

ARTICLE

Detering the Movement of an Invasive Fish: Individual Variation in Common Carp Responses to Acoustic and Stroboscopic Stimuli

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Abstract

Biological invasions erode ecosystem functioning and occur more frequently in freshwater ecosystems than in terrestrial environments. Nonphysical deterrents may be used to limit invasive fish dispersal, without altering the stream-flow or connectivity of a watershed. Little is currently known about how behavioral variation among individuals may affect the efficacy of a deterrent, although such variation has been shown to affect fish dispersal in other contexts, such as range expansion. Furthermore, deterrent effectiveness is rarely tested when fish are motivated to disperse. Across a control, CO₂, and CO₂ + deterrent treatment, we quantified the avoidance response of invasive Common Carp *Cyprinus carpio* to a combined acoustic-stroboscopic deterrent. In the CO₂ treatment, we motivated individuals to enter a novel environment by degrading the home chamber of a choice arena with a continuous infusion of CO₂. In the CO₂ + deterrent treatment we introduced acoustic and stroboscopic stimuli to delay the departure of the fish and evaluate the efficacy of the deterrent. Finally, we tested a subset of the fish multiple times to determine whether they consistently responded to the same concentration of CO₂. We found that the acoustic and stroboscopic deterrent could detain the fish in an increasingly unfavorable environment. Common Carp took only 195 and 131 s, respectively, to swim between the chambers during the control and CO₂ treatment but took an average of 596 s in the CO₂ + deterrent treatment. High CO₂ concentrations in the CO₂ + deterrent treatment led to most fish eventually dispersing toward the deterrent stimuli. Avoidance behavior varied widely within the CO₂ + deterrent treatment, and Common Carp expressed repeatable differences in the tank-inflow CO₂ concentrations that were observed during chamber departure. Such interindividual variation in deterrent avoidance indicates that some individuals within a given species are more likely to move past a deterrent than others.

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Received June 30, 2021; accepted October 6, 2021

Biological invasion rates have increased over the past several decades due to anthropogenic influences (Ricciardi 2007; Seebens et al. 2017) and now represent a significant threat to the stability of global biodiversity (Britton et al. 2011). Freshwater ecosystems have received proportionately more invasive species than terrestrial ecosystems (Vitousek et al. 1997; Ricciardi and MacIsaac 2011), decreasing their productivity (Gallardo et al. 2016) and eroding their ecological resilience and resistance to environmental change (Downing et al. 2012). Preventing a species introduction is far more effective at minimizing ecological disruptions than mitigating the adverse effects of a species once it has been introduced (Leung et al. 2002; Lodge et al. 2006, 2016). Within freshwater ecosystems, barriers that prevent the movement of an invasive species can be valuable tools for conservation, as they can limit range expansions (Taft 2000; Noatch and Suski 2012). However, structural deterrents (e.g., dams or screens) are not always feasible due to ecological or economic considerations such as requirements for unimpeded stream flow or native fish passage (Noatch and Suski 2012; Wittmann et al. 2014).

Nonphysical deterrents can avoid these problems while still slowing or stopping the dispersal of invasive species into novel environments. Furthermore, while attaining perfect species specificity may not be feasible, many nonphysical deterrents may target species of interest to a greater extent than other native species (Bzonek et al. 2021b). Acoustic and strobe-light stimuli are two emerging deterrents that have shown varying promise under certain site- and species-specific conditions (Brown 2000; Noatch and Suski 2012; Vetter et al. 2015; Zielinski and Sorensen 2017; Dennis and Sorensen 2020a). These stimuli could be deployed in primary dispersal pathways, such as navigational locks and canals (USACE 2019) to limit the dispersal of invasive freshwater fishes. If deterrents can reliably produce avoidance responses in such pathways, further upstream dispersal may be halted (Noatch and Suski 2012).

Sound has many characteristics that make it a promising species-specific deterrent. Underwater sound can travel at high speeds, produce a directional signal, and remain unimpeded by turbidity or ambient light levels (Popper and Carlson 1998). Furthermore, species with specialized hearing anatomy can be targeted with acoustic deterrents. Species in the superorder Ostariophysii have a Weberian apparatus, a specialized connection between the inner ear and swim bladder (Popper and Carlson 1998). This connection allows ostophysian fish to perceive sound pressure waves in addition to perceiving particle motion (Popper and Fay 1993). By sensing both components of sound, these species can hear across a greater range of frequencies at a lower sound intensity than others (Lovell et al. 2006; Popper and Fay 2011). All of the species in the order Cypriniformes have this connection, including three

invasive species of high conservation concern in North America, Common Carp *Cyprinus carpio*, Silver Carp *Hypophthalmichthys molitrix*, and Bighead Carp *H. nobilis*. All are highly invasive and have had detrimental effects in many waterbodies (Weber and Brown 2009; Solomon et al. 2016). As a result, the use of acoustic deterrents to limit the dispersal of sound-pressure-sensitive carp is receiving intense interest (Vetter et al. 2015, 2017a; Murchy et al. 2017; Zielinski and Sorensen 2017; Dennis and Sorensen 2020b). Acoustic deterrents have been found to produce a greater avoidance response in species with specialized hearing anatomy than in species without specialized hearing anatomy (Bzonek et al. 2021b).

