

Research Article

Short-term behavioural response of common carp, *Cyprinus carpio*, to acoustic and stroboscopic stimuli

Paul A. Bzonek^{1,2,*}, Jaewoo Kim³ and Nicholas E. Mandrak^{1,2}

¹Department of Ecology & Evolutionary Biology, University of Toronto, 27 King's College Circle, Toronto, Ontario, M5S 1A1 Canada

²Department of Biological Sciences, University of Toronto Scarborough, 1265 Military Trail, Scarborough, Ontario, M1C 1A4 Canada

³Golder Associates Ltd., 102, 2535 – 3rd Avenue S.E., Calgary, Alberta, T2A 7W5 Canada

Author e-mails: paul.bzonek@mail.utoronto.ca (PB), jaewoo_kim@golder.com (JK), nicholas.mandrak@utoronto.ca (NM)

*Corresponding author

Citation: Bzonek PA, Kim J, Mandrak NE (2020) Short-term behavioural response of common carp, *Cyprinus carpio*, to acoustic and stroboscopic stimuli. *Management of Biological Invasions* 11(2): 279–292, <https://doi.org/10.3391/mbi.2020.11.2.07>

Received: 14 March 2019

Accepted: 22 November 2019

Published: 30 March 2020

Thematic editor: Matthew Barnes

Copyright: © Bzonek et al.

This is an open access article distributed under terms of the Creative Commons Attribution License (Attribution 4.0 International - CC BY 4.0).

OPEN ACCESS

Abstract

Deterrents that limit the dispersal of non-native fishes into waterways are important tools for managing aquatic invasions. Acoustic and stroboscopic stimuli may be used to limit the dispersal of common carp (*Cyprinus carpio*), a widely invasive species. This study exposed wild-caught common carp to stroboscopic, acoustic, or combined-stimuli treatments, to observe changes made in their activity and in the number of passes made across the deterrent. Mixed-effects models determined that for all treatments, common carp spent more time moving actively during the stimulus and post-stimulus periods than during the control period. Common carp deterrent passes differed according to treatments. In the stroboscopic treatment, passes only increased during the post-stimulus period, in the acoustic treatment there were no significant differences across stimulus periods, and in the combined treatment passes decreased during the stimulus period. These results indicate that stimulus-induced behavioural changes may be sustained for short periods of time (> 30 min) after the deactivation of a stimulus deterrent. Our study found a muted avoidance response in comparison to other acoustic deterrent studies, likely due to the lack of sufficient stimulus refuge. Finally, individuals that were exposed to both stimuli did not express additive behavioural responses in comparison to individuals that were only exposed to one stimulus type. Our findings highlight important considerations for deterrent technologies and directly quantify the behavioural response of combined deterrent stimuli.

Key words: non-structural deterrent, behavioural deterrent, aquatic invasive species

Introduction

Biological invasions are a major threat to global biodiversity (Britton et al. 2011), with a disproportionate vulnerability found in freshwater ecosystems (Ricciardi et al. 2011). These systems are characterized by high species richness (Dudgeon et al. 2006) and strong trophic linkages that can be dramatically altered by the introduction of an invasive species (Gallardo et al. 2016). Furthermore, the potential for species invasions or range expansions has dramatically increased through anthropogenic vectors such as live trade, shipping, intentional animal release, and canal passage (Pagnucco et al. 2015). These vectors have led to a greater proportion of non-indigenous

species occupying freshwater ecosystems (Vitousek et al. 1997; Ricciardi et al. 2011). Mitigating the spread of invasive species is a high conservation priority, as the establishment of even a single species can lead to significant, and often irreversible, ecological consequences (Vitule et al. 2009; Wittmann et al. 2014). Once an aquatic species has invaded a novel environment, its eradication is often extremely difficult, and the costs of active management are generally very high (Leung et al. 2002).

Non-structural deterrents have been employed to obstruct fish movement, and limit the propagule pressure of an invasion front without modifying the physical structure of a waterway (Noatch et al. 2012). Fish movement can be obstructed by altering stream flow, as done with high-velocity dams (Haro et al. 2004), or fish movement can be obstructed by introducing new stimuli to the system to surpass the physiological tolerances of fishes, as done with electrical or chemical systems. Finally, fishes can be deterred from continued movement by making a targeted region undesirable, as done with chemical, acoustic, or visual technologies (Noatch et al. 2012). Non-structural deterrents avoid some of the disadvantages of physical barriers including expensive installations, impediments to water flow, and the maintenance required to remove clogging or biofouling (Flammang et al. 2014).

Acoustic deterrents were initially investigated as a tool to reduce the level of fish impingement upon nearby power plants (Hocutt 1980; Maes et al. 2004). The sound frequencies tested have ranged from infrasound to ultrasound (Hocutt 1980; Haymes et al. 1986; Knudsen et al. 1997; Mann et al. 1997) and produced a range of avoidance responses across a variety of species. More recently, broadband sound has been investigated as a potential non-structural deterrent to prevent the continued dispersal of bigheaded carps throughout the Mississippi River Basin and into the Great Lakes. Vetter et al. (2015) consistently deterred silver carp *Hypophthalmichthys molitrix* 11 times, and bighead Carp (*Hypophthalmichthys nobilis*) 20 times (Vetter et al. 2017) away from the source of a marine-motor recording. Additional lab studies have continued to find bigheaded carps expressing an avoidance response to acoustic stimuli (Murchy et al. 2016, 2017; Zielinski et al. 2017).

Acoustic deterrent reliability could be further improved by combining additional sensory modalities and adding redundancy to fish avoidance responses (Popper et al. 1998; Taylor et al. 2005; Flammang et al. 2014; Dennis et al. 2019). Strobe lights can be added to an acoustic deterrent relatively easily (Ruebush et al. 2012) and provide a secondary directional stimulus that engages new sensory systems. As a stand-alone deterrent, strobe lights lack consistency across species and under varying turbidity and background light-intensity levels (McIninch et al. 1987; Nemeth et al. 1992; Simmons et al. 2004; Noatch et al. 2012). The flashing pattern of the stimulus may increase deterrent efficacy in comparison to continuous light

(Popper et al. 1998). Sullivan et al. (2016) found that stand-alone strobe lights were effective across a broad range of light and pulsing frequencies in deterring largemouth bass (*Micropterus salmoides*).

