



A complex sound coupled with an air curtain blocks invasive carp passage without habituation in a laboratory flume

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Abstract Invasive bigheaded carp are currently advancing upstream in the Mississippi River and threaten to invade its headwaters. The possibility that sound projected into navigation locks might block this invasion is being considered and four types of complex sound have been shown to have promise: an outboard-motor sound, a proprietary cyclic sound, air curtains, and the (coupling) pairing of this proprietary sound with an air curtain. In a laboratory study, we systematically tested the effects of these stimuli on invasive bighead carp and common carp, as well as the native largemouth bass (which lack hearing specializations), in a darkened laboratory flume. We were

specifically interested in whether the outboard-motor sound or the proprietary sound might be more effective at blocking and deterring fishes (i.e., does the type of complex sound matter), and whether coupling either of these sounds with an air curtain might enhance their effectiveness. We found that the proprietary sound was more effective than the outboard-motor sound at both deterring and blocking common carp as well as deterring bighead carp. The largemouth bass were less affected by both sounds. We also found that when an air curtain was coupled to either sound, the combined stimulus became more effective at blocking all three species. This was especially true for the proprietary sound which when coupled with an air curtain blocked 97% of bighead carp. The proprietary sound coupled with the air curtain has promise to block bigheaded carp and should be considered for field tests.

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Introduction

The bighead carp (*Hypophthalmichthys nobilis*) and its congener the silver carp (*H. molitrix*), hereafter referred to as bigheaded carp, were introduced from Asia to the Mississippi River Basin in the 1970s and

are now spreading into the upper reaches of the Mississippi River and toward the Laurentian Great Lakes (Kolar et al. 2007; Chapman and Hoff 2011; Lubejko et al. 2017; <https://www.asiancarp.us/index.html>). These microphagous fishes are altering this river's food web (Kolar et al. 2007; Patel et al. 2010; Wang et al. 2018), which is already impaired by the common carp (*Cyprinus carpio*) introduced over a century ago from Europe (Sorensen and Bajer 2011). In addition to being voracious feeders, silver carp jump out of the water when disturbed reducing the recreational value of the river for public fishing and boating. Although many strategies have been proposed to stop the upstream spread of bigheaded carps, the possibility of blocking carp passage through navigation locks using sound has been suggested to have special promise (Vetter et al. 2015; Murchy et al. 2017; Zielinski and Sorensen 2017). In particular, the carps (like all ostariophysan fishes) are especially sensitive to sound (Ladich and Fay 2013; Vetter et al. 2018). Sound can also be easily and safely projected into the water (Popper and Carlson 1998; Noatch and Suski 2012). Indeed, several promising sound stimuli have already been identified for bigheaded carp (Taylor et al. 2005; Zielinski et al. 2014; Vetter et al. 2015) although which one(s) might offer the greatest promise has yet to be determined.

Pure tones (single frequency), complex sounds (sounds containing multiple frequencies) and air curtains (bubbling systems that produce low-frequency sounds together with visual and hydrodynamic cues) have all been tested on bigheaded and common carps and shown to have promise in different sets of experiments. Using well-lit outdoor mazes with a speaker system, Vetter et al. (2015) established that while silver carp are seemingly unaffected by exposure to continuous pure tones (500, 1000, 1500 or 2000 Hz), they are deterred by the continuous complex sound of a 100 horsepower (hp) outboard-motor containing frequencies between 20 and 10,000 Hz. Later, Murchy et al. (2017) confirmed that this outboard-motor sound prevented 90% of bighead and silver carps from entering a channel separating two well-lit ponds. However, when a similar (40hp) outboard-motor sound was later tested by Zielinski and Sorensen (2017) in a low-light laboratory maze in which the speaker systems were concealed from sight, they found that this sound only repelled about 75% of bigheaded and common carps and that this rate

dropped with repeated exposure (i.e., carp habituated). These results seemingly demonstrate that while an outboard-motor sound can deter carps in the laboratory, they also show that testing conditions including the presence of visual cues (visible speakers) can alter this response so different deterrents need to be directly compared using identical protocols. Thus, these studies do not provide much insight into why complex sounds deter carp (or other fishes) or whether some types of complex sound may be more effective than others.

Laboratory and field tests have also shown that air curtains (streams of bubbles emitted by submersed pipes which produce low-frequency complex sound as well as visual and tactile cues [Zielinski et al. 2014]) can block invasive bigheaded and common carps. In particular, two laboratory studies have demonstrated that air curtains can repeatedly block up to 80% of both common carp and bigheaded carps in near total darkness for several hours (Zielinski et al. 2014; Zielinski and Sorensen 2016). Further, a field test in a small creek showed that an air curtain could block 60% of downstream swimming juvenile common carp, but that it was ineffective against upstream migrating adults (Zielinski and Sorensen 2015). The promise of air curtains is tempered by the fact they can be both relatively expensive and complicated to install and operate because of the need to produce large volumes of air, and that fast flowing and deeper waters (greater than 10–20 m) may also reduce their efficiency because of bubble dispersal and coalescence. Additionally, all tests of air curtains conducted to date have used different testing protocols than those used for the outboard-motor sound precluding direct comparisons between these stimuli.

In addition to tests of complex sound and air curtains alone, there have been several tests of a commercially available fish deterrent system, which couples a proprietary 20–2000 Hz complex cyclic sound with an air curtain. This system has blocked at least 95% of both silver and bighead carps in a laboratory raceway and a small creek (Taylor et al. 2005; Ruebush et al. 2012). Other fish species have not been directly tested, although tests of a similarly coupled system showed it could divert downstream swimming Atlantic salmon (*Salmo salar*) (Welton et al. 2002). This deterrent system is known as a “Bio-Acoustic Fish Fence” or “BAFF” (Fish Guidance Systems Ltd “FGS”; Southampton, UK; <http://www>.