Light is another species-specific stimulus that can act as a nonphysical deterrent to fish movement (Brown 2000; Schilt 2007; Noatch and Suski 2012). Light is a primary source of information for many teleosts, and there is wide variation in sensory capabilities among species (Lin et al. 2017), which may allow it to act as a species-specific nonphysical deterrent. Strobe lights are the most commonly used light stimuli used to deter fish (Richards et al. 2007), as they may be less susceptible to habituation due to the discontinuous nature of the signal (Popper and Carlson 1998). However, Dennis and Sorensen (2020b) noted that a high-intensity constant light produced a greater avoidance response than a strobe light in Bighead Carp. Vetter et al. (2019) suggested that strobe lights may temporarily impair vision in Common Carp, but they recommend further behavioral studies to evaluate the effect of strobe lights on carp movement. Sullivan et al. (2016) found that Largemouth Bass *Micropterus salmoides* were repelled by strobe lights across a wide range of light wavelengths and pulsing frequencies. A number of studies had some measure of success in the use of stroboscopic light as a component of or as a “stand-alone,” nonphysical deterrent (Nemeth and Anderson 1992; Brown 2000; Königson et al. 2002; Richards et al. 2007; Kates et al. 2012; Sullivan et al. 2016).

Significant knowledge gaps remain in the development of nonstructural deterrents. For example, consistent behavioral variation among individuals of the same species is known to influence spatial use and dispersal (Wilson and McLaughlin 2007; Chapman et al. 2011; Harrison et al. 2015; Myles-Gonzalez et al. 2015), but there has been limited investigation of the role of such variation in deterrent efficacy (Bzonek et al. 2021a). Additionally, while acoustic and stroboscopic deterrents have shown significant success in laboratory settings (Vetter et al. 2017b; Dennis and Sorensen 2020b), few studies have observed how fish interact with a deterrent when they are motivated to emigrate from their current environment or immigrate to a new one (but see Cupp et al. 2017). We attempted to address such knowledge gaps in this study. To assess the repeatability of interindividual behavioral

variation, we conducted repeated trials on a subset of individuals. To address fish motivation, we attempted to push individuals out of the “home chamber” of a two-chamber “shuttle box” by progressively degrading its environment with increasing CO₂. Carbon dioxide was used to reduce environmental quality, as past studies with similar choice-arena environments have used CO₂ to motivate fish to leave their occupied chamber (Kates et al. 2012; Dennis et al. 2015, 2016; Cupp et al. 2017; Tucker et al. 2018).

The goal of this study was to determine whether acoustic and stroboscopic deterrents are effective at blocking the passage of Common Carp in a choice arena. We also investigated whether individuals had meaningful differences from each other in response to the deterrents. We used CO₂ as a motivator and a response metric to assess deterrent efficacy. We made three predictions. First, we predicted that adding CO₂ into the home chamber of a choice arena would motivate Common Carp to swim into an adjoining novel chamber. Second, we predicted that activating the acoustic and stroboscopic deterrents in the novel chamber would cause the fish to persist longer within elevated CO₂ concentrations to avoid the deterrents. Finally, we predicted that there would be consistent differences among individuals in their avoidance responses across repeated trials.

METHODS

Experimental animals.—The experimental procedures were conducted with approval from the University of Toronto University Animal Care Committee (AUP 20011687). Seventy-six juvenile Common Carp (mass = 7.52 ± 1.70 g; fork length = 75.52 ± 6.75 mm; mean \pm SD) were obtained from Osage Catfisheries, Inc. (Osage Beach, Missouri) and transported to the University of Toronto Scarborough aquatics vivarium. Prior to the trials, the fish were anaesthetized in a solution of 6 mg/L eugenol, diluted with 49 mg/L ethanol, and outfitted with an external tag (FTF-69; Floy tag; Seattle) for identification. The Common Carp were acclimated in the vivarium for at least 23 d posttransport and 16 d posttagging before running trials. The individuals were housed in two 700-L living streams (LS-700; Frigid Units, Inc., Toledo, Ohio) and one 600-L round tank (SS Filtration and Development Co. Ltd., Oakville, Ontario) at $20.8 \pm 1.0^\circ\text{C}$. The fish were fed ~2% biomass daily (3-mm sinking pellets, New Life International, Homestead, Florida). Following the data collection period, the remaining fish were euthanized by an overdose of eugenol (18 mg/L) diluted in ethanol (150 mg/L).

Experimental design.—The Common Carp were randomly assigned to undergo a single trial ($n = 55$) or repeated trials ($n = 21$). The trials were randomly divided among three treatments: a control treatment, a CO₂ treatment, and a CO₂ + deterrent treatment. In the control

treatment, an aerator pumped ambient air into both the home and novel chambers through their respective buffer tanks. In the CO₂ treatment, CO₂ was pumped into the home chamber, motivating individuals to move into the novel chamber that was oxygenated with ambient air. In the CO₂ + deterrent treatment, CO₂ was again pumped into the home chamber. Additionally, acoustic and stroboscopic deterrents were activated in the novel chamber to behaviorally detain the fish in the home chamber.

The repeatability of movement behavior was assessed through repeated trials during which individuals would undergo one trial a day for three consecutive days. Each fish that was used in the repeated trials was assigned to the same treatment for all of the trials. Only the first trial of each repeated-trial challenge was included in the single-trial analysis.

The trials were conducted in a modified shuttle-box choice arena (Loligo, Inc., Hobro, Denmark) following the procedures that are described by Kates et al. (2012). The arena was comprised of two large chambers (80.5 cm in diameter) with a connecting channel (20.2 \times 12.6 cm). Each chamber had independent water circulation and was connected to an external water buffer tank where CO₂ concentration was controlled. The fish were acclimated in the home chamber. The CO₂ concentration of the home chamber was modified by bubbling CO₂ into the chamber's respective buffer tank (Figure 1). Compressed gas (CD 50, Praxair, 99.5% CO₂) was continuously pumped into the buffer tank at 1 psi (6,895 Pa), which slowly increased the concentration of CO₂ over time. Ambient air was bubbled into the novel chamber. The mirrored water circulation of the two chambers minimized water exchange across the connecting channel but still allowed for fish to leave the occupied chamber to the novel chamber (Serrano et al. 2010). We defined a fish to have left the home chamber once its body had passed the halfway line of the connecting channel. The fish were tracked via live feed of an overhead webcam (C270 HD Webcam, Logitech, Newark, California) to minimize observational disturbance.