A combined acoustic-strobe-light deterrent may be useful in managing common carp, *Cyprinus carpio* dispersal. Common carp is a globally invasive species (Chumchal et al. 2005) that dominates natural communities (Weber et al. 2009). As common carp consumes aquatic vegetation, it re-suspends sediment and excretes high levels of nutrients that can lead to algae blooms. Additionally, it reduces macrophyte abundance and habitat for benthic invertebrates (Parkos III et al. 2003; Chumchal et al. 2005; Weber et al. 2009). These characteristics have led to substantial international efforts towards controlling its spread, or limiting its ecological damage (Weber et al. 2009) and an interest in management-related behavioural studies (Sisler et al. 2008; Huntingford et al. 2010; Zielinski et al. 2014, 2017).

Common carp and other large-bodied invasive cyprinids are a major conservation concern to the Great Lakes basin (Lougheed et al. 1998; Cudmore et al. 2011). These cyprinids are in the superorder Ostariophysi, which have a specialized connection between their inner ear and swim bladder (Popper et al. 1998). This connection, termed the Weberian apparatus, allows for compressions in the swim bladder caused by sound waves to be transmitted to the inner ear, and gives carps a hearing advantage compared to species without this anatomical feature (Lovell et al. 2006; Popper et al. 2011). Common carp can detect frequencies from 100-2000 Hz at sound-pressure levels lower than 100 dB re 1 μ Pa RMS (Kojima et al. 2005). Zielinski et al. (2017) found that, in the absence of any visual stimuli, common carp behaved similarly to bighead and silver carps when exposed to complex sound, however, Murchy et al. (2016) observed that with visual stimuli, common carp avoidance to complex sound expressed potential habituation, and was considerably muted in comparison to the two other species. Bighead, common, and silver carps all have similar dark-adapted visual sensitivity, but common carp has expressed a greater electroretinography response and recovery to strobe lights than the other two species (Vetter et al. 2019).

In our study, common carp were exposed to either acoustic, stroboscopic, or both stimuli to quantify how behaviours differed before, during, and after a stimulus was applied. Behaviour was quantified by the duration of active movement (activity) and the number of passes made across the stimulus centered within the experimental tank (passes). We predicted that activity levels would increase, and that passing frequency would decrease during the stimulus period. Additionally, we predicted that the magnitude of behavioural response would be greater for the combined stimuli treatments than for the individual acoustic or strobe-light treatments.

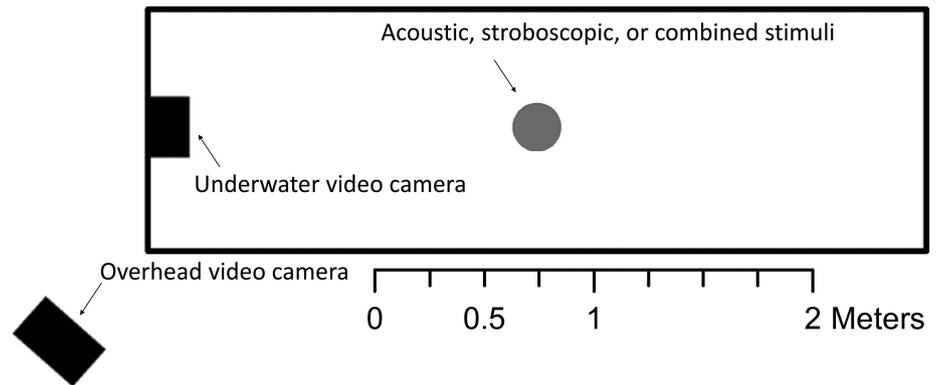


Figure 1. Layout of experimental tanks with video cameras represented with black boxes, and stimuli represented with the gray circle. The experimental stimulus was always placed in the middle of the tank.

Materials and methods

Study Animals

Wild, adult common carp were collected, by boat electrofishing in Hamilton Harbour, Lake Ontario, and held at the Aquatic Life Research Facility at the Canada Centre for Inland Waters (Burlington, ON). In total, 53 common carp were used, with an average weight of 3.80 ± 1.23 kg (Mean \pm SD), and an average fork length of 569.5 ± 47.4 mm. Fish weight did not differ across the three treatment types ($F_{2, 33} = 2.73$, $p > 0.05$). Captured common carp were bathed in a formalin treatment (125 ppm) for one hour on three consecutive days to prevent parasite and disease transfer. The treated fish were maintained in large aerated recirculating tanks (650 L tank x 4, 1650 L tank x 2) with dechlorinated water (12–15 °C) for 13 ± 9 days before being placed in experimental tanks.

Common carp were identified with a FD-94 anchor tag (Floy Tag & Manufacturing Inc. Seattle WA) inserted into fish musculature below dorsal fin with a fine fabric tag. Prior to fish tagging, individuals were anaesthetized with a Portable Electroshock System (PES, Smith-Root Inc., Vancouver, WA) following the procedure outlined in Jaewoo et al. (2017), then weighed, measured and photographed. Fish were fed daily, (1–1.5% body weight) with commercial fish food (Profishent Trout Chow, Martin Mills, Inc., Elmira, ON), and maintained in a 12 h light: dark photoperiod. After data collection, fish were euthanized via percussion stunning and destruction of the brain.

Experiment

Trials were conducted in three experimental tanks measuring 3.56 m long, 1.10 m wide, and 0.39 m deep. The behavioural responses to acoustic, strobe-light, and combined stimuli were recorded in 1080 p and 60 fps with one underwater camera (Hero 4, GoPro, San Mateo, CA), and one overhead camcorder (XA 25, Canon, Brampton, ON) positioned in the left end of the tank (Figure 1).

To minimize isolation stress and risk perception (Huntingford et al. 2010), each trial held three common carp at a time. The fish schooled throughout trials so one individual was randomly selected to be the focal fish and represent the movement of the group (Vetter et al. 2015). Each fish per group had a uniquely coloured anchor tag and flagging tape of the same colour was added to the end of each tag to allow for improved fish identification during video analysis. Focal fish were reused as non-focal fish in trials of a different treatment.

After fish tagging or trial completion, common carp were held for at least 24 hours before they could be selected for a trial. Once an individual was selected for a trial, they were acclimated to the experimental tank for 19 ± 2 hours, with the inactive stimulus equipment placed in the tank at least 45 minutes prior to trial initiation. All three fish were placed in the top left corner of the tank and allowed to move freely throughout the acclimation period. Trials with missing video data due to camera movement or battery failure were removed, leaving a total of 36 trials split across acoustic ($n = 11$), stroboscopic ($n = 12$), and combined ($n = 13$) treatments.

