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The effect of light stimuli on dark-adapted visual sensitivity in invasive silver carp *Hypophthalmichthys molitrix* and bighead carp *H. nobilis*

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Non-physical barriers, including the use of underwater strobe lights alone or paired with sound or bubbles, are being considered as a means to prevent the upstream migration of invasive silver carp *Hypophthalmichthys molitrix* and bighead carp *H. nobilis*. To optimize potential optical deterrents, it is necessary to understand the visual sensitivity of the fishes. Dark-adapted *H. molitrix* and *H. nobilis* were found to possess broad visual sensitivity between 470 to 620 nm with peak spectral sensitivity at 540 nm for *H. molitrix* and 560 nm in *H. nobilis*. To assess the effect of a strobe light on vision, dark-adapted *H. molitrix*, *H. nobilis and* common carp *Cyprinus carpio*, were exposed to three different 5 s trains (100, 200, or 500 ms on–off flashes) of white light and the recovery of visual sensitivity was determined by measuring the b-wave amplitude of the electroretinogram (ERG). For all species, the longest recoveries were observed in response to the 500 ms flash trains (*H. molitrix* mean ± SE = 702.0 ± 89.8 s; *H. nobilis* 648.0 ± 116.0 s; *C. carpio* 480 ± 180.0 s). The results suggest that strobe lights can temporarily depress visual sensitivity, which may render optical barriers less effective.

KEYWORDS

electroretinography, fish vision, *H. molitrix*, *H. nobilis*, nonphysical barrier, strobe lights

1 | INTRODUCTION

Since their accidental introduction in the southern part of the USA in the 1970s (Kolar *et al*., 2007), silver carp *Hypophthalmichthys molitrix* (Valenciennes 1884) and bighead carp *Hypophthalmichthys nobilis* (Richardson 1845) carp, collectively termed bigheaded carp, have migrated northwards through the Mississippi River drainage and now threaten the Laurentian Great Lakes (Moy *et al*., 2011; Sass *et al*., 2010). These filter feeders outcompete native species such as paddlefish *Polyodon spathula* (Walbum 1792) (Schrank *et al*., 2003), bigmouth buffalo *Ictiobus cyprinellus* (Valenciennes 1884) (Irons *et al*., 2007) and gizzard shad *Dorosoma cepedianum* (LeSueur 1818) (Sampson *et al*., 2009) and threaten the trophic structure (Sass *et al*., 2014; Solomon *et al*., 2016) in regions with abundant *Hypophthalmichthys* spp. populations.

Currently, fisheries managers are working to develop effective methods for controlling the range expansion of *H. molitrix* and *H. nobilis* and a variety of non-physical barriers are being examined, however the sensory physiology of the target species remains largely unexplored. Recent studies have shown that both *H. molitrix* and *H. nobilis* can hear higher frequency sound than has been previously reported (Vetter *et al*., 2018) which is important for the design of acoustical deterrents. Jumping in *H. molitrix* is probably mediated both by sound and water turbulence, suggesting differential input to the lateral line and inner ear stimulates this behaviour (Vetter & Mensinger, 2016; Vetter *et al*., 2017,b). However, the visual capability for both species remains unknown. While filter-feeding behaviour combined with their turbid water environment probably reduces the need for high visual acuity, the retention of large, well-developed eyes suggests that visual sensitivity remains an important factor in their natural history.

For the past 60 years, strobe lights have been investigated as a method to modulate fish behaviour with varied results (Brown, 2000; Noatch & Suski, 2012; Popper & Carlson, 1998; Schilt, 2007). While some recent studies have found strobe lights to be effective in deterring or altering fish swimming (Hamel *et al*., 2008; Kim & Mandrak,

2017), others found no effect on behaviour (Flammang *et al*., 2014; Miehls *et al*., 2017; Mussen *et al*., 2014; Stewart *et al*., 2014; Table 1). The efficacy of strobe lights affecting fish behaviour most likely depends on the species' visual and spectral sensitivity and environmental conditions, such as ambient light and water turbidity. For strobes to be optimal, the spectrum of light used should be correlated with the visual and spectral sensitivity of the target species. Unfortunately, the strobe-light stimulus parameters used in fish behaviour studies are quite varied, with several studies failing to detail specifics about the light stimulus that would allow independent verification (Table 1).