To measure the water chemistry of the choice arena, water samples were collected immediately after the trial from the center of the home chamber and near the home chamber inflow port. Water chemistry was measured at the two locations to determine whether there was spatial variation in CO₂ concentrations throughout home chamber. A preliminary investigation determined that water chemistry did not differ across collection location in the control treatment. Total alkalinity (mg/L CaCO₃) and CO₂ (mg/L CO₂) were calculated from the water samples with digital titration kits (Hach Company, Loveland, Colorado, USA; Titrator Model 16900; CO₂ Kit 2272700 and total alkalinity Kit 2271900; Kates et al. 2012; Dennis et al. 2015). The partial pressure of CO₂ ($p\text{CO}_2$) was estimated with alkalinity and pH using the CO₂calc app

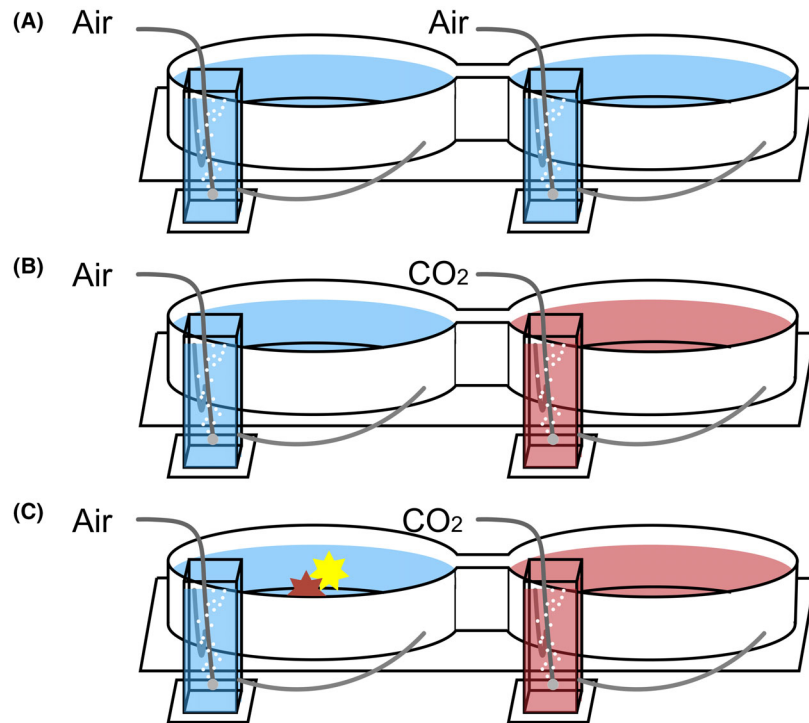


FIGURE 1. Experimental design for (A) control, (B) CO₂, and (C) CO₂ + deterrent treatments. Common Carp were acclimated in the home (right) chamber and free to travel to the novel (left) chamber during a trial. The red and yellow stars represent the acoustic and strobe-light stimuli. The blue water represents oxygenated water, bubbled with ambient air, and the red water represents water bubbled with carbon dioxide.

(Robbins et al. 2010). The choice arena was drained and refilled with water that was dechlorinated by carbon filtration between each trial.

Deterrent stimuli.—The acoustic stimulus was a 3-s loop combining a 200–1400 Hz sweep, a 200–1500 Hz band sweep, and a recording of a 4-stroke 50 hp outboard motor. This was the same stimulus that was used in Bzonek et al. (2020), Bzonek et al. (2021a), and Bzonek et al. (2021b), where we used the same stimulus across multiple studies to allow for direct comparisons between lab and field contexts. The stimulus was emitted from the speaker with a sound pressure level of 142 decibels (dB) re 1 μ Pa at 1 m from the source (Figures S1, S2 available in the Supplement in the online version of this article). Similar stimulus sound-pressure levels have been used effectively for cyprinids in other acoustic-deterrent studies (Vetter et al. 2015; Zielinski and Sorensen 2017). The combined tones of the acoustic stimulus overlapped in frequency with the hearing sensitivity of Common Carp (Popper 1972). The audio was played through an underwater speaker (Lubell LL916H, Lubell Labs, Inc., Columbus, Ohio). The outboard motor component of the stimulus was recorded 1 m away from the signal with a hydrophone (M8E51-C35, sensitivity at 250 Hz = -164 dBV (decibel voltage ratio), GeoSpectrum Technologies, Inc., Dartmouth, Nova Scotia) connected to a JASCO Ocean Sound

Meter (JASCO, Halifax, Nova Scotia). The stroboscopic stimulus was a white light (Figure S3) that was produced with a 110 V random flashing underwater SeeBrite strobe light that operated with a frequency of 1–20 Hz (Seebrite LED, I.A.S. Ltd., Vancouver). The strobe light produced $51 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^2$ of radiation between 400 and 700 nm at a distance of 1 m from the source (measured by LP-80, AccuPAR, Pullman, Washington). The deterrents remained in the novel chamber across all three treatments.