Each trial lasted for 90 minutes and consisted of three components: a 30-minute control period; a 30-minute stimulus period; and, a 30-minute post-stimulus period. The same focal fish was observed for all periods of each trial. Two behavioural conditions were observed for every trial; the total duration of active movement (s), and the number of passes made across the deterrent. An individual was considered active if it was pumping its pectoral fins or travelling at a velocity greater than $0.05 \text{ m}\cdot\text{sec}^{-1}$. This velocity was used as it was an observed midpoint in velocities between deliberate fish movement and incidental movement observed when fish are maintaining position within the water column. Velocity was assessed by manually observing fish movement across distance markers placed in tank. The main goal of the activity measurement was to differentiate between the movement of general exploratory behaviour and inactive stationary behaviour. A fish was considered to have passed a deterrent once the midpoint of its body had passed the deterrents placed in the middle of the tank. All recorded trials were observed and scored with Behavioural Observation Research Interactive Software (Friard et al. 2016). Each video was viewed by one of two observers to quantify passes across the deterrent and durations of active movement.

Behavioural Stimuli

The acoustic stimulus was a four-second loop that combined a 200–1400 Hz sweep, a 200–1500 Hz band sweep, and a recording of a 50 hp outboard motor that had an energy peak at ~ 1300 Hz. When combined, these components produce a signal that ranges in frequency across the hearing sensitivity of common carp (Popper 1972), while simultaneously changing

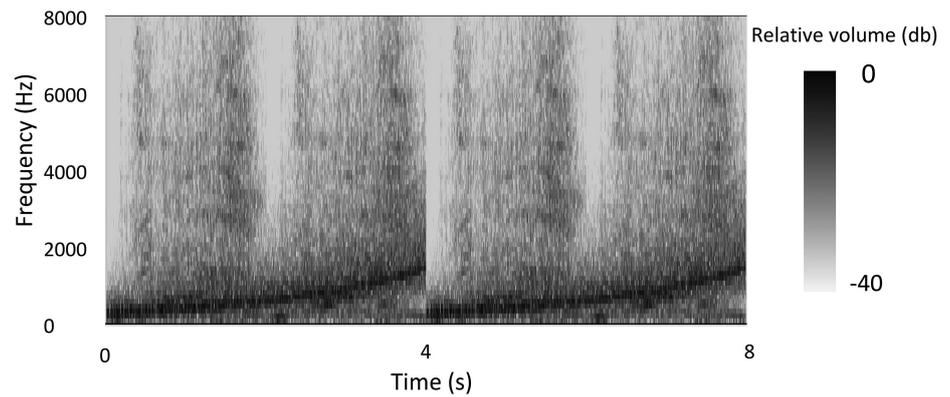


Figure 2. Spectrogram of the acoustic stimulus displaying changes in sound pressure over time for frequencies between 0 and 8000 Hz. The spectrogram was plotted using Audacity (Version 2.1.1.0) with a frequency resolution of 7.8 Hz, produced by a Hanning moving window.

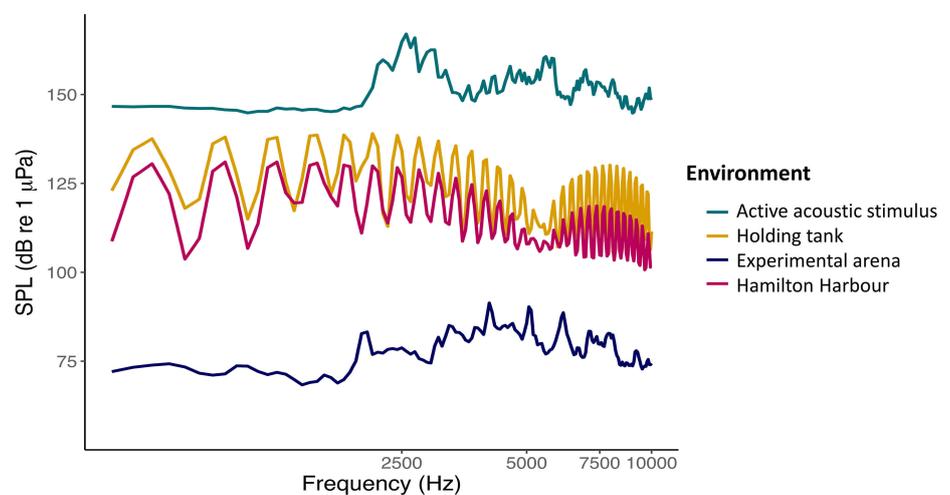


Figure 3. Power spectrum for the RMS sound pressure level of the acoustic stimulus 5 cm from the speaker (blue line), and for ambient noise in the holding tank (yellow line), experimental arena (purple line), and Hamilton Harbour (blue line). Power spectrums are plotted with a frequency resolution of 62 Hz.

over time to reduce the likelihood of habituation (Figure 2). The stimulus was produced with an underwater speaker (Lubell LL916H, Lubell Labs Inc., Columbus, OH) placed in the center of the experimental tank. Sound intensity ranged from 117–128 dB re 1 μ Pa RMS during ambient conditions to 160–167 dB re 1 μ Pa RMS during the acoustic and combined treatments (Figure 3). Common carp were captured from Hamilton Harbour, which had a background sound pressure level of 112 dB re 1 μ Pa RMS and were acclimated in holding tanks with sound pressure levels of 131 dB re 1 μ Pa RMS.

The stroboscopic stimulus used in this study was a 110 V random-flashing underwater strobe light that operated with a frequency of 1–20 Hz (Seebrite LED, I.A.S. Ltd, Vancouver, BC). The strobe light was placed in the center of the experimental tank where it produced white light in 360° throughout the water column. Peak light intensity ranged from 1–66 lux in ambient conditions to 300–17090 lux during the acoustic and combined treatments. The strobe light produced 51 μ mol s⁻¹ m² of light radiation between 400 and 700 nm at a distance of 1 m from the source (LP-80, AccuPAR, Pullman, WA).