In both North America and their native range in China, *H. molitrix* and *H. nobilis* predominately inhabit turbid water (Kolar *et al*., 2007; Yi *et al*., 2010; Yih & Liang, 1964) environments, where light is scattered by dissolved particulates, including plankton and down welling light is shifted to higher wavelengths compared with clearer water environments (Sundarabalan & Shanmugam, 2015). Therefore, it is likely that the spectral sensitivity of *H. molitrix* and *H. nobilis* evolved for a turbid light environment. The relative intensity of stroboscopic displays is maximized with decreasing environmental light, which suggests that a light deterrent may be optimal under scotopic conditions. In this study, the dark-adapted visual sensitivity of *H. molitrix* and *H. nobilis* was used to evaluate the effect of a strobe-light stimulus on visual sensitivity.

2 | MATERIAL AND METHODS

2.1 | Animal husbandry

Hypophthalmichthys molitrix (n = 10, mean ± SD standard length, L_S = 11.9 ± 1.8 cm), *H. nobilis* (n = 10, L_S = 12.1 ± 0.8 cm) and *C. carpio* (n = 3, L_S = 7.7 ± 0.5 cm) were obtained from the U.S. Geological Survey Columbia Environmental Resources Center, Columbia, MO. At the University of Minnesota-Duluth, *H. molitrix* and *H. nobilis* were housed in a 1230 l recirculating tank maintained between 19 and 22°C and equipped with a biological, chemical and mechanical filtration system (Fluval FX6 High Performance Canister Filter, Fluval; www.fluvalaquatics.com). Daily feeding consisted of liquid algae mixture (~300 ml; 1:1 *Chorella* sp. and *Spirulina* sp.; Bulk Foods; www.bulkfoods.com). A Prohibited Invasive Species Permit (#391) from the Minnesota Department of Natural Resources and an Injurious Wildlife Permit (MA-98346B-0) from the US Fish and Wildlife Service were obtained prior to acquisition of the animals and the fish were kept in a locked room with restricted access. *Cyprinus carpio* were kept in an 80 l recirculating tank maintained between 19 and 22°C and equipped with the same filtration system and fed goldfish flakes (Tetra Werke, Melle, Germany) daily. All fish were held at a 16 h:8 h (L:D) photoperiod and tested between 08.00 and 17.00 hours. Experiments were conducted in accordance with protocol 1604-33658A approved by the Institutional Animal Care and Use Committee of the University of Minnesota.

2.2 | Electroretinography preparation

Electroretinography (ERG) was conducted to determine the spectral sensitivities of *H. molitrix* (n = 5) and *H. nobilis* (n = 5). All experiments were conducted in a dark room. Fishes were anesthetized using buffered 0.005% MS-222 and a tail pinch was used to confirm that the surgical level of anaesthesia was obtained. The fish were then immersed in the solution to the ventral border of the eye and held in place within an experimental acrylic tank (31 × 15 × 8 cm) housed within a sheet-metal faraday cage (77 × 67 × 96 cm). Fish were ventilated *via* a tube inserted in the buccal cavity with recirculating water containing 0.005% MS-222.

A small incision was made in the eye at the limbus and a 0.02 mm diameter silver–silver chloride recording electrode was inserted into the vitreous humour. A reference electrode was placed rostrally between the nostrils. After electrode implantation, fish were dark adapted for at least 30 min prior to testing. Electroretinograms were first amplified (x100) and filtered (1 Hz low pass, 3 kHz high pass; World Precision Instrument Inc.; www.wpiinc.com) and then digitized and recorded using a PowerLab4/SP data acquisition system and

TABLE 1 Summary of studies examining the effect of strobe lights on fish behaviour

Species	Strobe frequency (Hz)	Stimulus duration (h)	Strobe intensity	Strobe wavelength	Behaviour affected	Other stimuli evaluated	Reference
Osmerus mordax°	7.5	4	2634 lumens	Not specified	Yes	None	Hamel *et al*. (2008)
O. mordax°	6	4	6585 lumens	Not specified	Yes	None	Hamel *et al*. (2008)
Cyprinus carpio	1–20	0.5	11,274.33 lx	Not specified	Yes	None	Kim and Mandrak (2017)
Sander vitreus	8 & 16	16	650 lumens	Not specified	No	Sound	Flammang *et al*. (2014)
Oncorhynchus tshawytscha	8	2	> 200 lumens	Not specified	No	None	Mussen *et al*. (2014)
Esox masquinongy	1	2	Not specified[a]	Not specified	No	Sound and bubbles	Stewart *et al*. (2014)
Petromyzon marinus	6	Overnight	Not specified	Not specified	No	Sound and bubbles	Miehls *et al*. (2017)
O. tshawytscha	3	Day or night	847.44 lx @ 1 m	Not specified	Yes	Sound and bubbles[b]	Perry *et al*. (2014)
Hypophthalmichthys molitrix & *H. nobilis*	Not specified	Variable, multi-day	Not specified	Not specified	Yes	Sound and Bubbles[b]	Ruebush *et al*. (2012)