In each trial, an individual fish was placed in the choice arena to acclimate for 60 min, during which time ambient air was bubbled into both buffer tanks. After acclimation, a gate between the chambers was raised, allowing the individual to leave the home chamber. The CO₂ and acoustic/stroboscopic deterrents were activated immediately before lifting the gate. Latency to leave was measured as the duration of time (s) between lifting the gate and the fish leaving the home chamber. If the fish took longer than 20 min to leave, the trial was ceased and a time of 20 min was assigned to the trial (3.7% of trials; McLean and McLaughlin 2018). If the fish lost equilibrium (0.9% of trials) or was excessively gulping air (9.3% of trials), the trial was terminated to minimize distress and the termination time was applied to the latency to leave (Kates et al. 2012; Dennis et al. 2015). The termination time was applied to the latency time, as the fish were free to leave

at any time before displaying such erratic behavior, but the capacity of the fish to depart would be impaired after displaying such behaviors.

Choice-arena profiles.—The acoustic and stroboscopic stimuli were defined within the choice arena. Root mean square sound pressure (Figure 2A), peak light intensity (Figure 2B), and mean water velocity (Figure S4A) were measured at 26 points on a grid of 15-cm spacing within

the occupied chamber and connecting channel. Measurements at each grid point were taken for 0.5 min and mapped using the inverse distance weighting function in ArcGIS (ArcGIS Desktop, Environmental Systems Research Institute, 10.3, Redlands, California). Sound pressure was recorded by two hydrophones at a sampling rate of 128k Hz (M8E51-C0, sensitivity at 250 Hz = -199 dBV; M8E51-C35, sensitivity at 250 Hz = -164 dBV,

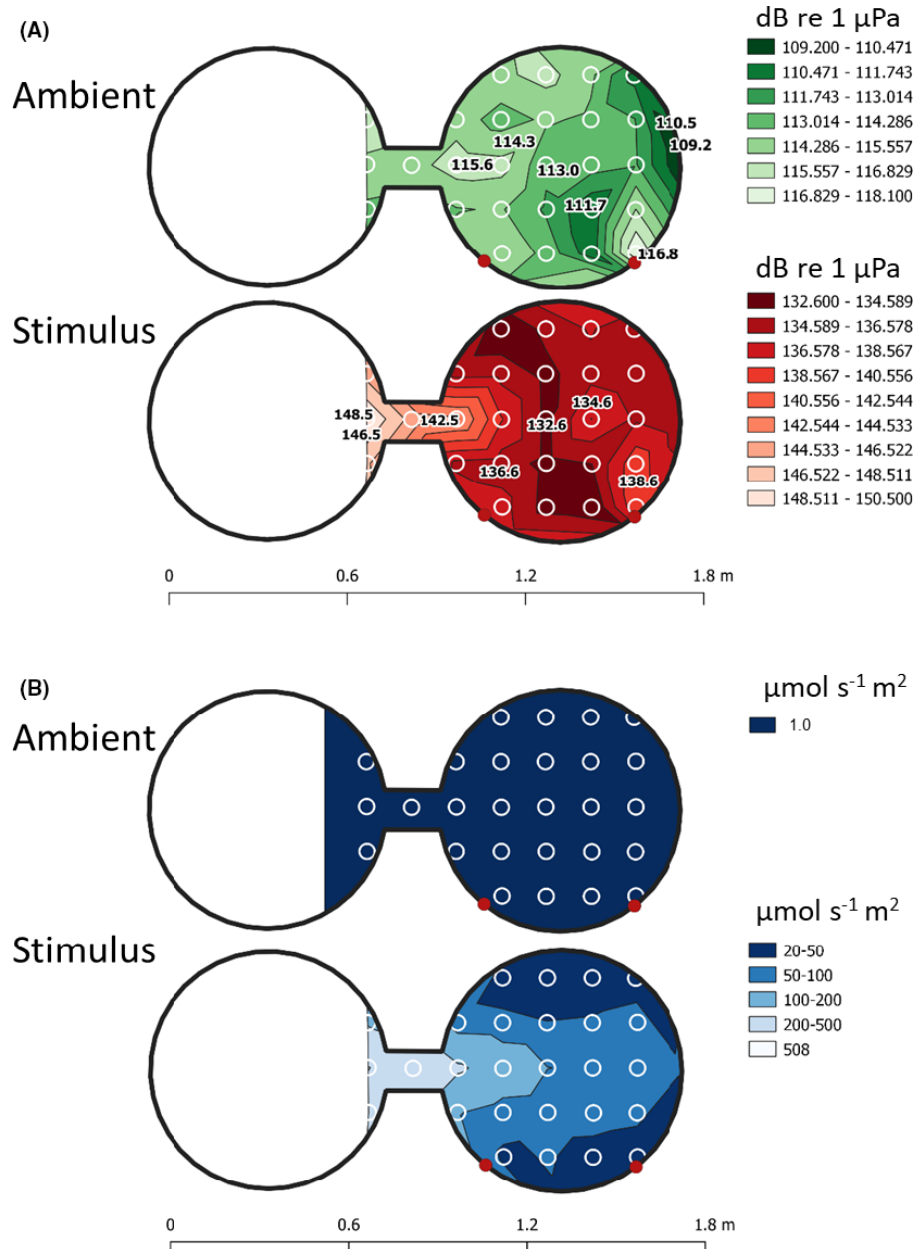


FIGURE 2. (A) Sound and (B) light profiles of the occupied chamber and connecting channel under ambient and stimulus conditions. The root mean square sound pressure ranged from 109 to 118 dB re 1 μ Pa under ambient conditions and 132 to 150 dB re 1 μ Pa during the stimulus treatments. Peak illuminance was 1 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^2$ under ambient conditions and ranged 23–508 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^2$ during the CO_2 + opposition treatments. No data were collected in the white region due to obstructions that were caused by the acoustic and strobe-light apparatus. The white rings indicate where the data measurements were taken.