fish-guide.com/) and has seemingly been perfected over several decades in the field (Welton et al. 2002; Perry et al. 2014). Welton et al. (2002) hypothesized that BAFF systems enhance the efficacy of sound as a fish deterrent by entraining sound within the bubble stream creating a “wall of sound” but did not present sound mapping data to evaluate this possibility. Others speculate, but also fail to test, the possibility that coupled sound and air curtain deterrent systems produce strong sound pressure and particle acceleration gradients that are aversive to fishes (Domenico 1982; Zielinski et al. 2014). Of course, the type of complex cyclic (broadband) sound used in the BAFF system designed for bigheaded carps may also be more effective than other types of complex sounds (David Lambert, Fish Guidance Systems Ltd., Southampton, U.K., personal communication). In any case, while these BAFF studies using this proprietary sound are interesting and appear promising from a theoretical perspective, an understanding of their practical value to wild carps is complicated by three aspects of extant studies. First, the hatchery test by Taylor et al. (2005) only examined the response of bighead carp and only tested the effects of the proprietary sound when coupled with the air curtain. Thus, both the role of the (potentially expensive) air curtain in blocking bighead carp passage compared to the proprietary sound alone and its possible effects on other fish species (a concern to fisheries managers) are presently unknown. Second, the field test by Ruebush et al. (2012) was complicated by their inability to control the number and species of wild stream fishes that encountered the BAFF system, along with their sporadic addition of high-intensity lights to the BAFF which made it impossible to determine which stimuli were driving avoidance responses. Third, BAFF studies have also used different protocols than the ones used in the tests examining the air curtain and outboard-motor sound making direct comparisons between these studies challenging. So while it is clear that pure sounds are less effective than complex sounds at deterring bigheaded carp in the laboratory, it is simply not yet clear whether different types of complex sound are more effective at deterring carps than others or whether coupling complex sound with an air curtain actually enhances its ability to block carps. It is also unclear how these different types of sound stimuli impact fishes other than carps, especially those that lack the hearing sensitivity of carps.

The overarching goal of this study was to identify a type of sound stimulus that might be particularly effective at deterring and blocking invasive carps while having minimal effects on other fish species. We were especially interested in determining whether the proprietary sound coupled with an air curtain has special promise that might justify the expense and complexity of purchasing and installing a commercially available fish deterrent system. To accomplish this goal, we asked two questions of interest from a basic perspective. First, we asked whether invasive carps or other fishes are sensitive to the nature of complex sound (i.e., is there a difference in the responses of fishes to an outboard-motor sound versus a proprietary-cyclic sound). Second, we asked whether coupling an air curtain to a complex sound makes it more effective at blocking carps or other fishes than either the complex sound or air curtain alone, and if one type of combined sound-air curtain system might be more effective than the other. To answer these questions, we tested groups of bighead carp, common carp and largemouth bass (*Micropterus salmoides*, a non-ostariophysan lacking hearing specializations) in a darkened laboratory flume and repeatedly exposed these fishes to two types of complex sound when coupled (or not) to an air curtain.

Materials and methods

Experimental design

We tested the effects of exposing groups of three fish species (bighead carp, common carp, largemouth bass) to five types of sound stimuli (an outboard-motor sound, a proprietary cyclic sound, an air curtain, an air curtain coupled with the outboard-motor sound, and an air curtain coupled with the proprietary sound) to determine which type of sound (if any) was most effective at stopping carps. We accomplished this in three steps. First, in a series of control experiments, we examined the constancy of each species' swimming behavior within our laboratory flume in the absence of sound stimuli allowing us to confirm that it did not change over time. Second, we examined the effect of exposing groups of each species of fish to the five types of sound stimuli to determine if fish distribution and swimming behavior changed with sound exposure. Third, we used the results from the second set of

experiments to calculate efficiencies of blockage and deterrence to compare the effects of different stimuli between and within species to answer our questions about whether differences between complex sounds might exist, and whether coupling them with an air curtain enhances their efficacy, as well as which might be best for carps.

We conducted a grand total of 18 experiments, each of which tested one type of sound stimulus on one species (i.e., we tested each of the three species with no stimulus [control], the outboard-motor sound, the proprietary sound, an air curtain, the outboard-motor sound coupled with an air curtain, and the proprietary sound coupled with an air curtain). Each experiment consisted of 8 trials in which a different group of 10 previously untested (naïve) fish of the same species was tested on a randomly chosen stimulus. Each trial started with a 1-h acclimation period (no stimulus), followed by 8 sets of exposure periods each of which started with a 6-min pre-test period (no stimulus), followed by a 6-min test period (stimulus on [or not in the 3 control experiments]), and then a 10-min recovery period (no stimulus). Fish were exposed 8 times because that was the average number of times that adult silver carp have been noted to challenge a navigational lock in the Mississippi River (Sara Tripp, Missouri Department of Conservation, Cape Girardeau, MO, personal communication). All trials were conducted between 0900 and 2100 h and in near-darkness (< 1 lx, similar to light levels we have measured at > 1 m in the Mississippi River). Fish position was recorded during pre-test and test periods using low-light cameras and analyzed after trials by quantifying both the number of times fish crossed the midline of the flume where the deterrent system was located (i.e., passage rates), and the average number of fish found within 1 m of the deterrent system (i.e., fish distribution). We examined distribution and movement during both the pre-test and test periods to provide estimates of changes in basal behavior (i.e., during pre-test periods) and behaviors induced by exposure itself (i.e., during test periods). We were unable to collect distribution data for experiments that used the air curtain because air bubbles interfered with our ability to determine exact fish location, although we could deduce when fish crossed the bubble stream.

Fish

Juvenile fishes were obtained from a commercial fish farm (Osage Catfisheries; Osage Beach, MO). Common carp (TL: 91 ± 12 mm; mean \pm SD) and largemouth bass (TL: 119 ± 22 mm) were held in flow-through circular tanks (300 L; 1 m diameter) and fed 2.5 mm floating pellets (Skretting, Tooele, Utah), while bighead carp (TL: 142 ± 15 mm) were maintained in circular tanks (1000 L; 2 m diameter) and fed a diet of *Spirulina* and *Chlorella* algae (Hansen et al. 2014). All tanks were supplied with 18 °C well water, aerated using air stones, dimly illuminated (5 lx; 16 h day: 8 h night) and relatively quiet (80–100 dB ref. 1 μ Pa). All procedures were approved by the University of Minnesota Institutional Animal Care and Use Committee (Protocol: 1712-35381A) and all necessary federal and state permits were obtained.

Laboratory flume

Trials were performed in a custom-built indoor elliptical fiberglass flume (8 m long \times 1 m wide channel \times 0.3 m water depth; 1.0 m wall height) (Fig. 1). Two speakers (FGS MkII 15-100; Fish Guidance System Ltd.; Southampton, UK) along with two porous pipes (AD100T; PentairAES; Apopka, FL) were placed in the center of each channel of the flume. These pipes produced a continuous stream of fine air bubbles (1–5 mm diameter). Concrete blocks with foam pads were placed on the exterior side of the walls and along the floor of the flume to minimize sound reverberation, ensuring that the sound pressure dropped to background levels (60–80 dB ref 1 μ Pa) on the other side of the flume so that fish could escape the sound to these refuges (like a large river) (Fig. 1). Fish movement was monitored using a combination of overhead and underwater cameras and dim infrared lights (VT-IR1 and VT-IR2; Vitek; Valencia, CA; 840 nm wavelength, < 1 lx). Bighead carp were tested in slowly flowing water (1.66 cm/s) because pilot studies showed they shoaled better and swam more actively under these conditions, while common carp and largemouth bass were tested in still water (water inflow was turned off before trials started).