[a] Authors note that the strobe visibility was 3.2 km.
[b] These studies only evaluated a combined sound, bubble and strobe-light stimulus.

LabChart 7 software (AD Instruments; www.adinstruments.com). Upon completion of the experiment, to distinguish experimental fish from naïve fish, the tip of the caudal fin (dorsal fork) was removed while the experimental fish were still anesthetized. After this procedure, the fish were then allowed to recover in isolation before being reintroduced to the tank. This surgical procedure is minimally invasive and is optimal for recording ERGs.

2.3 | Electroretinography experimental procedure

The light stimulus consisted of a 200 ms flash of monochromatic light from 400 to 700 nm at 10 nm increments that were presented in random order. The b-wave amplitude of the ERG was used as the response criterion with amplitude determined from the peak of the b-wave to the baseline. A 100 W quartz tungsten-halogen lamp (model 6333; Newport; Stratford, CT) powered by a constant power supply (model 68,938; Newport) provided the illumination, which was passed through a monochromator (model 77,250; Newport) and regulated by an Oriel Electronic Shutter (model 76,994; Newport). The monochromatic light stimulus was filtered with neutral density filters (0.1 to 3.0) and transmitted to the eye *via* a fibre optic (model 77,632; Newport). Light intensity was measured using an Orphir radiant power energy meter (model 70,260; Newport) and probe (model 70,268; Newport). Mean irradiance needed to elicit a response was compared using a repeated measures ANOVA with a *post hoc* Holm-Sidak test (SigmaPlot 12; www.sigmaplot.co.uk).

2.4 | Strobe-light stimulus

The ERGs showed *Hypophthalmichthys* spp.were maximally sensitive to wavelengths around 560 nm (Figure 1) and therefore monochromatic (560 nm) light flashes were used to establish a criterion ERG response for naïve fish. However, to ensure an ERG would be elicited after the strobe stimulus, the maximum irradiance output from the light source at 560 nm (7.031 e−15 1 photons cm^{-2} s^{-1}) was used during recovery experiments. Once the criterion response was established, fish were exposed to the first of three strobe stimuli presented in random order. A LED light (240 V, 10 watt, 760.0 lumen, white light, colour temperature: 60,000 Kelvin; Lighting EVER; www.lightingever.com) was used as the light stimulus and was controlled by the PowerLab4/SP (ADinstruments; www.adinstruments.com). The LED provided broad-spectrum white light, with the majority of the energy contained in two peaks: a narrow peak at 460 nm and a broader peak centred around 550 nm (Figure 2a). The strobe consisted of a series of flashes that were 100, 200, or 500 ms in duration with 100, 200 or 500 interpulse intervals, respectively, resulting in 5 s trains of 100 ms on–off (n = 50 total flashes), 200 ms on–off (n = 25), or 500 ms on–off (n = 5) giving a total of 2500 ms of illumination during each 5 s train (stimuli are referred to as: 100, 200 and 500 ms). Following the final light stimulus in each flash train, a 200 ms flash (560 nm) was presented every 60–90 s until the b-wave had returned to original levels (at least to 90% of the criterion amplitude). *Hypophthalmichthys molitrix* (n = 5), *H. nobilis* (n = 5) and *C. carpio* (n = 3) were tested under all three strobe conditions. Each fish was exposed to all three stimuli types (100, 200 and 500 ms) with the presentation order randomized. All fish examined were naïve to the ERG procedure and had not been used in the previous experiment to determine the visual sensitivity. Following recovery of 90% of the criterion response, a 10 min recovery period was provided prior to the next strobe train. The 560 nm flash was again used to establish the b-wave amplitude and if this was not at least 90% of the first criterion amplitude, further time was provided to restore the original dark-adapted sensitivity. A repeated measures ANOVA was used to compare the mean recovery times (to ≥ 90.0% of the criterion response). Data are reported as mean ± 1 SE.