GeoSpectrum Technologies, Inc.) connected to a JASCO Ocean Sound Meter (JASCO). The higher sensitivity hydrophone (M8E51-C0) was used to record ambient sound pressures, and the lower sensitivity hydrophone (M8E51-C35) was used to record the louder stimulus sound pressures. Peak light radiation ($\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^2$) was measured under ambient and stimulus conditions with a PAR meter that was sensitive to frequencies between 400 and 700 nm (LP-80, AccuPAR, Pullman, Washington). Water velocity was measured using an acoustic doppler velocimeter (SonTec Flow Tracker2 Handheld-ADV; San Diego, California, USA).

Statistical analysis.— In the single-run trials, latency to leave and departing CO_2 concentrations (measured at tank center and tank inflow) were compared across control ($n = 18$), CO_2 ($n = 18$), and CO_2 + deterrent ($n = 20$) treatments with nonparametric Kruskal–Wallis tests. A Kruskal–Wallis test was used because the data did not meet the assumptions of normality (Shapiro–Wilk test, visual inspection of residuals). To account for the multiple dependent variables, a Holm–Bonferroni correction was applied. Adjusted P -values are presented in the statistical analyses. Post hoc analyses were conducted with a Tukey and Kramer test using the PMCMR package (Pohlert 2014). The frequency of excessive gulping observed across treatments was compared with a chi-square test.

To determine whether the Common Carp that completed repeated trials expressed consistent differences among individuals, repeatability was measured for the behavioral metrics of latency to leave, CO_2 center, and CO_2 inflow. Treatment type was included as a fixed effect, and fish identity was included as a random effect (Dingemans and Dochtermann 2013). Adjusted R values were constructed with the package rptR (Stoffel et al. 2017). Repeatability ranges from 0 to 1 and is the ratio of the variation among individuals divided by the total variation (both among and within individuals; Bell et al. 2009; Wolak et al. 2012; Stoffel et al. 2017). Repeatability is high when responses vary widely among individuals but each individual behaves consistently over time. To check for the potential habituation of Common Carp to repeated handling and trials, an ANCOVA was constructed with treatment type as a factor and trial number as a covariate. All of the statistical analyses were conducted with the statistical software R (R Core Team 2018).

RESULTS

The presence of the acoustic and stroboscopic deterrents significantly altered the behavior of the Common Carp. Latency to depart the home chamber differed across the three treatments (Kruskal–Wallis test: $\text{df} = 2$, $\chi^2 = 19.8$, $P < 0.001$). Individuals took significantly longer to leave the home chamber during the CO_2 + deterrent treatment

than during the control treatment (Tukey and Kramer post hoc; $P < 0.01$) or CO_2 treatment ($P < 0.001$). The control treatment did not significantly differ from the CO_2 treatment ($P = 0.77$). Most (61%) of the Common Carp left in less than a minute during the control and CO_2 treatments (Figure 3A), but latency to leave was over twice as long in the CO_2 + deterrent treatment (Table 1). Some of the fish never left and remained in the home chamber with increasing CO_2 until they displayed excessive gulping or loss of equilibrium. Such erratic, hypercapnic behavior occurred more frequently ($\chi^2 = 14.0$, $\text{df} = 2$, $P < 0.001$) in the CO_2 + deterrent treatment (23% of trial) than in the control (0%) or CO_2 treatment (3%). If the trials with excessive gulping or loss of equilibrium are removed, the new results do not meaningfully change (Kruskal–Wallis test: $\text{df} = 2$, $\chi^2 = 19.3$, $P < 0.001$).

The prolonged latency to leave in the CO_2 + deterrent treatment led to significant differences in departure CO_2 concentrations across the three treatments. These differences occurred at both the chamber center ($\text{df} = 2$, $\chi^2 = 14.4$, $P < 0.001$) and near the chamber inflow ($\text{df} = 2$, $\chi^2 = 29.1$, $P < 0.001$; Figures 3, S5). The CO_2

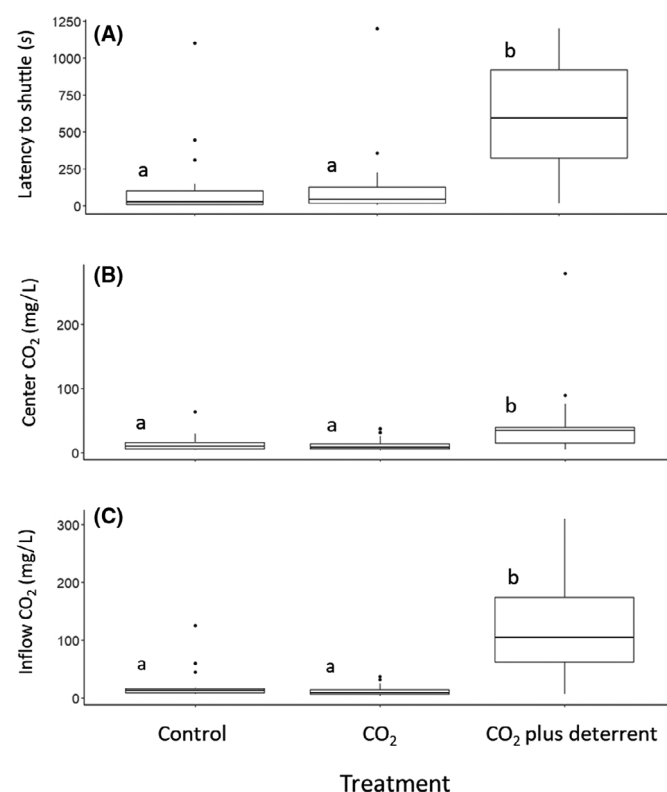


FIGURE 3. Average (A) latency to leave the home chamber and departing CO_2 concentrations at the (B) tank center and (C) tank inflow port. For all dependent variables, the CO_2 + deterrent treatment produced significantly higher values than the control or CO_2 treatments. Each box depicts the median, 25th, and 75th percentile value.