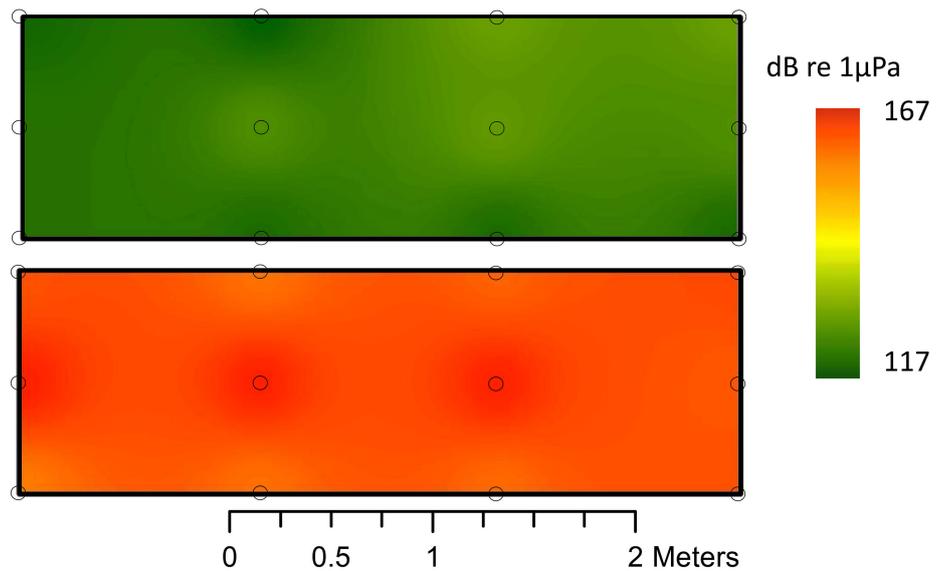


Figure 4. Sound-pressure levels (dB re 1 μ Pa RMS with 30 sec audio recording) of the experimental tank under ambient (upper) and stimulus (lower) conditions. Black rings represent where measurements were taken at a depth of 0.2 m. Sound-pressure levels are plotted with the peak power frequencies of the stimulus and ambient acoustic environments.

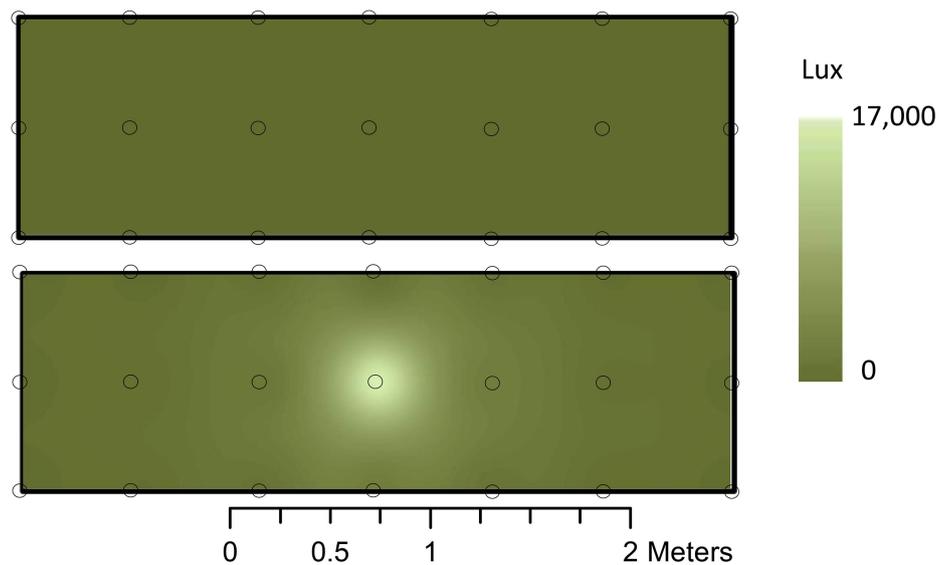


Figure 5. Light intensity levels (peak Lux facing source with 30 sec recording) of the experimental tank under ambient (upper) and strobe-light (lower) conditions. Black rings represent where measurements were taken at a depth of 0.2 m.

Sound pressure (Figure 4) and light intensity (Figure 5) were measured for 30 s in a 3×4 measurement grid along the experimental tank and mapped using the IDW function in ArcGIS 10.3 (ESRI, Redlands, CA) (ESRI 2014). Sound-pressure levels were measured with two hydrophones at a sampling rate of 128 kHz (M8E51-C0, sensitivity @ 250 Hz = -199 dBV; M8E51-C35, sensitivity @ 250 Hz = -164 dBV, GeoSpectrum Technologies Inc., Dartmouth, NS) connected to a JASCO Ocean Sound Meter (JASCO, Halifax, NS). The higher sensitivity hydrophone (M8E51-C0) was used to measure the ambient sound pressures of Hamilton Harbour, the holding tank, and the experimental tank. The lower sensitivity hydrophone

(M8E51-C35) was used to measure stimulus sound pressures, and record the motor component of the acoustic stimulus. Peak strobe-light illuminance was measured for ambient and stimulus treatments with a lux meter (MW700, Milwaukee Electronics Kft., Hungary).

Data Analysis

Common carp activity duration and deterrent passes were analysed separately as dependant variables to be compared among treatment type and stimulus period. Activity was square-power transformed and passes-across-deterrents were square-root transformed to improve normality. The data were analysed with linear mixed-effects models fit by restricted maximum likelihood. Each trial observed the repeated measures of common carp response across the control, stimulus, and post-stimulus periods. To account for the repeated measures within a trial, stimulus period was nested within the random-factor of fish identity. Treatment type and stimulus period were measured as fixed effects, and the variance structure was allowed to differ across both factors. Linear mixed-effects models were constructed with the nlme package (Pinheiro et al. 2018) in the statistical program R (R Core Team 2018). Significant differences across fixed-effects factors were quantified with a mixed model ANOVA to obtain degrees of freedom, F-statistics and P-values (Reber et al. 2008; Allen et al. 2014). Holm-Bonferroni corrected alpha levels of $\alpha = 0.025$ ($0.05/2$) were applied to account for the two dependant variables. Post-hoc pairwise comparisons were tested with Tukey's HSD, using the lsmeans package (Allen et al. 2014).

Results

Exposing common carp to aversive stimuli resulted in significant changes in durations of active movement across the control, stimulus and post-stimulus periods ($F_{2, 64} = 31.19$, $p < 0.001$) (Figure 6). The duration of active movement did not significantly differ between the acoustic, stroboscopic, or combined treatments ($F_{2, 37} = 2.86$, $p = 0.07$), and there were no interaction effects between stimulus period and treatment type ($F_{4, 64} = 0.91$, $p = 0.46$). Duration of activity was highest during the post-stimulus period (mean \pm SD; Light: 1352 ± 249 s; Sound: 1353 ± 285 s; Combined: 1406 ± 351 s), followed by the stimulus period (Light: 1207 ± 423 s; Sound: 1200 ± 300 s; Combined: 1222 ± 460 s), and finally the control period (Light: 814 ± 394 s; Sound: 952 ± 448 s; Combined: 1108 ± 421 s).