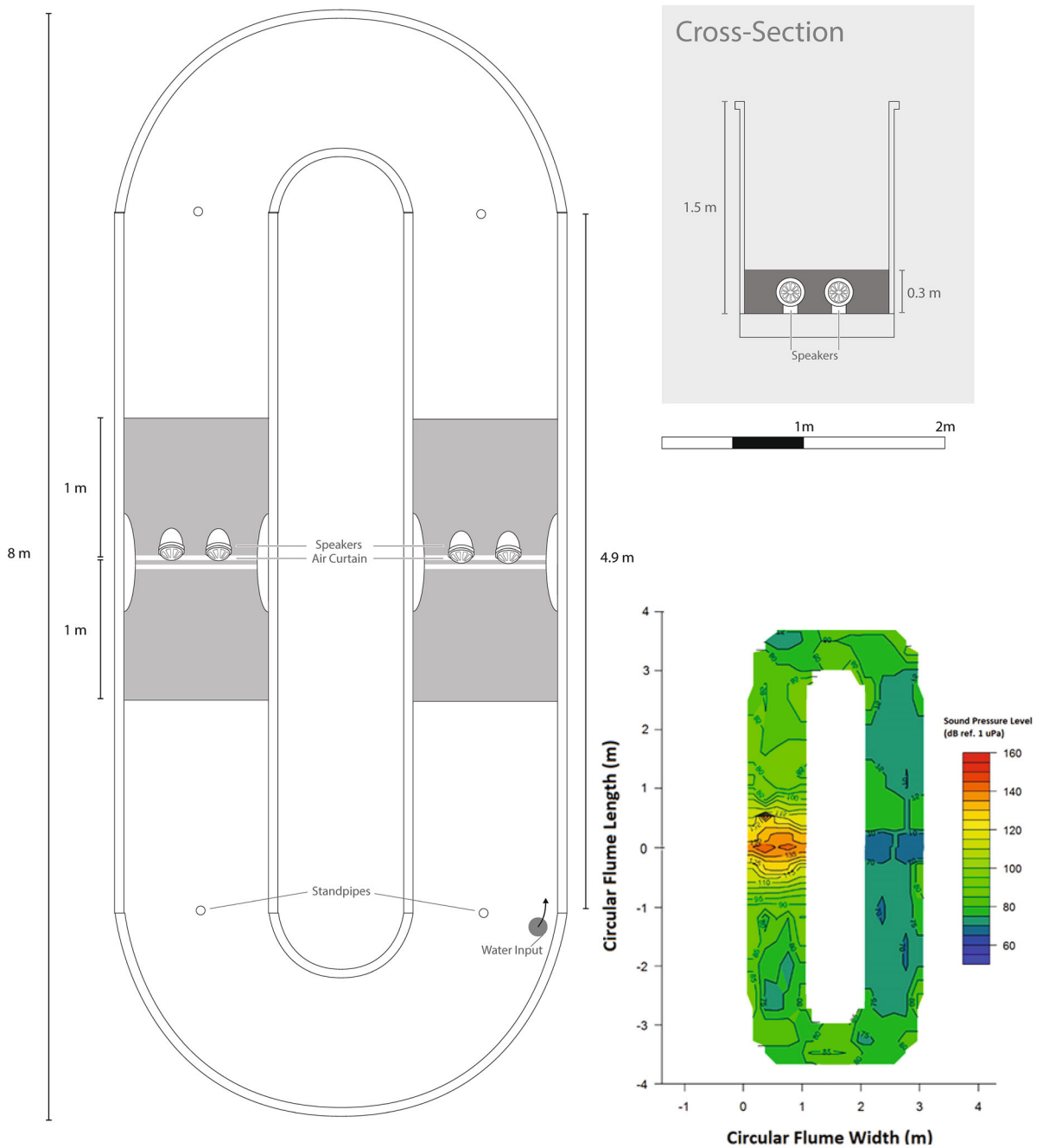


Fig. 1 Schematic drawing of an overhead and cross-sectional view of the elliptical fiberglass flume with a contour map of sound pressure to its right. Two underwater speakers and an air curtain were placed in each of the two 4.9 m channels. The grey box around the speakers and air curtain denotes a 1 m area away from the deterrent system. Water inflow to the tank is indicated by a black circle and the direction of flow (when on) is marked

by the blue arrow. Standpipes ensured that water depth was maintained at 0.3 m. Bottom-right panel shows a plan view of the sound pressure level in dB (ref 1 μPa) for the outboard-motor sound at 500 Hz played on the western speaker system. Sound levels on the east (right) side of the flume receded to background levels

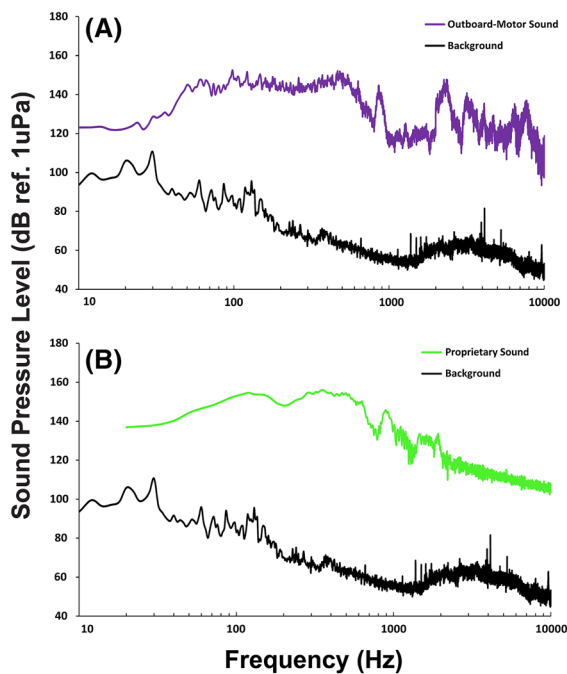


Fig. 2 Sound pressure level power spectrum of the: **a** outboard-motor sound (purple line), and **b** proprietary sound (green line) measured 5 cm from the speaker in the flume with background noise (black lines) as a reference. Sound pressure level measurements are provided at a 2 Hz bandwidth as described by Zielinski and Sorensen (2017)