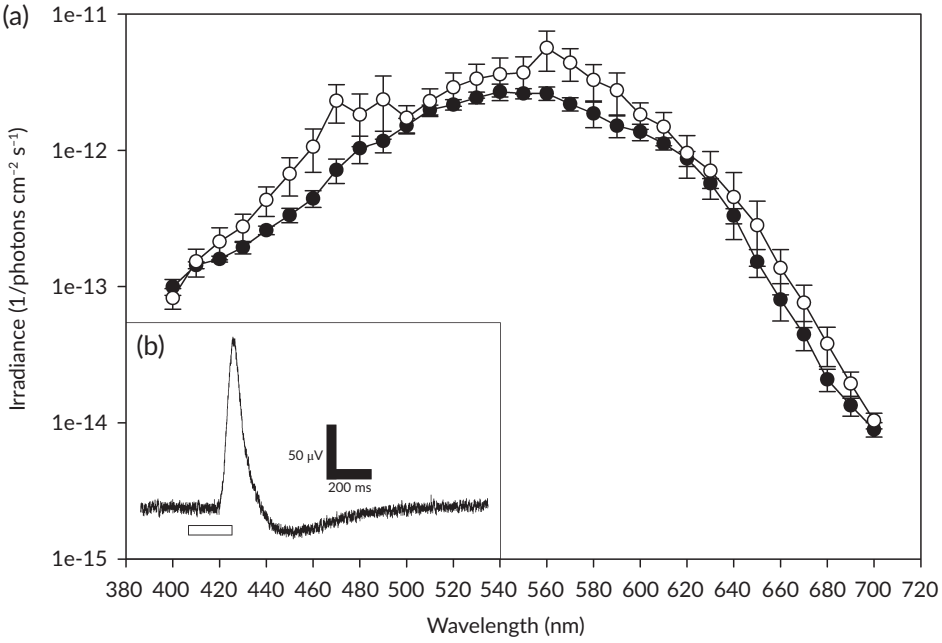

FIGURE 1 (a) The mean (± SE) irradiance needed to invoke the criterion at each wavelength examined for *Hypophthalmichthys molitrix* (–●–; n = 5) and *H. nobilis* (–○–; n = 5). Lines connecting the symbols are for illustrative purposes only. (b) Representative ERG b-wave from a dark-adapted *H. nobilis* in response to a 200 ms flash of 560 nm light. ▭, The stimulus