Exposing common carp to aversive stimuli also resulted in significant changes for the number of passes made across the control, stimulus and post-stimulus periods ($F_{2, 64} = 15.52$, $p < 0.001$) (Figure 7). The number of passes did not significantly differ between the three treatments ($F_{2, 37} = 2.40$, $p = 0.11$), but there were significant interactions between stimulus period and treatment type ($F_{4, 64} = 5.80$, $p < 0.001$). In the acoustic treatment, deterrent

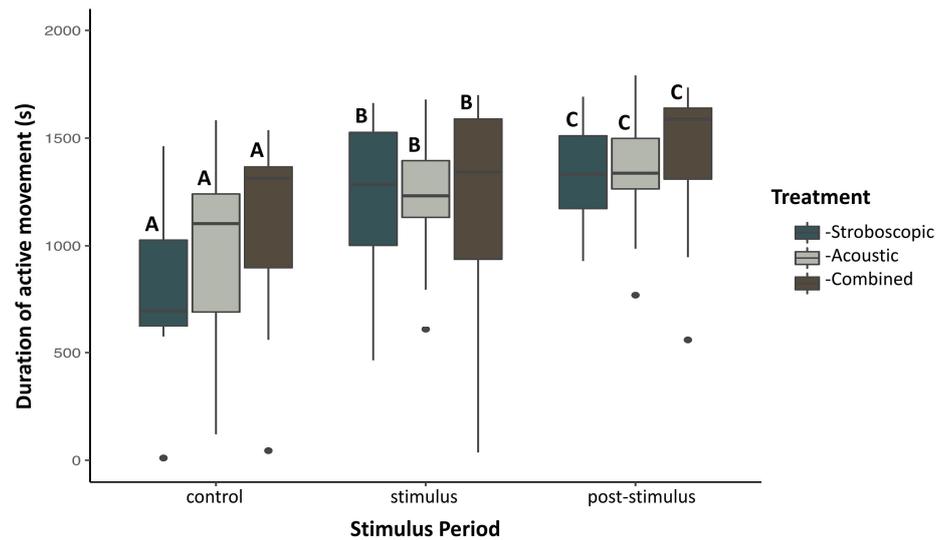


Figure 6. Common carp activity across treatment type and stimulus levels. As indicated by lettering, activity levels were significantly different ($p < 0.05$) across stimulus periods, but not across treatment type, as determined by a Tukey's HSD tests.

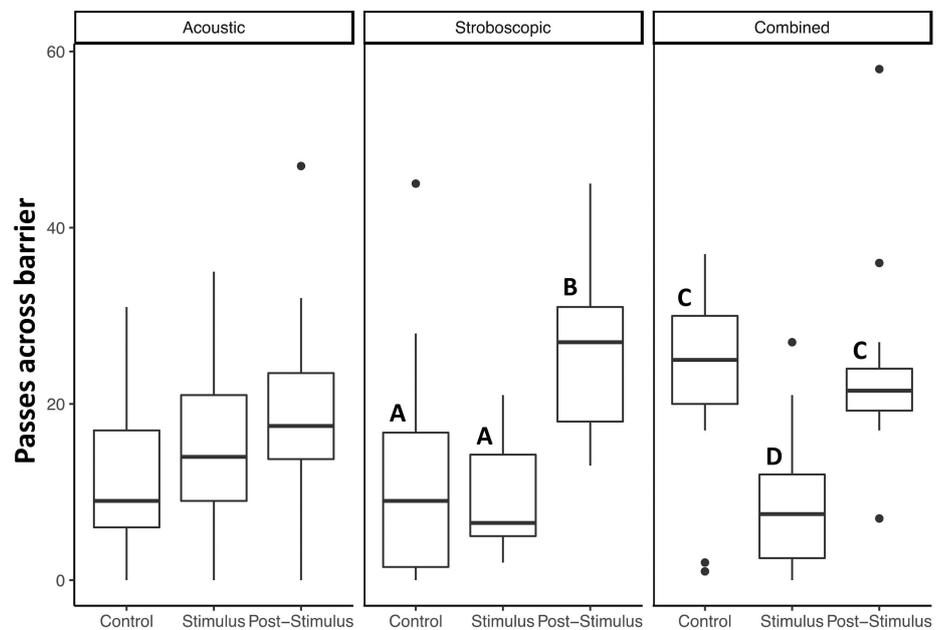


Figure 7. Number of passes made by common carp across the deterrent for each treatment type and stimulus period. Significant differences ($p < 0.05$) within treatments were determined using Tukey's HSD tests and the results represented by letters.

passes did not differ between periods (control: 11 ± 9 ; stimulus: 15 ± 11 ; post-stimulus: 19 ± 12) and fish expressed high variation in latency of first passing (control: 647 ± 640 s; stimulus: 302 ± 542 ; post-stimulus: 229 ± 566). In the stroboscopic treatment, the post-stimulus period had significantly more passes (26 ± 10) than the control (13 ± 14) or stimulus period (9 ± 7). Fish latency to the first deterrent pass was also much shorter in the post-stimulus period (52 ± 65 s) than the control (674 ± 850 s) or stimulus (445 ± 492) periods. Finally, the combined treatment had significantly lower passing rates during the stimulus period (Combined: 9 ± 8) than during the control (22 ± 11) or post-stimulus period (24 ± 13). Both the stimulus and post-

stimulus periods had long latencies to first deterrent pass (555 ± 514 s; 507 ± 629 s) in comparison to the control period (66 ± 48).

Discussion

Common carp increased their activity as the acoustic, strobe-light or combined stimuli were turned-on, and further increased their activity once the stimulus was deactivated (Figure 6). These results show that both acoustic and stroboscopic stimuli can produce a behavioural response in common carp that exists during, and after deterrent activation. The common carp were likely exhibiting a fright (Königson et al. 2002) and avoidance response to the stimuli, as seen in other laboratory studies for stroboscopic (Kim et al. 2017) or acoustic stimuli (Murchy et al. 2016; Zielinski et al. 2017). Stroboscopic deterrents have also been found to increase blood-cortisol levels, an indicator of stress, in other freshwater fishes (Richards et al. 2007).

Each treatment had a different effect on common carp deterrent passes. In the stroboscopic treatment, passes only increased after the stimulus ceased, while in the acoustic treatment, deterrent passes never significantly differed from the control. In the combined treatment, the deterrents altered the passing rate as predicted, with a significant decrease in passing rates during the stimulus period (Figure 7). In both the stroboscopic and combined treatment, passing rates were significantly higher in the post-stimulus period than the stimulus period. This increase in passing rates is likely associated with the corresponding increase in post-stimulus activity. When the stimuli were in operation, individuals spent more time actively moving but, to avoid proximity to the source of the stimulus, did not express a corresponding increase in passes across the deterrent. Once the stimulus stopped, individuals began passing across the deterrent more frequently, matching their elevated post-stimulus activity levels.