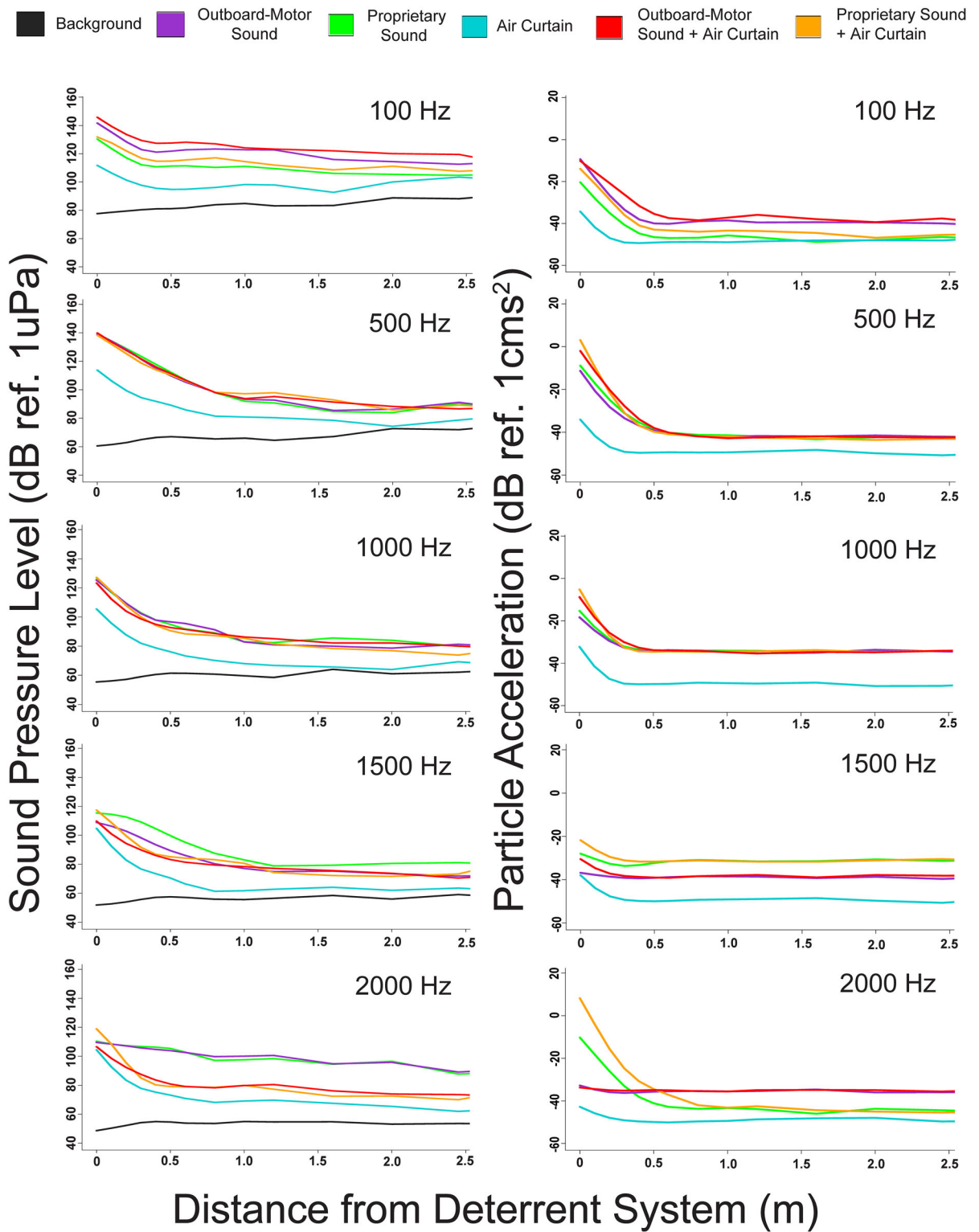
Sound stimuli

For the outboard-motor sound, we used the recording of the 40 hp outboard-motor employed and described by Zielinski and Sorensen (2017). This complex sound was played continuously during each test period and contains frequencies between 20 and 10,000 Hz. Its power spectrum is shown in Fig. 2a. For the proprietary sound, we used the recording previously used and described by both Taylor et al. (2005) and Ruebush et al. (2012). This complex sound has been described as being comprised of “cyclic sound bursts between 20 and 2000 Hz” (Taylor et al. 2005). This sound was obtained from Fish Guidance Systems Ltd., [“Sound 7”; Southampton, UK]. Figure 2b shows its power spectrum. For the air curtain, we used porous pipes supplied with an air flowrate of 1.2 L s^{-1} as previously described by Zielinski et al. (2014). The air curtain was carefully positioned immediately at the front of the speakers to optimize sound transfer into the air curtain (as monitored by a hydrophone, see below), effectively coupling these stimuli to closely

Fig. 3 Sound pressure level (dB ref. $1 \mu\text{Pa}$) and particle acceleration (dB ref. 1 cm s^{-2}) at 100, 500, 1000, 1500 and 2000 Hz measured within 2.5 m of the deterrent system during exposure to the outboard-motor sound (purple lines), the proprietary sound (green lines), the air curtain (blue lines), the outboard-motor sound coupled with an air curtain (red lines), and the proprietary sound coupled with an air curtain (orange lines). Ambient background sound levels within the elliptical flume are shown as a black line. Reported sound measurements were taken at a 0.15 m depth along the midpoint of the flume

mimic a BAFF (personal communication; Andy Turnpenny, FGS, Southampton, UK). Speaker output was carefully adjusted to produce target peak sound pressure levels of 140 dB ref. $1 \mu\text{Pa}$ directly in front of each speaker [the level used in Murchy et al. (2016) and Zielinski and Sorensen (2017)].

Sound pressure (dB_{rms} ref $1 \mu\text{Pa}$) and particle acceleration (dB_{rms} ref 1 cm s^{-2}) for all sound stimuli were mapped (Fig. 3). Sound pressure measurements were acquired using a C55 hydrophone (sensitivity: $-163.5 \text{ dB ref } 1 \text{ V}/\mu\text{Pa}$; frequency range: 0.01–100 kHz) with an integral power amplifier (Cetacean Research, Seattle, WA), sampled at 44.1 kHz and digitized using a TASCAM US-122mkII (TEAC, Montebello, CA) USB audio interface. Acoustic particle acceleration measurements were acquired using a neutrally buoyant triaxial accelerometer [sensitivity: $100 \text{ mV}/(\text{m/s}^2)$; frequency range: 0.5–5000 Hz] connected to a signal conditioner (model # W356A12 and 482C05, PCB Piezotronics, Depew, NY), sampled at 16 kHz and digitized using a USB-1208FS-Plus data acquisition board (Measurement Computing Corporation, Norton, MA). The hydrophone and accelerometer were mounted on a PVC probe, similar in design to that of Zeddies et al. (2012), placed at a depth of 0.15 m and measurements taken at 0.25 m intervals across the width of the channel. Sound measurements were taken at: 0.00, 0.10, 0.20, 0.30, 0.40, 0.50, 0.60, 0.80, 1.00, 1.20, 1.60, 2.00, 2.40, 3.00, 3.60, 4.20, 5.40, and 6.60 m away from the speaker system. At each location, the sound stimulus was recorded for 5-s which was then split into 10–0.5 s batches and averaged. A custom Matlab graphical user interface developed by Zielinski and Sorensen (2017) was used to analyze and transform the pressure and particle acceleration waveforms into the frequency domain. Particle acceleration values along the x, y and z planes were then combined



to obtain the overall magnitude of particle acceleration [calculated as $\sqrt{(x^2 + y^2 + z^2)}$] (Radford et al. 2012).