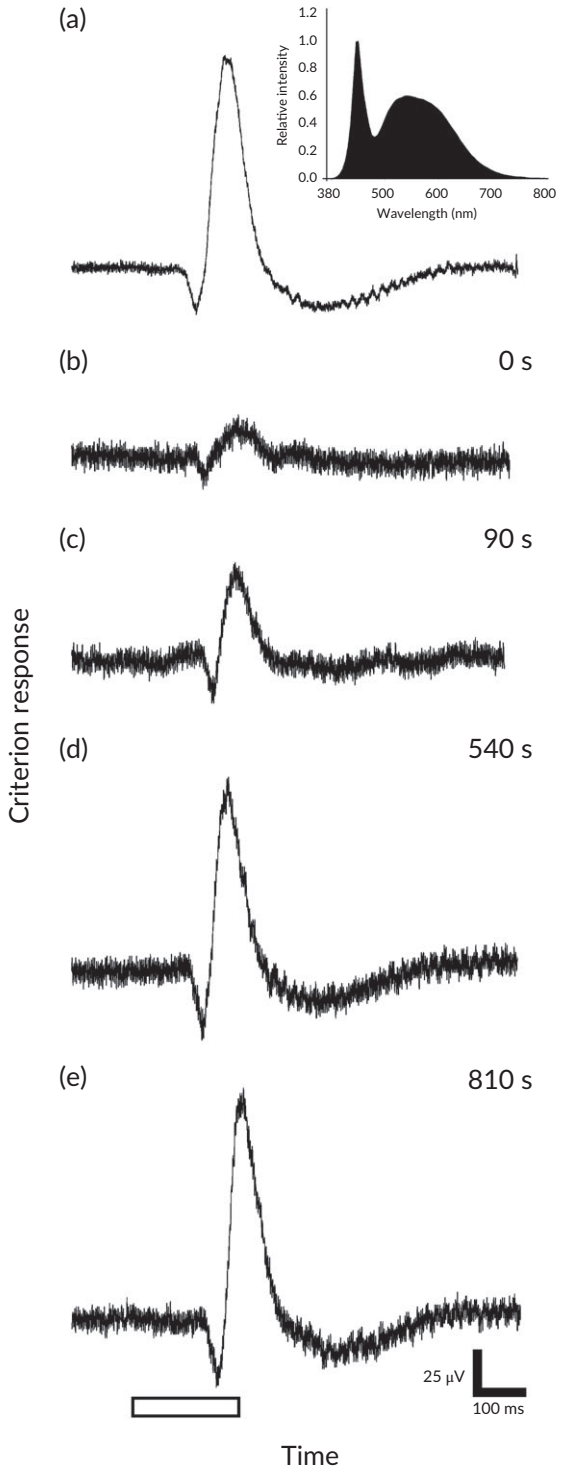

FIGURE 2 Representative electroretininograph (ERG) b-waves recorded from a single *Hypophthalmichthys molitrix* exposed to a strobe stimulus (500 ms train). (a) Criterion ERG in response to 560 nm light with (inset) example LED light emission spectrum for broad-spectrum white light. (b)–(e) ERGs elicited using the same 560 nm flash but at 0, 90, 540, and 810 s, respectively, after the strobe stimulus. ▭, When the stimulus was presented

3 | RESULTS

Both *H. molitrix* and *H. nobilis* showed broad spectral sensitivity between 470 and 620 nm. *H. molitrix*, were maximally sensitive at 540 nm however, this peak sensitivity was contained within a range of wavelengths (510–570 nm) that were significantly (ANOVA: $F_{4,30}$ = 8.6, P < 0.05) more sensitive than the other wavelengths evaluated. *H. nobilis* had peak sensitivity at 560 nm and the mean irradiance needed to evoke an ERG response was significantly (ANOVA: $F_{4,30}$ = 37.9; P < 0.05) lower than that for all over wavelengths evaluated. However, similar to *H. molitrix*, *H. nobilis* was significantly more sensitive to the surrounding wavelengths between 530 and 580 nm, than to the wavelengths above or below this range.

For *H. molitrix* and *H. nobilis*, exposure to the strobe stimuli resulted in an immediate reduction in the criterion ERG response amplitude (Figure 2). These reductions varied from 100.0%–58.0% (*H. nobilis*) and 100.0%–66.4% (*H. molitrix*) of pre-strobe b-wave amplitudes (100.0% = completely extinguished ERG; Figure 3). Recovery to > 50.0% of the criterion response amplitude occurred within the first 120 s for all *H. molitrix* and *H. nobilis* exposed to the 100 and 200 ms strobe stimuli. However, it took *H. molitrix* and *H. nobilis* up to 360 s to regain at least 50.0% of the criterion response to the 500 ms train. For both *H. molitrix* and *H. nobilis*, recovery time to ≥ 90.0% of the criterion response was greater when fish were exposed to the 500 ms train (mean ± 1 SE *H. molitrix* = 702.0 ± 89.8 s; *H. nobilis* = 648.0 ± 116.0 s) than either the 100 ms (*H. molitrix* = 367.5 ± 69.7 s; *H. nobilis* = 315.0 ± 51.2 s) or 200 ms (*H. molitrix* = 282.0 ± 45.1 s; *H. nobilis* = 285.0 ± 28.7 s) strobes (Figure 4), however this difference was not significant (ANOVA: *H. molitrix* $F_{2,4}$ = 6.8; P > 0.05; *H. nobilis* $F_{2,4}$ = 5.6; P > 0.05).

For *C. carpio*, recovery ERG responses were extinguished immediately after all strobe exposures, regardless of the duration. However, after 60 s, all *C. carpio* exposed to the 100and 200 ms flash trains had regained at least 50.0% of the criterion response, while 50.0% recovery in response to the 500 ms strobe duration took up to 240 s (Figure 3). Furthermore, there was no significant difference in recovery time to ≥ 90.0% of the criterion response between any of the strobe-flash durations (100 ms: 220.0 ± 80.0 s; 200 ms: 180.0 ± 60.0 s; 500 ms: 480 ± 180.0 s; Figure 4). For all species, both the strobe stimulus and the 560 nm flash were bright enough to evoke a small a-wave (Figure 2).