The lack of response in passes during the acoustic treatment may have been influenced by the conditions of the experimental tank. There was no refugia from the acoustic or stroboscopic stimuli, a scenario unlikely in naturalized settings. The common carp in our study experienced a minimum sound-pressure of 160 dB re 1 μ Pa during the stimulus period. Goldfish, *Carassius auratus*, exposed to 170 dB re 1 μ Pa for 24 hours expressed a temporary threshold-shift in hearing ability (Smith et al. 2004). While our study only exposed individuals to the stimulus for a period of 30 minutes, the signal strength was considerable and may have temporarily altered fish hearing physiology. Additionally, our study used mature, wild-caught individuals of large size relative to the experimental tank. When exposed to any of the aversive stimuli, individuals were constrained in the space that they had to express a behavioural response. Common carp exposed to the acoustic deterrent may have continued passing across the deterrent in order to find suitable stimulus refuge.

When interpreting our results, it is also important to consider the environmental conditions of the experimental tank. Sound pressure and particle motion are both affected by tank size, water depth, and surface substrate (Gray et al. 2016), factors that would differ considerably between our laboratory environment and natural settings. Within our experimental tank, fish are exposed to an irregular acoustic field where sound pressure must drop to zero at the water-fibreglass wall boundary, but particle motion can be reflected back into the tank (Rogers et al. 2016; Zielinski et al. 2017). Additionally, fish were held in clear water with very low turbidity. Turbidity is likely to affect fish responses to stroboscopic stimuli (McIninch et al. 1987) and should be considered when evaluating site conditions for non-structural deterrent deployment.

The magnitudes of behavioural responses were fairly conserved across the acoustic, stroboscopic, and combined treatments. This similarity of behavioural responses across treatment type was unexpected as acoustic and stroboscopic stimuli impact different sensory systems. Due to the high intensity of the acoustic and strobe-light stimuli, and the small experimental tanks relative to fish size, common carp may have been expressing a strong response to each stimulus individually, leaving little room for additive responses when the stimuli were combined. Alternately, the addition of multiple deterrent stimuli may not increase common carp behavioural responses beyond the magnitude produced by each individual stimulus. In the second scenario, the benefit of integrating multiple deterrent technologies would be to increase system redundancy rather than to modulate the magnitude of response in target fishes. As acoustic stimuli are detected by the octavo-lateralis system and strobe-light stimuli are detected by the visual system, a comprehensive deterrent may be more robust across a greater range of environmental conditions than individual deterrents on their own (Noatch et al. 2012). Additional deterrent stimuli may also interact synergistically (Dennis et al. 2019). Taylor et al. (2005) found that the addition of bubble curtains to acoustic stimuli increased the sound-pressure gradient and further defined the acoustic field around the deterrent.

Non-structural deterrents are an emerging tool that may be used to limit the propagule pressure of invading common carp or other fishes. This study found that stroboscopic and acoustic stimuli produced short-term changes in common carp behaviour, but that the combination of both stimuli did not produce an additive behavioural response. Common carp durations of active movement increased during, and after stimulus exposure. The frequency of passes made across the deterrent varied according to treatment type. In the combined stroboscopic and acoustic treatment, fewer passes were made during the stimulus period than during the control or post-stimulus period. These behavioural changes are likely signs of negative phono- and photo-taxis, but the magnitude of response was

muted in comparison to other studies that provided greater stimulus refuge or were not limited by small-tank acoustics. Future studies should continue to investigate the behavioural responses of common carp and Asian carps to multimodal, non-structural deterrents within realistic field environments.

Acknowledgements

We would like to thank everyone who assisted in the data collection process; C. Bondy, C. Chandler, B. Doyle, D. Fillipi, M. Jarrah, A. McLean, and S. Muhammad. We also acknowledge those who assisted in the capture and maintenance of wild common carp; B. Aucoin, S. Best, B. Bomback, J. Boudreau, A. Buse, D. Campbell, M. Choi, K. Crawford, S. Epifani, C. Illes, D. Marson, A. Mehlenbacher, A. Price, E. Su, J. Seguin, and E. Ratajczyk. This research was funded by the Fisheries and Oceans Canada Asian Carp Program managed by B. Cudmore. Members of the Mandrak lab provided valuable support and advice. This study was conducted according to the Animal Use Protocol approved by the Animal Care Committee at Canada Centre for Inland Waters. Finally, the authors wish to acknowledge the anonymous reviewers who provided extensive feedback to improve this manuscript.