Statistical analysis

We used a stepwise approach to analyze our data. First, we analyzed the control (no stimulus) experiments to confirm that there was no effect of the passage of time on each species' passage rate and distribution. Next (having confirmed there was no effect of time), we examined the impact that each sound stimulus had on fish movement. Finally, we compared the results of specific sets of experiments (i.e., specific stimuli and species) to answer our two questions. We developed this stepwise approach after extensively evaluating various statistical models including generalized linear mixed models using binomial and Poisson distributions (Matthew Galloway, Statistical Consulting Center, University of Minnesota, Minneapolis, MN; personal communication). The stepwise approach we developed was not only statistically valid but both simpler (mixed models containing all species and stimuli had four-way interactions that were difficult to resolve and not always relevant) and more powerful than models as it permitted direct a priori comparisons to address our specific questions. All analyses were performed using JMP Pro 13 (SAS Institute Inc.; Cary, NC).

All analyses of all experiments started by transforming data to meet the assumptions of normalcy and homogeneity of variance (verified by examining fitted residuals; Anscombe and Tukey 1963). Passage rate data for each trial was square root transformed while distribution data were $\log_{10} + 1$ transformed as suggested by Sokal and Rohlf (1995). The passage rate and distribution data obtained in the control experiments were next analyzed by species using one-way repeated measures ANOVAs with the main effect being "test-number" (i.e., time in flume) and "fish group number" entered as a random effect (to account for repeated measurements). Next, passage rate and distribution data for each of the five sound experiments were analyzed using two-way repeated measures factorial ANOVAs with the two main effects being "treatment" (i.e., pre-test [no stimulus] or test [stimulus]) and "test-number" (i.e., repeated exposure to the treatment), along with "fish group number" entered as a random effect. If a treatment effect was observed ($p < 0.05$), we then used paired t-tests

corrected for multiple comparisons (Bonferroni correction) to compare each pre-test with its matched test value to ascertain exactly which test-numbers differed due to sound exposure ($p < 0.05$). Similarly, if a test-number (i.e. repeated exposure) effect was described ($p < 0.05$), we used two one-way repeated measures ANOVAs to test for changes in fish movement due to repeated sound exposure by examining both changes in pre-test (baseline movement) and test (responses to sound) values. If the ANOVA was significant ($p < 0.05$), we used a linear regression analysis to determine if passage rates or the number of fish near the deterrent system was increasing (habituating) or decreasing (sensitizing).

Finally, to answer our questions of whether there is a difference in the response of fish to the outboard-motor sound versus the proprietary sound (Question 1) and whether coupling an air curtain with complex sound makes either complex sound more effective and which one is most effective (Question 2), we calculated blockage and deterrence efficiencies for the different experiments. It was necessary to calculate efficiencies both because absolute passage rates varied between species and the responsiveness of largemouth bass changed with repeated exposures to sound stimuli so direct comparisons of raw passage rates were not meaningful. Blockage efficiencies were calculated by dividing the number of passages observed when the sound stimulus was on (i.e., test period) by the number of passages when the sound stimulus was off (i.e., pre-test period), subtracting this value from 1, and then multiplying by 100. Deterrence efficiencies were calculated in a similar manner using the average number of fish seen within 1 m of the deterrent for each 6-min pre-test and test period. Blockage and deterrence efficiency data also met the assumptions of normalcy and homogeneity of variances. We first performed 2-way repeated measures factorial ANOVAs (one for blockage efficiency, one for deterrence efficiency) with the two main effects being "stimulus" and "species" along with "fish group number" as a random effect. If any of the main effects were found significant ($p < 0.05$), we then used a series of paired t-tests corrected for multiple comparisons (Bonferroni correction) to answer our questions. In particular, to test whether the outboard-motor sound differed from the proprietary sound (Question 1), paired t-tests between the two complex sounds were employed using efficiency data for each species. To test whether

coupling sound with an air curtain enhanced the effectiveness of sound deterrents (Question 2), we used paired t-tests to determine if each coupled sound and air curtain stimulus was more effective than sound or the air curtain alone. Lastly, we performed paired t-tests to determine whether the proprietary sound was more effective than the outboard-motor sound when both were coupled with an air curtain (i.e., which was the best deterrent system). Overall blockage and deterrence efficiencies (mean \pm SD) for each species and experiment were also calculated using all test values for each experiment to aid comparisons between sound stimuli. Results were then compiled by question and are described below by species with control experiments first, followed by the relevant sound experiments, and finally a comparison of the sound stimuli. All figures displaying passage rate and distribution data are presented as box-and-whisker plots (with medians, means and inter-quartile ranges) because these raw data were not normally distributed.

Results

The distribution of sound stimuli (sound maps)

All 5 sound stimuli attenuated to background levels by 3–4 m for sound pressure and 1 m for particle acceleration (Fig. 3). Although many small differences were evident in the sound field associated with each sound stimulus, three trends seemed notable. First, the air curtain consistently produced lower sound pressure and particle acceleration amplitudes than the sounds alone at all frequencies (Fig. 3). Second, notably sharp sound pressure gradients were observed at 1500 Hz and 2000 Hz for both complex sounds when coupled with the air curtain (Fig. 3). Third, when the proprietary sound was coupled to the air curtain, it generated especially sharp particle acceleration gradients at 2000 Hz (Fig. 3).

Question 1: Are bighead carp, common carp, and largemouth bass sensitive to the nature of complex sound (i.e., Is there a difference between an outboard-motor sound and the proprietary sound)?