4 | DISCUSSION

The spectral sensitivity curves for dark-adapted *H. molitrix* and *H. nobilis* were similar, with both species demonstrating peak sensitivity to green wavelengths although the *H. nobilis* peak was slightly red-shifted (*H. molitrix* 540 nm; *H. nobilis* 560 nm). Both *Hypophthalmichthys* spp. had more red-shifted spectral sensitivity than has been reported for dark-adapted *C. carpio*, which have peak sensitivity at 523 nm (Witkovsky, 1968). In turbid water, dissolved organic matter and minerals absorb downwelling light and thus the available light is slightly red-shifted (~600 nm; Guthrie, 1986) and the dark-adapted visual sensitivities of these carp species are consistent with the prevailing wavelengths in their environment.

For all carp species, ERGs were extinguished or greatly reduced (> 50.0%) immediately after exposure to the strobe stimuli, with recovery times correlated with flash duration in each train. For *H. molitrix*

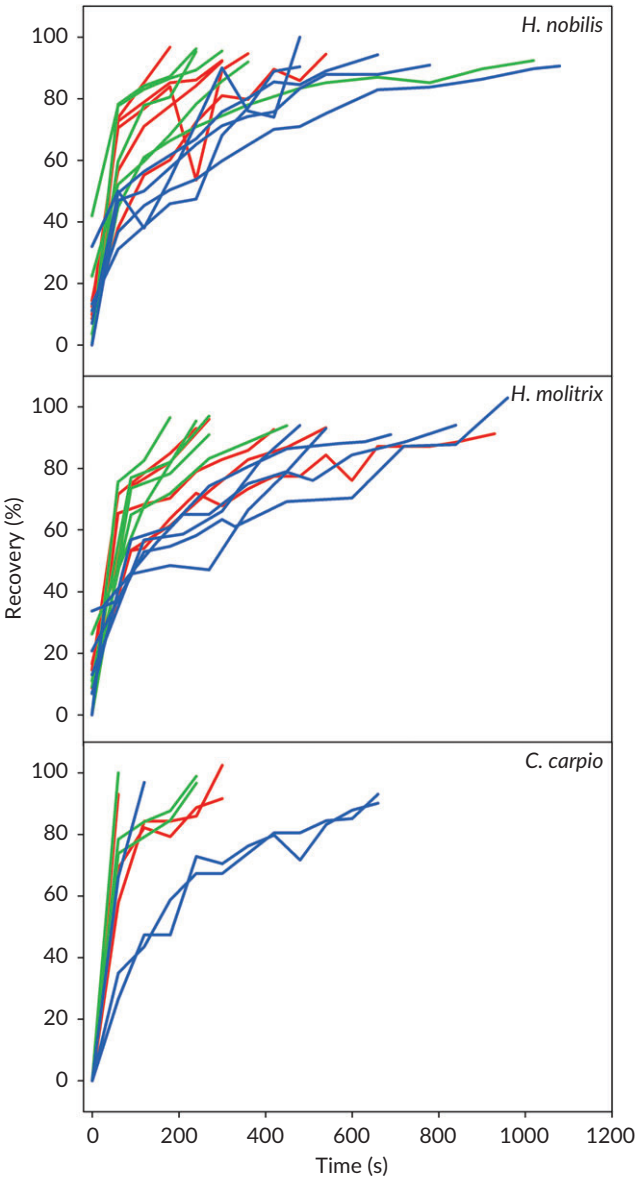

FIGURE 3 Time to recovery of ≥ 90.0% ERG criterion response for individual *Hypophthalmichthys nobilis* (n = 5), *H. molitrix* (n = 5), and *Cyprinus carpio* (n = 3) tested with 560 nm strobe flash of 100, 200 and 500 ms duration. (——) 100 ms, (——) 200 ms and (——) 500 ms