TABLE 1. Summary of trial data for latency to depart the home chamber and departing CO₂ concentrations at the center and at the inflow port of the home chamber. The values were compared across control, CO₂, and CO₂ + deterrent treatments. The pCO₂ values were estimated from alkalinity and pH with the CO₂calc app (Robbins et al. 2010). The values are presented as mean ± SD.

Treatment	Latency to leave (s)	Tank center			Tank inflow		
		CO ₂ (mg/L)	pCO ₂ (µatm)	pH	CO ₂ (mg/L)	pCO ₂ (µatm)	pH
Control	195 ± 377	11.9 ± 9.7	3,866 ± 2,288	7.1 ± 0.3	12.1 ± 9.6	3,806 ± 2,357	7.1 ± 0.3
CO ₂	131 ± 270	14.0 ± 14.1	4,471 ± 3,930	7.1 ± 0.3	22.1 ± 30.5	5,124 ± 6,872	7.2 ± 0.4
CO ₂ + deterrent	596 ± 367	44.5 ± 60.0	11,444 ± 13,468	6.7 ± 0.4	126.7 ± 88.0	20,565 ± 14,517	6.4 ± 0.4

concentrations were higher in the CO₂ + deterrent treatment than the control treatment (Tukey and Kramer post hoc; chamber center: $P < 0.01$; chamber inflow: $P < 0.001$) and CO₂ treatment (chamber center: $P < 0.01$; chamber inflow: $P < 0.001$). The control treatment did not differ from the CO₂ treatment in CO₂ concentrations (chamber center: $P = 0.89$; chamber inflow: $P = 0.42$). The chamber inflow had higher CO₂ concentrations than the chamber center (Table 1), and the trials with a higher CO₂ concentration had a larger difference between the tank-center and tank-inflow concentrations (Figure S6).

Some individuals consistently left the home chamber at lower CO₂ concentrations than others. The tank-inflow CO₂ concentrations that were observed during departure expressed significant repeatability ($R = 0.33$, $CI = [0.04, 0.60]$; Figure 4). However, avoidance behavior was not

repeatable for latency to leave ($R = 0.20$, $CI = [0, 0.49]$), or for tank-center CO₂ concentrations during departure ($R = 0.22$, $CI = [0, 0.52]$). Common Carp did not express habituation to the repeated trials, as trial number did not significantly influence latency to leave (ANCOVA $F_{2, 57} = 0.02$, $P = 0.878$).

DISCUSSION

Our goal was to quantify how acoustic and stroboscopic deterrents altered the movement behavior of invasive Common Carp. We found strong evidence that these combined deterrents can deter movement in a controlled environment. Our first prediction, that increasing environmental CO₂ would motivate Common Carp to leave their home chamber was not supported; in both the control and

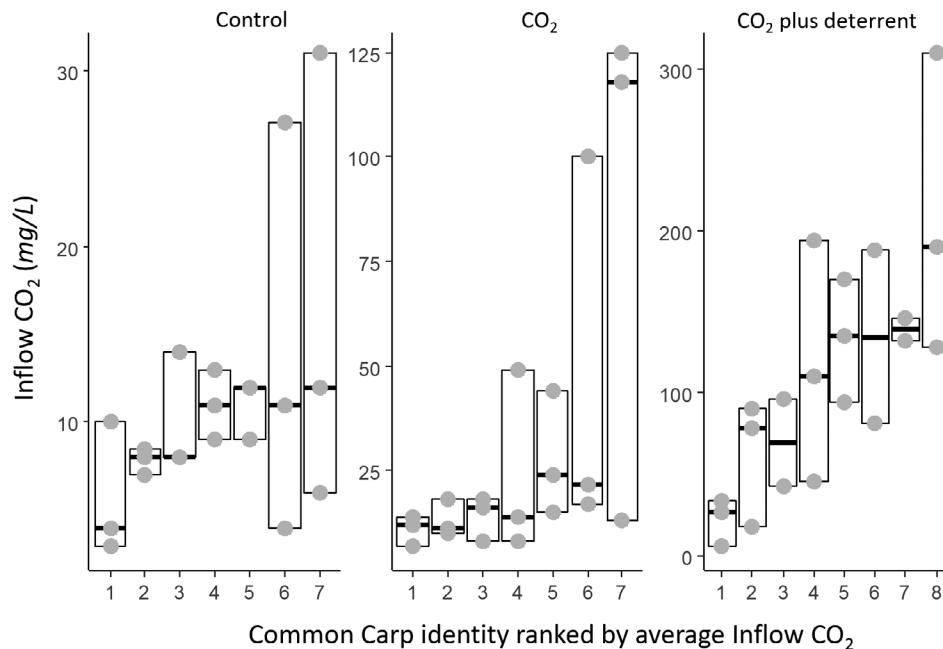


FIGURE 4. Repeatable Common Carp avoidance responses to inflow CO₂ concentrations. The box plots represent the CO₂ concentrations that were observed when the individuals departed the home chamber. Each box plot represents a unique fish, with box plots ranked by mean CO₂ concentrations. Each treatment used different groups of fish. The trials were repeated once per day for three consecutive days and individuals were randomly assigned to the control ($n = 7$), CO₂ ($n = 7$), or CO₂ + deterrent ($n = 8$) treatment. Within treatments, individuals consistently differed in the CO₂ concentrations that were required to induce home chamber departure.