References

- Allen ML, Elbroch LM, Casady DS, Wittmer HU (2014) Seasonal variation in the feeding ecology of pumas (*Puma concolor*) in northern California. *Canadian Journal of Zoology* 92: 397–403, <https://doi.org/10.1139/cjz-2013-0284>
- Britton JR, Gozlan RE, Copp GH (2011) Managing non-native fish in the environment. *Fish and Fisheries* 12: 256–274, <https://doi.org/10.1111/j.1467-2979.2010.00390.x>
- Chumchal MM, Nowlin WH, Drenner RW (2005) Biomass-dependent effects of common carp on water quality in shallow ponds. *Hydrobiologia* 545: 271–277, <https://doi.org/10.1007/s10750-005-3319-y>
- Cudmore B, Mandrak NE, Dettmers JM, Chapman DC, Kolar CS (2011) Binational ecological risk assessment of bigheaded carps (*Hypophthalmichthys* spp.) for the Great Lakes basin. Department of Fisheries and Oceans Canadian Science Advisory Secretariat Research Document 2011/114 : 1–57
- Dennis CE, Zielinski D, Sorensen PW (2019) A complex sound coupled with an air curtain blocks invasive carp passage without habituation in a laboratory flume. *Biological Invasions* 21: 2837–2855, <https://doi.org/10.1007/s10530-019-02017-6>
- Dudgeon D, Arthington AH, Gessner MO, Kawabata ZI, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard AH, Soto D, Stiassny MLJ, Sullivan CA (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Reviews* 81: 163, <https://doi.org/10.1017/S1464793105006950>
- Flammang MK, Weber MJ, Thul MD (2014) Laboratory evaluation of a bioacoustic bubble strobe light barrier for reducing walleye escapement. *North American Journal of Fisheries Management* 34: 1047–1054, <https://doi.org/10.1080/02755947.2014.943864>
- Friard O, Gamba M (2016) BORIS: A free, versatile open-source event-logging software for video/audio coding and live observations. *Methods in Ecology and Evolution* 7: 1325–1330, <https://doi.org/10.1111/2041-210X.12584>
- Gallardo B, Clavero M, Sánchez MI, Vilà M (2016) Global ecological impacts of invasive species in aquatic ecosystems. *Global Change Biology* 22: 151–163, <https://doi.org/10.1111/gcb.13004>
- Gray MD, Rogers PH, Popper AN, Hawkins AD, Fay RR (2016) The effects of noise on aquatic life; “large” Tank acoustics: how big is big enough? *Advances in Experimental Medicine and Biology* 875: 423–426, <https://doi.org/10.1007/978-1-4419-7311-5>
- Haro A, Castro-Santos T, Noreika J, Odeh M (2004) Swimming performance of upstream migrant fishes in open-channel flow: a new approach to predicting passage through velocity barriers. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 1590–1601, <https://doi.org/10.1139/f04-093>
- Haymes GT, Patrick PH (1986) Exclusion of adult alewife, *Alosa pseudoharengus*, using low-frequency sound for application at water intakes. *Canadian Journal of Fisheries and Aquatic Sciences* 43: 855–862, <https://doi.org/10.1139/f86-105>
- Hocutt CH (1980) Behavioral barriers and guidance systems. Power plants: Effects on fish and shellfish behavior. Academic Press, New York, 183–205, <https://doi.org/10.1016/B978-0-12-350950-5.50013-3>
- Huntingford F, Andrew G, Mackenzie S, Morera D, Coyle SM, Pilarczyk M, Kadri S (2010) Coping strategies in a strongly schooling fish, the common carp *Cyprinus carpio*. *Journal of Fish Biology* 76: 1576–1591, <https://doi.org/10.1111/j.1095-8649.2010.02582.x>

- Jaewoo K, Doyle B, Mandrak N (2017) Electrodesation of freshwater fishes for the surgical implantation of transmitters. *Canadian Journal of Zoology* 95: 574–579, <https://doi.org/10.1139/cjz-2016-0205>
- Kim J, Mandrak NE (2017) Effects of strobe lights on the behaviour of freshwater fishes. *Environmental Biology of Fishes* 100: 1427–1434, <https://doi.org/10.1007/s10641-017-0653-7>
- Knudsen FR, Knapp SM, Enger PS, Sand O, Schreck CB (1997) Infrasound produces flight and avoidance responses in Pacific juvenile salmonids. *Journal of Fish Biology* 51: 824–829, <https://doi.org/10.1006/jfbi.1997.0486>
- Kojima T, Ito H, Komada T, Taniuchi T, Akamatsu T (2005) Measurements of auditory sensitivity in common carp *Cyprinus carpio* by the auditory brainstem response. *Fisheries Science* 71: 95–100, <https://doi.org/10.1111/j.1444-2906.2005.00935.x>
- Königson S, Fjälling A, Lunneryd SG (2002) Reactions in individual fish to strobe light. Field and aquarium experiments performed on whitefish (*Coregonus lavaretus*). *Hydrobiologia* 483: 39–44, <https://doi.org/10.1023/A:1021342520542>
- Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA, Lamberti G (2002) An ounce of prevention or a pound of cure: Bioeconomic risk analysis of invasive species. *Proceedings of the Royal Society B* 269: 2407–2413, <https://doi.org/10.1098/rspb.2002.2179>
- Lougheed VL, Crosbie B, Chow-Fraser P (1998) Predictions on the effect of common carp (*Cyprinus carpio*) exclusion on water quality, zooplankton, and submergent macrophytes in a Great Lakes wetland. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 1189–1197, <https://doi.org/10.1139/f97-315>
- Lovell JM, Findlay MM, Nedwell JR, Pegg M (2006) The hearing abilities of the silver carp (*Hypophthalmichthys molitrix*) and bighead carp (*Aristichthys nobilis*). *Comparative Biochemistry and Physiology, Part A* 143: 286–291, <https://doi.org/10.1016/j.cbpa.2005.11.015>
- Maes J, Turmpenny WH, Lambert DR, Nedwell JR, Parmentier A, Ollevier F (2004) Field evaluation of a sound system to reduce estuarine fish intake rates at a power plant cooling water inlet. *Journal of Fish Biology* 64: 938–946, <https://doi.org/10.1111/j.1095-8649.2004.00360.x>
- Mann D, Zhongmin L, Popper, N (1997) A clupeid fish can detect ultrasound. *Nature* 389: 341, <https://doi.org/10.1038/38636>
- McIninch SP, Hocutt CH (1987) Effects of turbidity on estuarine fish response to strobe lights. *Journal of Applied Ichthyology* 3: 97–105, <https://doi.org/10.1111/j.1439-0426.1987.tb00460.x>
- Murchy K, Vetter B, Brey M, Amberg J, Gaikowski M, Mensinger A (2016) Not all carp are created equal: Impacts of broadband sound on common carp swimming behavior. *Proceedings of Meetings on Acoustics* 27: 010032, <https://doi.org/10.1121/2.0000314>
- Murchy KA, Cupp AR, Amberg JJ, Vetter BJ, Fredricks KT, Gaikowski MP, Mensinger AF (2017) Potential implications of acoustic stimuli as a non-physical barrier to silver carp and bighead carp. *Fisheries Management and Ecology* 24: 208–216, <https://doi.org/10.1111/fme.12220>
- Nemeth RS, Anderson JJ (1992) Response of juvenile coho and chinook salmon to strobe and mercury vapor lights. *North American Journal of Fisheries Management* 12: 684–692, [https://doi.org/10.1577/1548-8675\(1992\)012<0684:ROJCAC>2.3.CO;2](https://doi.org/10.1577/1548-8675(1992)012<0684:ROJCAC>2.3.CO;2)
- Noatch MR, Suski CD (2012) Non-physical barriers to deter fish movements. *Environmental Review* 20: 71–82, <https://doi.org/10.1139/a2012-001>
- Pagnucco KS, Maynard GA, Fera SA, Yan ND, Nalepa TF, Ricciardi A (2015) The future of species invasions in the Great Lakes-St. Lawrence River basin. *Journal of Great Lakes Research* 41: 96–107, <https://doi.org/10.1016/j.jglr.2014.11.004>
- Parkos III JJ, Santucci, Jr. VJ, Wahl DH (2003) Effects of adult common carp (*Cyprinus carpio*) on multiple trophic levels in shallow mesocosms. *Canadian Journal of Fisheries and Aquatic Sciences* 60: 182–192, <https://doi.org/10.1139/f03-011>
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2018) nlme: Linear and Nonlinear Mixed Effects Models
- Popper AN (1972) Pure-Tone Auditory Thresholds for the Carp, *Cyprinus carpio*. *The Journal of the Acoustical Society of America* 52: 1714–1717, <https://doi.org/10.1121/1.1913305>
- Popper AN, Carlson TJ (1998) Application of sound and other stimuli to control fish behavior. *Transactions of the American Fisheries Society* 127: 673–707, [https://doi.org/10.1577/1548-8659\(1998\)127<0673:AOSAOS>2.0.CO;2](https://doi.org/10.1577/1548-8659(1998)127<0673:AOSAOS>2.0.CO;2)
- Popper AN, Fay RR (2011) Rethinking sound detection by fishes. *Hearing Research* 273: 25–36, <https://doi.org/10.1016/j.heares.2009.12.023>
- R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Reber A, Castella G, Christe P, Chapuisat M (2008) Experimentally increased group diversity improves disease resistance in an ant species. *Ecology Letters* 11: 682–689, <https://doi.org/10.1111/j.1461-0248.2008.01177.x>
- Ricciardi A, MacIsaac HJ (2011) Impacts of biological invasions on freshwater ecosystems. In: Richardson DM (ed), Fifty years of invasion ecology: The legacy of Charles Elton. Blackwell Publishing Ltd., West Sussex, UK, pp 211–224, <https://doi.org/10.1002/9781444329988.ch16>