Bighead Carp Although somewhat variable, both bighead carp passage rates and their distribution (i.e., the number of bighead carp located near the inactive

deterrent) did not change during the course of the control experiment when stimuli were not played (Figs. 4a, 7a; Supplemental Tables 2, 4). In contrast, our test of the outboard-motor sound found both a treatment effect and a test-number (i.e., repeated exposure) effect on bighead carp passage rates (Supplemental Table 2) with differences observed in all 8 test periods of this experiment ($p < 0.05$ [after being corrected for multiple comparisons]; Fig. 4b), resulting in an overall blockage efficiency of $76 \pm 29\%$ (mean \pm SD) (Table 1). While pre-test passage rates did not change with repeated exposure during this experiment; test passage rates dropped, symptomatic of sensitization (Supplemental Tables 1, 2). When exposed to the outboard-motor sound, the number of bighead carp observed near the deterrent decreased only during the first test period ($p < 0.05$; Fig. 7b; Supplemental Tables 3, 4) resulting in an overall deterrence efficiency of $21 \pm 29\%$ (Table 2). In our test of the proprietary sound, a treatment effect but no test-number effect was observed in bighead carp passage rates (Supplemental Table 2) with differences being measurable at all 8 test periods ($p < 0.05$; Fig. 4c) and an overall blockage efficiency of $78 \pm 27\%$ (Table 1). When exposed to the proprietary sound, the number of bighead carp located near the deterrent dropped with differences being measured in 3 of 8 test periods ($p < 0.05$; Fig. 7c) with no effect of repeated exposure (Supplemental Tables 3, 4) resulting in an overall deterrence efficiency of $45 \pm 36\%$ (Table 2). Comparing the relative efficiencies of the proprietary sound and outboard-motor sound on bighead carp, we found no measurable difference between the two complex sound stimuli in their ability to block these carp ($p > 0.05$; Table 1, Supplemental Table 5), but we did find that the proprietary sound was much more effective than the outboard-motor sound at deterring them ($p < 0.05$; Table 2; Supplemental Table 6).

Common carp Both common carp passage rates and the number of common carp located near the deterrent did not change during the course of the control experiment (Figs. 5a, 7d; Supplemental Tables 2, 4). In our test of the outboard-motor sound, we found both a treatment effect and a test-number effect (i.e., repeated exposure) on common carp passage rates (Supplemental Table 2) with follow-up tests showing differences at 5 of 8 test periods ($p < 0.05$; Fig. 5b) and an overall blockage efficiency of $42 \pm 28\%$

BIGHEAD CARP

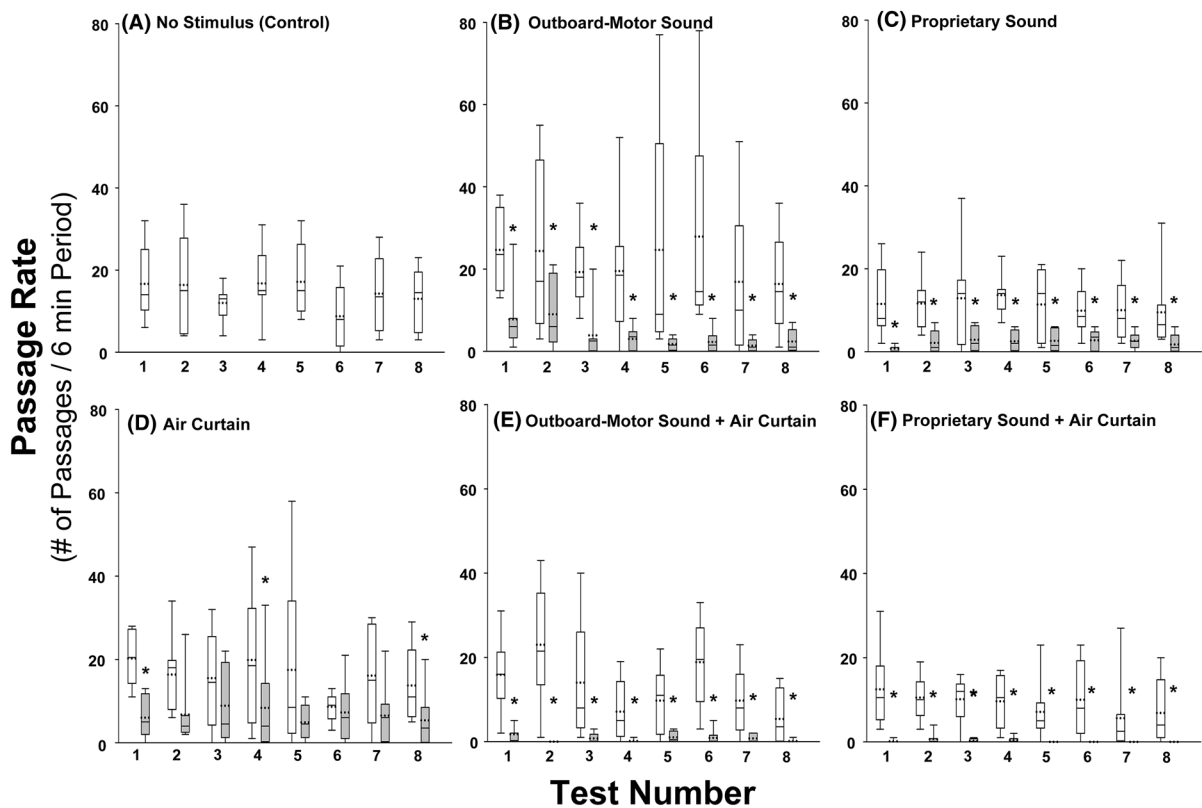


Fig. 4 Passage rates (i.e., the number of passages per 6-min pre-test or test period) of bighead carp to 5 types of sound stimuli across time: **a** no stimulus (control); **b** outboard-motor sound; **c** proprietary sound; **d** air curtain; **e** outboard-motor sound coupled with the air curtain; and **f** the proprietary sound coupled with the air curtain. Box-and-whisker plots in each panel show lower bound, 25th percentile, median (solid line), mean (dotted line), 75th percentile, and upper bound values for passage rates during pre-test periods (white bars) and test

periods (gray bars) over the course of eight consecutive periods (i.e., test numbers). Asterisks denote differences between pre-test and test passage rates for that specific test number ($p < 0.05$ [corrected for multiple comparison]). Eight trials each consisting of 10 naïve bighead carp were used to test each sound stimulus. In each trial, a naïve group of bighead carp were exposed to the stimulus (or not) during eight consecutive matched sets of pre-test and test periods ($N = 128$ observations)

(Table 1). Follow-up tests on both pre-test and test periods showed no change in common carp passage rates following repeated exposure to the outboard-motor sound (Supplemental Tables 1, 2). In contrast, there was no change in the number of common carp observed near the deterrent when exposed to this sound (Fig. 7e; Supplemental Tables 3, 4) with an overall deterrence efficiency of $14 \pm 19\%$ (Table 2). When exposed to the proprietary sound, a treatment effect but no test-number effect (Supplemental Table 2) was seen with follow-up tests showing reductions at all 8 test periods ($p < 0.05$; Fig. 5c) and an overall blockage efficiency of $79 \pm 19\%$ (Table 1). This was accompanied by a large decrease in the number of

common carp observed near the speakers with differences being measured in 5 of 8 test periods ($p < 0.05$; Fig. 7f) with no effect of repeated exposure (Supplemental Table 3, 4) resulting in an overall deterrence efficiency of $38 \pm 29\%$ (Table 2). Comparing the relative efficiencies of the proprietary sound and outboard-motor sound to alter common carp movement, we found that the proprietary sound was both more effective at blocking and deterring common carp ($p < 0.05$; Tables 1, 2; Supplemental Tables 5, 6).

