lit conditions. Behavioral sensitization was also noted with repeated exposure for Bighead Carp to all light stimuli in a dark flume, suggesting special promise in the field. Further, the response of fish to light was shown to be both species- and context-specific. With the exception of the 12 Hz strobing light, light was less effective at blocking bass than Bighead Carp in both the dark and dimly-lit flume, and actually increased bass passage in dimly-lit conditions. These blockage rates for Bighead Carp rival some of those seen for sound and air curtains for this species in the laboratory (Dennis et al. 2019). In summary, our results suggest that high-intensity constant light has promise to block Bighead Carp passage in both dimly-lit and dark background lighting conditions without having dramatic effects on Largemouth Bass, and calls for field tests.

Our most important finding was that high-intensity white light was effective at blocking Bighead Carp passages in both dark [1 lux] and dimly-lit [100 lux] conditions. We found that Bighead Carp passage was reduced by 80% when exposed to both constant and strobing high-intensity lights in a dark flume, and that this light deterrent became more effective with repeated exposure. To our knowledge, this is the first demonstration of sensitization (e.g., decreasing passages with repeated exposures) to high-intensity light in a fish. This trait could be advantageous in the field where fishes are exposed to a variety of other environmental stimuli and likely encounter a deterrent system multiple times. Interestingly, we also saw that a constant light was more effective than a strobing light at blocking Bighead Carp passage in our flume under dimly-lit conditions. This observation was not predicted based on the manner at which retinal sensitivity recovered to light exposure in study by Vetter et al. (2018), which suggested that longer durations of light exposure will reduce the fish’s ability to detect and potentially respond to a light deterrent. Hamel et al. (2008) suggested that strobing light may not be as effective at deterring fishes during daylight hours because of high ambient light levels. A constant light source may have provided a more prolonged contrast than strobing light under illuminated conditions, possibly making it easier for fish to detect. Because Bigheaded Carp are expected to repeatedly challenge locks and dams, the suggestion of sensitization is relevant and strongly warrant further study, especially in the field where conditions are very different.

Our study also demonstrated that the pulse frequency of high-intensity lights did not alter the effectiveness of light to block Bighead Carp passage in a dark laboratory flume but that it did seem to matter in brighter background lighting. Our finding that pulse frequency did not matter in
High-intensity light blocks Bighead Carp in a laboratory flume

darkness is consistent with previous behavioral studies on Largemouth Bass, Walleye and Rainbow Smelt (Hamel et al. 2008; Flammang et al. 2014; Sullivan et al. 2016) but was not predicted by retinal physiology which suggested that lower pulse frequencies should be less effective due to their greater recovery times from bleaching (i.e., change in opsin configuration that reduces the degree to which rods can be stimulated resulting in a decreased sensitivity to bright light) (Vetter et al. 2018). This difference would be explained if swimming carp changed their orientation to light, because this behavior would reduce retinal bleaching. However, we were unable to measure fish orientation to the light due to poor underwater video quality (we could only confidently observe passage across the light bar); future studies should examine whether the swimming behavior of fish influences their responsiveness to light. We also found that a constant light was equally effective for Bighead Carp under dimly-lit and dark conditions, while strobing lights were more effective for Bighead Carp in a dark flume. This may be important because in real-world applications, a 2 Hz strobing light could be preferable because this frequency has a low chance of inducing epileptic shock (Fisher et al. 2005). Notably, in a pilot study, we exposed Bighead Carp to a 2 Hz strobing light in a dark flume and also saw a similar 80% decline in passage rates (i.e. no apparent difference from 5 Hz or 12 Hz strobing light; Figure S1; Tables S9, S10). However, we still do not know if the 2 Hz strobing light affects other fish species or whether its effectiveness declines in a dimly-lit environment as we witnessed for the 5 Hz strobing light.

We also found that background lighting conditions altered the effectiveness of high-intensity lights in our study, especially for Largemouth Bass, suggesting that light could have some taxon-specificity in dimly-lit environments. While the reduction in Bighead Carp passage rate to the 5 Hz strobing light was less in a dimly-lit flume (only 30% compared to 80% in the dark flume), the different response of Largemouth Bass to high-intensity lights under dimly-lit (100 lux) and dark (1 lux) conditions was notable. In our study, Largemouth Bass passage was blocked by both strobing (85%) and constant light (60%) when tested in a dark flume; however when tested in a dimly-lit flume, Largemouth Bass were actually more likely to pass the light deterrent system when it was activated. This finding supports the findings of Sullivan et al. (2016) and Kim and Mandrak (2017) for Largemouth Bass under both darkness (Sullivan et al. 2016) and dimly-lit conditions (Kim and Mandrak 2017). Stewart et al. (2014) saw a similar increase in passage for age-0 Muskellunge in a laboratory raceway to a strobing light (1 Hz) in both dimly-lit and dark conditions. The seeming difference in the effectiveness of high-intensity light between Bighead Carp and Largemouth Bass could allow light to serve as a taxon-specific deterrent during the day in low turbidity waters; however, additional research on other fish species and ambient lighting conditions is needed.
Finally, our observation that Bighead Carp and Largemouth Bass responded differently to light emphasizes that careful examination of target species is needed and should include a broader range of river fishes. While pulse frequency and background lighting did not dramatically alter blockage efficiencies in Bighead Carp, we found that strobing lights were more effective than a constant light at blocking Largemouth Bass in a dark flume. Previous research on salmonids suggests that strobing lights are more effective than constant light although responses are notably context- and species-specific, especially in the field (Brett and MacKinnon 1953; Haymes et al. 1984; Nemeth and Anderson 1992). These results contrast with those of Sullivan et al. (2016) who show that Largemouth Bass were deterred equally by both constant and strobing lights. This could be due to the different behavioral measures used to assess the effectiveness of the light deterrent system – either fish displacement (Sullivan et al. 2016) or blockage (this study). Largemouth Bass also showed signs of habituation to the constant light, a notable difference from the sensitization we observed in Bighead Carp. It is possible that the response of Largemouth Bass to high-intensity lights may be different in flowing water, and studies in the field should examine this variable. However, the results of this study suggest that free-swimming bass will actively avoid high-intensity light in darkness but might be attracted in dimly-lit environments. These results indicate that high-intensity light could function as a taxon-specific barrier in some cases.