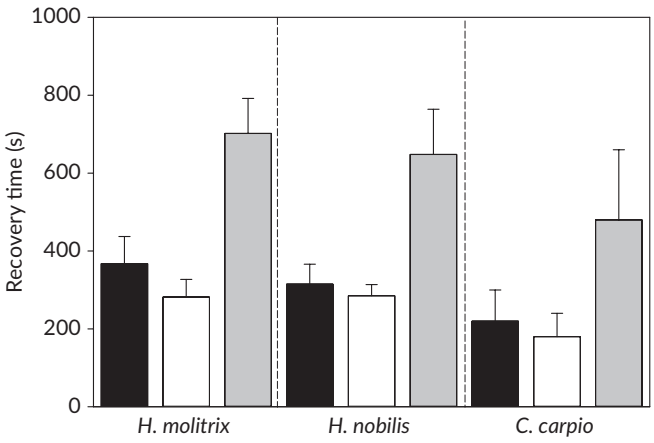

FIGURE 4 Mean (+ SE) time of recovery to ≥ 90.0% of the criterion response for *Hypophthalmichthys molitrix*, *H. nobilis*, and *Cyprinus Carpio* when exposed to 560 nm strobe flash of 100 (■), 200 (□) and 500 ms (▣) duration

and *H. nobilis*, > 50.0% recovery of the criterion ERG was achieved much quicker (within the first 2 min) after exposure to the shorter strobe durations. Although *C. carpio* were the only species to demonstrate a completely extinguished ERG immediately following every strobe exposure, regardless of the duration, this species also had the quickest recovery times to both > 50.0% and ≥ 90.0% of the criterion response for all strobe-flash durations. Although the results did not show any significant differences in recovery times, the findings do suggest that even brief exposure to strobe lights can temporarily impair carp vision. Future studies, particularly behavioural evaluations, are necessary to better understand how a strobe-light barrier would affect fish movement.

Temporal reduction in visual sensitivity could explain why studies have reported varied results in the efficacy of strobe lights in modulating fish swimming behaviour (Flammang *et al*., 2014; Hamel *et al*., 2008; Kim & Mandrak, 2017; Miehls *et al*., 2017; Mussen *et al*., 2014; Stewart *et al*., 2014). Many of these studies also examined the effect of a multi-modal non-physical barrier and combined strobe lights with sound or bubbles and reported mixed results. For instance, in a laboratory experiment Flammang *et al*. (2014) determined that strobe lights reduced the efficacy of a bubble–strobe-light barrier in preventing walleye *Sander vitreus* (Mitchill 1818) escapement from a simulated reservoir. Furthermore, Stewart *et al*. (2014) and Miehls *et al*. (2017) concluded that a bubble–strobe-light system was ineffective in altering the swimming behaviour of muskellunge *Esox masquinongy* Mitchill 1824 and sea lamprey *Petromyzon marinus* L. 1758, respectively. Alternatively, Perry *et al*. (2014) found that a combined bubble–strobe-light system was effective in diverting migrating Chinook salmon *Oncorhynchus tshawytscha* (Walbaum 1792). Similarly, a 2012 study reported that a bubble–strobe-light barrier was successful in preventing *H. molitrix* and *H. nobilis* from migrating upstream, but the researchers were unable to identify how many tagged fish remained in the area and challenged the barrier (Ruebush *et al*., 2012), which makes this study difficult to evaluate. In all of these studies, the strobe-stimulus parameters were highly varied and it was unclear if the strobe design factored in fish spectral sensitivity. Furthermore, in both of the latter examples, the strobe-flash frequency parameters were not provided which makes outside evaluation of the experiments and reproducibility difficult.

Although many strobe studies do not specify the wavelength of light used (Table 1), presumably, most of the experiments used white light. However, most fish have evolved visual sensitivity to prevailing wavelengths in their environment and thus have narrower spectral sensitivity than the broadband wavelengths of most strobes. Additionally, depending on water quality, certain wavelengths can be quickly attenuated and be relatively ineffective. Research investigating the use of monochromatic strobes designed for target species as a non-physical barrier could demonstrate an increased effectiveness. Additionally, it will also be important in the design of strobe deterrents, that the flicker fusion frequency of the visual system in each species be determined. The flicker fusion frequency is the rate at which a flashing light appears to be continuous. For *H. molitrix* and *H. nobilis*,

the flicker fusion threshold remains unknown, so it is unclear, even in the results presented in this study, what strobe frequencies are perceived as continuous illumination rather than flashing light by the carp. Hanyu and Ali (1963) studied ERG flicker-fusion frequency in goldfish *Carassius auratus* (L. 1758) and found that the values varied with temperature. They reported flicker-fusion thresholds of 67.2 ± 4.2 s^{-1} at 25°C and 24.4 ± 1.9 s^{-1} at 5°C. Therefore, these thresholds should also be determined for target species and considered when evaluating non-physical barriers containing strobe lights.