Largemouth bass The passage rate of largemouth bass was low but relatively constant and neither it, nor their proximity to the inactive deterrent system, changed during the course of the control experiment

Table 1 Blockage efficiencies (mean ± SD) of five sound stimuli for bighead carp, common carp and largemouth bass

	Outboard-motor sound	Proprietary sound	Air curtain	Outboard-motor sound + air curtain	Proprietary sound + air curtain
Bighead carp	76.42% (± 28.54) ^{ab b a ••}	77.81% (± 27.04) ^{ab a a ••}	59.65% (± 36.30) ^{• a a a ••}	90.24% (± 23.25) ^{• b a a •}	97.02% (± 13.20) ^{• a b a •}
Common carp	42.21% (± 28.14) ^{a a a ••}	79.40% (± 19.15) ^{b b a a ••}	63.86% (± 24.80) ^{• a a a ••}	88.07% (± 18.77) ^{• b a a •}	99.75% (± 1.17) ^{•• b b b •}
Largemouth bass	45.57% (± 37.38) ^{a a a ••}	50.38% (± 36.07) ^{a b a a ••}	68.02% (± 22.53) ^{• b a a ••}	71.24% (± 33.79) ^{• b a a •}	86.94% (± 23.81) ^{•• b b b •}

Four comparisons are shown next to each blockage efficiency: the first comparison being between the two complex sound stimuli alone; the second between the outboard-motor sound, air curtain, and outboard-motor sound coupled with the air curtain; the third between the proprietary sound, air curtain and proprietary sound coupled with the air curtain; and the fourth between the two complex sounds coupled with air curtains. Different lowercase letters denote differences ($p < 0.05$ [corrected for multiple comparisons]) in blockage efficiencies between the stimuli for specific comparisons, with “a” signifying the stimulus with the lowest blockage efficiency, and “b” denoting stimuli with higher efficiencies. Stimuli not being compared are denoted with a “•”. Eight trials of 10 naive bighead carp, common carp or largemouth bass were used to test each sound stimulus

(Figs. 6a, 7g; Supplemental Tables 2, 4). However, when tested with the outboard-motor sound, both a treatment effect and test-number effect (Supplemental Table 2) was observed for largemouth bass passage rates with follow-up tests revealing reductions in passage rate occurring at only two test-periods ($p < 0.05$; Fig. 6b) with an overall blockage efficiency of $46 \pm 37\%$ (Table 1). Decreases in both pre-test and test passage rates (i.e., sensitization) were observed with repeated exposure to the outboard-motor sound (Supplemental Tables 1, 2). In contrast, there was no change in the number of largemouth bass observed near the deterrent during this experiment (Fig. 7h; Supplemental Tables 3, 4) resulting in an overall deterrence efficiency of $26 \pm 27\%$ (Table 2). When tested with the proprietary sound, both a treatment effect and test-number effect (Supplemental Table 2) were seen with significant reductions in largemouth bass passage rates occurring during the first two test periods ($p < 0.05$; Fig. 6c) and an overall blockage efficiency of $50 \pm 36\%$ (Table 1). Small decreases in pre-test passage rates but not test passage rates were observed with repeated exposure to the proprietary sound (Supplemental Tables 1, 2). We also saw no change in the number of largemouth bass observed near the deterrent during the proprietary sound experiment (Fig. 7i; Supplemental Tables 3, 4) resulting in an overall deterrence efficiency of $35 \pm 32\%$ (Table 2). Comparing the relative efficiencies of the proprietary and outboard-motor sounds to alter largemouth bass movement, we found no difference in their abilities to either deter or block largemouth bass ($p > 0.05$; Tables 1, 2; Supplemental Tables 5, 6).

Question 2: Does coupling the air curtain with either the outboard-motor sound or the proprietary sound make either of them more effective than the sound or air curtain alone, and is one coupled system more effective than the other?

Bighead carp When bighead carp were exposed to the air curtain alone, we measured a treatment effect but no effect of test-number (i.e. repeated exposure) (Supplemental Table 2) on bighead carp passage rates with significant reductions being measured at 3 of 8 test periods ($p < 0.05$; Fig. 4d), resulting in an overall blockage efficiency of $60 \pm 36\%$ (Table 1). When bighead carp were exposed to the outboard-motor sound coupled with the air curtain, both a treatment

Table 2 Deterrence efficiencies (mean \pm SD) of the outboard-motor sound and proprietary sounds for bighead carp, common carp and largemouth bass

	Outboard-motor sound	Proprietary sound
Bighead carp	20.90% (\pm 28.98) ^b	45.28% (\pm 36.45) ^a
Common carp	13.84% (\pm 19.48) ^b	38.10% (\pm 28.69) ^a
Largemouth bass	25.57% (\pm 27.38) ^a	35.33% (\pm 32.02) ^a

For each species, different superscript letters denote significant differences ($p < 0.05$) in deterrence efficiencies with “a” symbolizing the stimulus with the highest deterrence efficiency, and “b” denoting stimuli with lower efficiencies. Eight trials of 10 naive bighead carp, common carp or largemouth bass were used to test each sound stimulus