- Richards NS, Chipps SR, Brown ML (2007) Stress response and avoidance behavior of fishes as influenced by high-frequency strobe lights. *North American Journal of Fisheries Management* 27: 1310–1315, <https://doi.org/10.1577/M06-239.1>
- Rogers PH, Hawkins AD, Popper AN, Fay RR, Gray MD (2016) The effects of noise on aquatic life; Parvulescu revisited: small tank acoustics for bioacousticians. *Advances in Experimental Medicine and Biology* 875: 423–426, <https://doi.org/10.1007/978-1-4419-7311-5>
- Ruebush BC, Sass GG, Chick JH, Stafford JD (2012) In-situ tests of sound-bubble-strobe light barrier technologies to prevent range expansions of Asian carp. *Aquatic Invasions* 7: 37–48, <https://doi.org/10.3391/ai.2012.7.1.005>
- Simmons MA, McKinstry CA, Cook CB, Tano DK, Faber DM, Francis S, Johnson RL, Simmons CS, Brown RS, Thorsten SL, LeCaire R (2004) Strobe light deterrent efficacy test and fish behavior determination at Grand Coulee Dam Third Powerplant Forebay. Springfield, VA, 2004, 139 pp, <https://doi.org/10.2172/962122>
- Sisler SP, Sorensen PW (2008) Common Carp and Goldfish discern conspecific identity using chemical cues. *Behaviour* 145: 1409–1425, <https://doi.org/10.1163/156853908785765881>
- Smith ME, Kane AS, Popper AN (2004) Acoustical stress and hearing sensitivity in fishes: does the linear threshold shift hypothesis hold water? *Journal of Experimental Biology* 207: 3591–3602, <https://doi.org/10.1242/jeb.01188>
- Sullivan BG, Wilson ADM, Gutowsky LFG, Patrick PH, Sills M, Cooke SJ (2016) The behavioral responses of a warmwater teleost to different spectra of light-emitting diodes. *North American Journal of Fisheries Management* 36: 1000–1005, <https://doi.org/10.1080/02755947.2016.1141123>
- Taylor RM, Pegg M, Chick JH (2005) Response of bighead carp to a bioacoustic behavioural fish guidance system. *Fisheries Management and Ecology* 12: 283–286, <https://doi.org/10.1111/j.1365-2400.2005.00446.x>
- Vetter BJ, Cupp AR, Fredricks KT, Gaikowski MP, Mensinger AF (2015) Acoustical deterrence of silver carp (*Hypophthalmichthys molitrix*). *Biological Invasions* 17: 3383–3392, <https://doi.org/10.1007/s10530-015-0964-6>
- Vetter BJ, Murchy KA, Cupp AR, Amberg JJ, Gaikowski MP, Mensinger AF (2017) Acoustic deterrence of bighead carp (*Hypophthalmichthys nobilis*) to a broadband sound stimulus. *Journal of Great Lakes Research* 43: 163–171, <https://doi.org/10.1016/j.jglr.2016.11.009>
- Vetter BJ, Rogers LS, Mensinger AF (2019) The effect of light stimuli on dark-adapted visual sensitivity in invasive silver carp *Hypophthalmichthys molitrix* and bighead carp *H. nobilis*. *Journal of Fish Biology* 95: 1–7, <https://doi.org/10.1111/jfb.13880>
- Vitousek PM, D'Antonio CM, Loope LL, Rejmanek M, Westbrooks R (1997) Introduced species: A significant component of human-caused global change. *New Zealand Journal of Ecology* 21: 1–16
- Vitule JRS, Freire CA, Simberloff D (2009) Introduction of non-native freshwater fish can certainly be bad. *Fish and Fisheries* 10: 98–108, <https://doi.org/10.1111/j.1467-2979.2008.00312.x>
- Weber MJ, Brown ML (2009) Effects of common carp on aquatic ecosystems 80 years after “Carp as a Dominant”: ecological insights for fisheries management. *Reviews in Fisheries Science* 17: 524–537, <https://doi.org/10.1080/10641260903189243>
- Wittmann ME, Cooke RM, Rothlisberger JD, Lodge DM (2014) Using structured expert judgment to assess invasive species prevention: Asian carp and the Mississippi-Great Lakes hydrologic connection. *Environmental Science & Technology* 48: 2150–2156, <https://doi.org/10.1021/es4043098>
- Zielinski DP, Voller VR, Svendsen JC, Hondzo M, Mensinger F, Sorensen P (2014) Laboratory experiments demonstrate that bubble curtains can effectively inhibit movement of common carp. *Ecological Engineering* 67: 95–103, <https://doi.org/10.1016/j.ecoleng.2014.03.003>
- Zielinski DP, Sorensen PW (2017) Silver, bighead, and common carp orient to acoustic particle motion when avoiding a complex sound. *PLoS ONE* 12: 1–20, <https://doi.org/10.1371/journal.pone.0180110>