The present study was limited to assessing the dark-adapted visual sensitivity of *Hypophthalmichthys* spp. This study examined scotopic visual sensitivity, which is primarily mediated by rods, because *H. molitrix* and *H. nobilis* live in low-light turbid environments both in North America and their native range in China and rod cells are probably important for carp vision. However, an examination of the photopic visual sensitivity, mediated by cone cells, would be an interesting comparison. Additionally, while the ERG is a commonly used method to determine spectral sensitivity in fish, it can only evaluate which wavelengths stimulate the photoreceptor cells of the retina and does not provide information on the higher order processing involved in image formation in the visual centres of the brain. Microspectrophotometry, a method that examines the spectral absorbance characteristics of the visual pigments contained within photoreceptors, coupled with behavioural experiments, would provide a more complete assessment of the visual capabilities of *H. molitrix* and *H. nobilis*.

All three carp species have relatively similar dark-adapted visual sensitivities, although *H. molitrix* and *H. nobilis* are more red-shifted. As these species are members of the same family and tend to inhabit similar turbid environments, it is not surprising that their vision would be similarly adapted. *Cyprinus carpio* primarily feeds on detritus and is therefore more likely to reside deeper in the water column than *H. molitrix* and *H. nobilis*, both of which are filter-feeders. Therefore, *C. carpio* may benefit from having vision that is less red-shifted. Furthermore, the results presented here demonstrated a significant difference between the effect of a strobe stimulus on *C. carpio* and the two *Hypophthalmichthys* spp. *Cyprinus carpio* exhibited a greater response to the strobe stimuli (*i.e.*, the fish demonstrated completely extinguished ERGs) but were able to recover vision more quickly than *H. molitrix* and *H. nobilis*. Therefore, although the photoreceptors in the *C. carpio* retina were more likely to become bleached, they also appeared to regenerate visual pigments more quickly.

Studies evaluating strobe lights as a non-physical barrier to fish passage assume a simple scenario: a fish approaches a flashing bright light and turns away. However, because of environmental conditions and fish visual physiology, the situation could be more complex. In the natural environment, light attenuation in water and ambient light levels are variable and can affect the range at which the fish will detect the stimulus. Presumably, as the fish approaches the strobe, the intensity increases and raises the question: at what distance does the light becomes an effective deterrent? At long distance, intermittently broadcast but very high intensity light could allow the fish to adjust to the strobe and reduce its deterrent effect. Furthermore, most freshwater fish have evolved in systems devoid of light sources during crepuscular or nocturnal conditions, when more sensitive rod photoreceptors are active (except from downwelling astral sources). In contrast, in marine systems, bioluminescence is common and examining how marine animals employ it may aid in developing more effective light deterrent systems. Spatial refuge is limited in the mid-water ocean environment and bioluminescent animals must balance the need for concealment against the advantages of bioluminescence. Stroboscopic displays are rare and most animals deploy quick single flashes or brief flash trains that can startle, freeze, or cause recipients to flee (Haddock *et al.*, 2010). Thus infrequent, high intensity flashes may be more effective than the continuous strobes that are typically evaluated in behavioural studies (Table 1). The data from this study suggest that in dim environments, bright flashes rapidly affect carp vision and that recovery periods are longer with increasing flash duration. The deterrence scenario assumed by strobe studies is possible, but we recommend behavioural assessments that examine deterrence rates in response to shorter light exposure times and that these studies also evaluate the likelihood and frequency of repeated barrier challenges. Finally, all field studies should also take into account environmental factors, such as turbidity and ambient light levels.

The results from the present study indicate that strobe stimuli can temporarily impair carp vision and the recovery times can vary depending on the flash duration. This coincides with the diverse results from behavioural experiments examining the effect of strobe lights on fish movement. When evaluating the efficacy of a strobe-light barrier, it is important that researchers evaluate the visual sensitivity of the species in question, conduct behavioural experiments, especially under natural settings, and provide more specific details regarding the light stimulus (*i.e.*, wavelength used, stimulus duration, flash duration). The present results provide a strong foundation on which behavioural studies can be designed to optimize the most effective strobe parameters to include in a deterrent system.

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