In conclusion, high-intensity light has promise for use as a deterrent to block Bighead Carp passage. Although our study provides an initial description of the effects of high-intensity light on fish passage, additional work in both the laboratory and especially the field would be helpful. In particular, studies examining how the intensity and spectrum of light might influence the behavioral responses of Bighead Carp to high-intensity light is still warranted (see Hamel et al. 2008; Ford et al. 2018; Hansen et al. 2018). Field studies using free-swimming wild fishes are also needed to truly understand how effective these light deterrent system might be and whether ambient lighting or turbidity levels are important factors. Nevertheless, at present, high-intensity light appears to have almost as much promise as sound to block Bighead Carp, especially in clear waters (Dennis et al. 2019). It could thus serve as an additional option for resource managers. For example, high-intensity light might be preferable to budget-constrained managers trying to stop most carp in shallow clear waters where light transmission would not be impeded by suspended particulates. Although light may be constrained by water clarity, it could perhaps be combined with sound or a coupled sound and air curtain system (bio-acoustic fish fence or BAFF) (Ruebush et al. 2012) to improve efficacy. These combinations all warrant testing. It is also important to note that no behavioral deterrent is likely to be 100% effective at blocking carp passage.
because they are generally thought to rely on behavioral preferences which can vary with individual (e.g., personality), so these systems should be combined with other control options (e.g., commercial fishing, improving native piscivorous fishes) to improve their chance of success. While we expect that Silver Carp will likely respond to high-intensity light in a similar manner as Bighead Carp, future studies on high-intensity lights should test all species of carp.

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Ethics and Permits

All procedures were approved by the University of Minnesota Institutional Animal Care and Use Committee (Protocol: 1712-35381A). Importation of Bighead Carp was approved by both federal (Injurious Wildlife; United States Fish and Wildlife Service; Permit Number: MA03394C-0) and state (Prohibited Invasive Species; Minnesota Department of Natural Resources; Permit Number: 294) agencies.

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Supplementary material

The following supplementary material is available for this article:

- **Table S1.** Summary of studies examining the effect of high-intensity light on fish behavior.
- **Table S2.** Generalized linear mixed model (GLMM) results for Bighead Carp exposed to Constant Light [0Hz], 5Hz Strobing Light and 12Hz Strobing Light in a dark flume [1 lux].
- **Table S3.** Generalized linear mixed model (GLMM) results for Largemouth Bass exposed to Constant Light [0Hz], 5Hz Strobing Light and 12Hz Strobing Light in a dark flume [1 lux].
- **Table S4.** Generalized linear mixed model (GLMM) results for Bighead Carp exposed to Constant Light [0Hz] and 5Hz Strobing Light in a dimly-lit flume [100 lux].
- **Table S5.** Generalized linear mixed model (GLMM) results for Largemouth Bass exposed to Constant Light [0Hz] and 5Hz Strobing Light in a dimly-lit flume [100 lux].
- **Table S6.** Z-test results for comparisons between the linear trend observed in the pre-test or test periods for light stimulus experiments relative to the linear trend observed during the No-Treatment Control. Significant $z$-values indicate either habituation (increased passage rates over time) or sensitization (decrease in passage rates over time) due to repeated exposure to the light stimulus.
- **Table S7.** Z-test results for comparisons between mean passage rates during the test periods for all combinations of light stimuli. Significant $z$-values indicate that the stimuli differ in their effectiveness to reduce passage rates.
- **Table S8.** Z-test results for comparisons between species for each light stimulus. Significant $z$-values indicate that the stimulus is more effective at blocking passage rates for one species than the other species.
- **Table S9.** Generalized linear mixed model (GLMM) results for Bighead Carp exposed to Constant Light [0Hz], 2Hz Strobing Light, 5Hz Strobing Light and 12Hz Strobing Light in a dark flume [1 lux].
- **Table S10.** Z-test results for comparisons between mean passage rates during the test periods for all combinations of light stimuli. Significant $z$-values indicate that the stimuli differ in their effectiveness to reduce passage rates.

**Figure S1.** Passage rate and blockage efficiency for Bighead Carp during a test of a 2Hz white strobing light in a dark flume [1 lux].

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