CO₂ treatments, the fish moved to the novel chamber before CO₂ was meaningfully elevated. Our second prediction, that Common Carp exhibited an avoidance response to acoustic and stroboscopic deterrents, was strongly supported. Individuals were deterred from leaving an increasingly unfavorable environment when the acoustic and stroboscopic deterrents were active. Finally, our third prediction, that individuals would perform consistently across trials and that there would be interindividual variation of responses, was supported. The inflow CO₂ concentrations that were required to motivate the Common Carp to leave the occupied chamber were consistent within individuals and differed widely among individuals.

Limitations and Assumptions

This study intended to motivate fish to depart the home chamber in the CO₂ treatment and then assess the deterrent's efficacy in motivated fish with the CO₂ + deterrent treatment. Common Carp quickly departed the home chamber in both the control and CO₂ treatments, making it difficult to determine the significance of CO₂ as a tool to motivate fish departure. However, past studies have consistently shown that elevated CO₂ concentrations will motivate fish to leave their occupied chamber (Kates et al. 2012; Dennis et al. 2015, 2016; Cupp et al. 2017; Tucker et al. 2018; Tucker and Suski 2019). The agreement among past studies indicates that as CO₂ concentrations increased in the CO₂ + deterrent treatment, individuals likely experienced a greater impulse to leave the home chamber.

Additionally, this study did not observe acoustic and stroboscopic deterrents in isolation but, rather, deterrents in opposition to elevated CO₂. Exposure to CO₂ may have altered fish avoidance behavior, as CO₂ has been observed to alter freshwater fish behavior in other contexts, such as movement velocity and alarm cue response (Tix et al. 2017a, 2017b). Previous acoustic and stroboscopic deterrent studies have deployed the same stimuli toward Common Carp, without the addition of CO₂, and the fish were observed to express mild avoidance responses in both lab (Bzonek et al. 2020) and field (Bzonek et al. 2021a, 2021b) trials.

Single-Trial Challenge

Individuals that were subjected to the acoustic and stroboscopic deterrents were compelled to remain in their original environment, even as conditions became increasingly unsuitable over time. In fact, the deterrents increased fish latency to depart threefold, and multiple individuals never advanced toward the novel chamber, instead remaining within the home chamber until they lost equilibrium due to the high CO₂ concentrations. These results highlight that within a laboratory environment, combined acoustic and stroboscopic deterrents can produce a strong avoidance response that limits the passage of Common Carp.

However, it is worth noting that after significant environmental degradation most individuals could be compelled to interact with the deterrents. This was done in the CO₂ + deterrent treatment by producing a hypercapnic environment that could only be escaped by advancing toward the acoustic and stroboscopic deterrents. Under these conditions, 26 of 34 individuals eventually did advance toward the deterrents. One implication of these findings is that nonphysical deterrents that rely on behavioral-based avoidance (i.e., acoustic, stroboscopic) will produce a less robust response than stimuli that can alter environmental conditions beyond the physiological tolerances of target species (e.g., CO₂, electricity). However, if the goal of behaviorally based deterrents is only to deflect fish movement (Zielinski and Sorensen 2016) or deter the fish for short periods (e.g., lock operation; Cupp et al. 2017), then they would not need to produce the same response strength as physiology-altering deterrents.

During the control and CO₂ treatments, the fish typically left the occupied chamber in under 1 min. Due to the rapid departure times, CO₂ did not have time to build up. Our study observed fish departure from the occupied chamber at ~22 mg/L, whereas previous studies that did not use a lift gate found chamber departure at >100 mg/L CO₂. Thus, it is unlikely that the early departing response in the CO₂ treatment was an avoidance behavior, as CO₂ levels were low compared with those of other studies (Kates et al. 2012; Dennis et al. 2015; Tucker et al. 2018). Instead, the immediate chamber departure in both the control and CO₂ treatments may have been an exploratory response to the novel environment (Wilson and Godin 2009) that became available once the gate was lifted.

Repeated-Trial Challenge

Common Carp expressed repeatable interindividual differences in the inflow CO₂ concentration that was necessary to motivate individuals to leave the home chamber. Repeatability indicates that individuals are behaviorally consistent and that differences are maintained between individuals over time (Bell et al. 2009). Here, some Common Carp consistently left at higher inflow CO₂ concentrations than others. Our findings support past choice-arena studies that describe high interindividual variation (~threefold differences within treatments; Kates et al. 2012; Dennis et al. 2016; Cupp et al. 2017) and repeatability (Tucker and Suski 2019) in the CO₂ concentrations that are required to induce shuttling in other fish species.

Variation in metabolic phenotype or physiological condition could drive interindividual variation in the level of CO₂ that is required to produce a given behavioral response. Hasler et al. (2017) found that the tolerance to CO₂ of Largemouth Bass was repeatable and correlated with a measure of anaerobic swimming capacity. Alternately, if there is a spectrum of behavioral temperament

(Réale et al. 2007), fish would require differing levels of CO₂-induced motivation to leave the home chamber. Behavioral temperament has not yet been found to influence fish avoidance to CO₂ within a choice arena (Tucker et al. 2018; Tucker and Suski 2019). The final explanation for consistent differences in avoidance may be differing spatial use within the home chamber.

Choice-Arena Environment

This is the first study that measured both tank-inflow and tank-centre CO₂ concentrations; previous studies have monitored only inflow CO₂ (Kates et al. 2012; Dennis et al. 2015). Carbon dioxide concentrations differed dramatically between the center and inflow regions of the occupied chamber (Figure S6). As CO₂ concentrations increased, the difference between chamber-center and chamber-inflow concentrations also increased. Thus, as trial duration and concomitant CO₂ concentrations increase, the differences in concentration between the tank center and tank inflow were exacerbated. This indicates that CO₂ is not thoroughly mixing throughout the chamber, and an individual's location within the choice arena would have meaningful effects on the CO₂ that is experienced by the test subject. If individuals consistently differed in their spatial occupation of the choice arena, some individuals may be minimizing their CO₂ exposure through their spatial-use behavior. Individuals that repeatedly find low-CO₂ microhabitats would be able to tolerate higher inflow concentrations than other fish. It is difficult to isolate whether differences in avoidance response are due to direct variation in physiology and behavior or whether behavior is driving consistent differences in spatial use that results in altered CO₂ exposure.

The inflow CO₂ concentration is likely more relevant than the center CO₂ concentration, as the fish often displayed thigmotaxis and rested near the tank edges during acclimation (P. A. Bzonek, personal observation). This may be due to the increased flow rates (Figure S4A) or greater perceived cover found along the edges. Additionally, the inflow CO₂ concentrations were higher and more dynamic than the tank-center concentrations. The rapid CO₂ changes near the tank inflow may have driven departure responses, as tank-inflow CO₂ was the only metric that exhibited repeatable interindividual variation in the responses of the Common Carp.

Another factor that may have influenced the departing behavior of Common Carp is the particle acceleration of the acoustic stimulus. In addition to sound pressure, acoustic energy produces a directional particle-acceleration field that Common Carp detect and orient toward (Zielinski and Sorensen 2017). During the CO₂ + deterrent treatment, the fish may have interacted with an irregular particle-acceleration field that was created by particle reflection off the choice-arena walls and floor (Gray et al. 2016; Rogers et al. 2016). The particle-acceleration field of

our choice arena was irregular, with a high-amplitude pocket in the occupied tank (Figure S4B). The Common Carp in our study may have aligned their orientation with the choice-arena particle-acceleration field, which would vary dramatically between lab- and field-scale environments (Gray et al. 2016).

Applications of Nonstructural Deterrents

Dispersal is a major vector for the introduction and spread of aquatic invasive species (Rahel et al. 2008), and it can be affected by anthropogenic structures that alter waterbody connectivity (Hirsch et al. 2017). Navigation locks have been proposed as potential sites for nonphysical deterrent deployment (USACE 2014, 2019; Schneider et al. 2018). When navigation locks open for ship transport, emigrating fish are presented with a decision that is analogous to that presented in this study—remain in the current environment or enter a novel region. Within the simplified and small-scale conditions of our laboratory study, invasive Common Carp were less likely and slower to enter the novel environment when acoustic and stroboscopic deterrents were present.

We also found that Common Carp expressed repeatability in their avoidance of CO₂. Some individuals consistently tolerated higher CO₂ concentrations than others before moving toward the deterrents. The variation in avoidance responses could be caused by fish varying in their physiological tolerances to CO₂ (Hasler et al. 2017), their behavioral temperament (Réale et al. 2007), or their spatial use within the home chamber. Regardless of the source of variation, these results indicate that the effectiveness of nonphysical deterrents may differ among individual fish of the same species. Past studies have established that different fish species can express a broad range of responses to a given deterrent (Murchy et al. 2016; Putland and Mensinger 2019; Bzonek et al. 2021b), but fewer studies have described the importance of interindividual variation within species. If interindividual variation is high, the effectiveness of deterrents may vary within a population. Furthermore, nonstructural deterrents with <100% efficacy may act as physiological/behavioral filters such that individuals that disperse across the deterrent represent a nonrandom subset of the population that challenges the deterrent. Such behavioral filtering has been observed along invasion fronts (Cote et al. 2010; Myles-Gonzalez et al. 2015), where individuals at an invasion front may express more dispersive behavior than individuals from established areas. The addition of nonstructural deterrents along an invasion front could further discretize behavioral variation along an invasion front and result in selection for dispersive behavior. In addition to ongoing research on nonphysical deterrent efficacy in the lab and field, future research should address the potential role of individual physiological and behavioral variation on deterrent success.

The avoidance found here and in other studies (Vetter et al. 2015; Kim and Mandrak 2017; Murchy et al. 2017) indicates that acoustic or stroboscopic deterrents may be effective tools for limiting the dispersal of invasive fishes into novel environments. Furthermore, these stimuli could be combined with additional nonphysical technologies (Ruebush et al. 2012; Flammang et al. 2014), such as bubble walls, CO₂, pheromones, or electricity, to produce a more comprehensive deterrent. Ideally, comprehensive deterrents would involve stimuli of varying biological rationale (Noatch and Suski 2012) and engage multiple sensory or physiological systems to introduce redundancy or produce a more robust response. Future research should investigate whether acoustic, stroboscopic, and other combined nonphysical deterrents reduce Common Carp exploration within a lock environment. Field experiments should also be undertaken to address how environmental factors such as turbidity, stimulus intensity, and flow regime influence fish behavior.

ACKNOWLEDGMENTS

We thank Michael Bedford, Erik Dean, Joanne Gui, Tej Heer, Mona Jarrah, and Evan Turner for assisting during the data collection process. Rowshyra Castaneda, Fielding Montgomery, Meagan Kindree, and Alex Van Nynatten provided helpful comments. Members of the Mandrak lab provided valuable support and advice, and Dennis Higgs kindly loaned useful equipment to the project. Finally, we would like to thank the anonymous reviewers for providing extensive and valuable feedback that improved the manuscript.

All of the authors provided substantial contributions to the conception and design of this study and the interpretation of the data. P.A.B. and P.D.E. collected data and drafted the manuscript. All critically revised and approved the manuscript for publication. This study was conducted according to the Animal Utilization Protocol approved by the University of Toronto Scarborough Local Animal Care Committee (AUP 20011687) and was funded by the Fisheries and Oceans Canada Asian Carp Program. The authors declare no conflicts of interest. The data that support the findings of this study are openly available at the Harvard Dataverse at <https://doi.org/10.7910/DVN/SXSMIZ>.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.