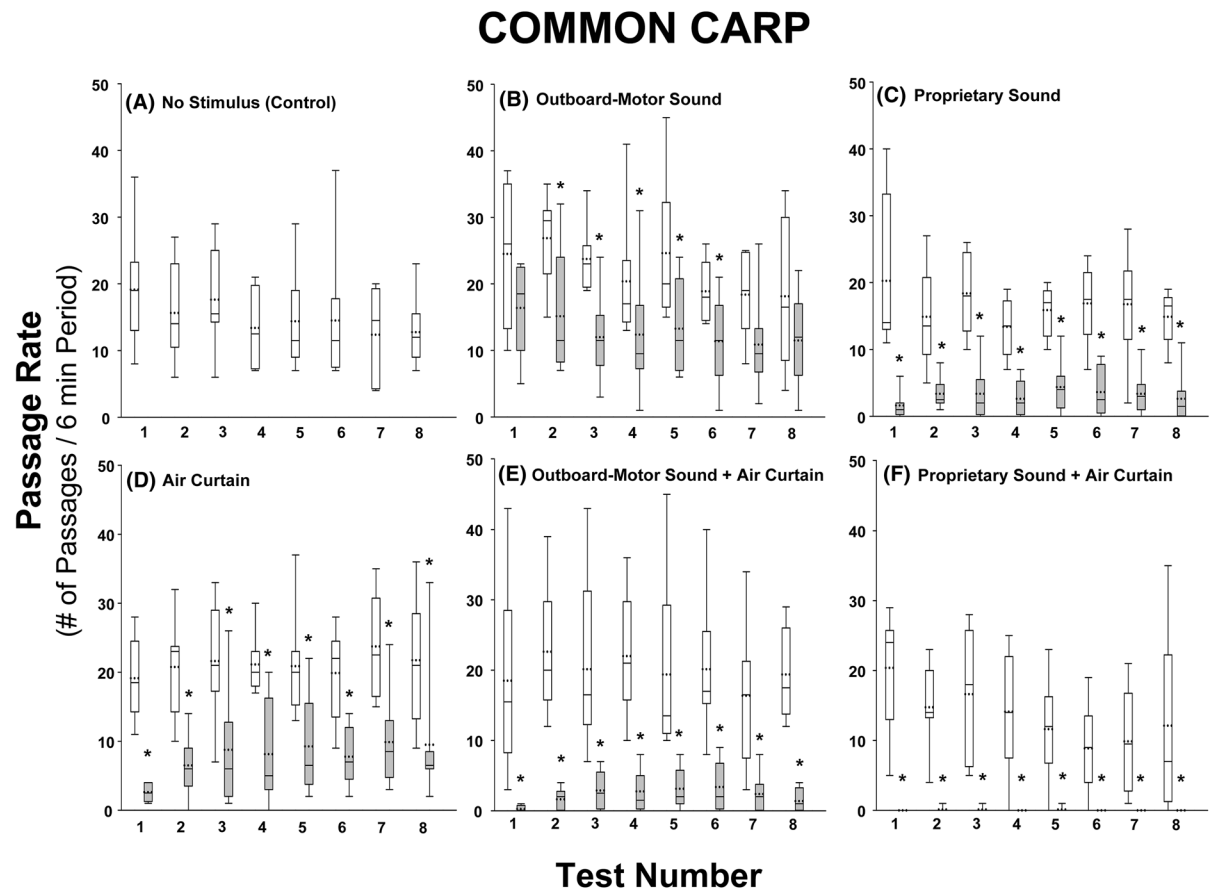


Fig. 5 Passage rates of common carp (i.e., number of passages per 6-min pre-test or test period) to 5 sound stimuli across time: **a** no stimulus (control); **b** outboard-motor sound; **c** proprietary sound; **d** air curtain; **e** outboard-motor sound coupled with an air curtain; and **f** the proprietary sound coupled with an air curtain. Box and whisker plots in each panel show lower bound, 25th percentile, median (solid line), mean (dotted line), 75th percentile, and upper bound values for passage rates during pre-test periods (white bars) and test periods (gray bars) over the

effect and a test-number effect were seen (Supplementary Table 2), with significant reductions in passage rates being noted during all 8 test periods

course of eight consecutive periods (i.e., test numbers). Asterisks denote differences between pre-test and test passage rates for that specific test period ($p < 0.05$ [corrected for multiple comparisons]). Eight trials each consisting of 10 naive common carp were used to test each sound stimulus. In each trial, a naive group of common carp were exposed to 8 consecutive matched sets of pre-test and test periods ($N = 128$ observations)

($p < 0.05$; Fig. 4e) resulting in a blockage efficiency of $90 \pm 23\%$ (Table 1). A small decline in pre-test passage rates (i.e., sensitization), but no change during

LARGEMOUTH BASS

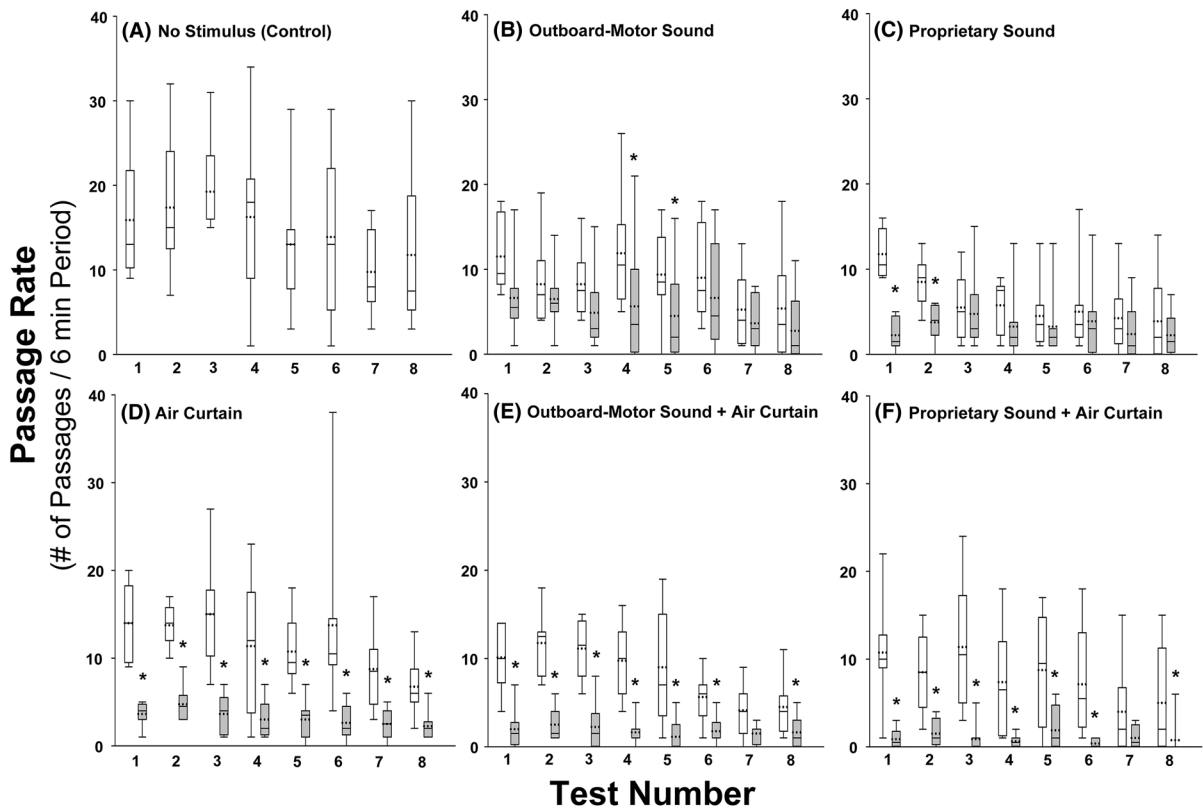


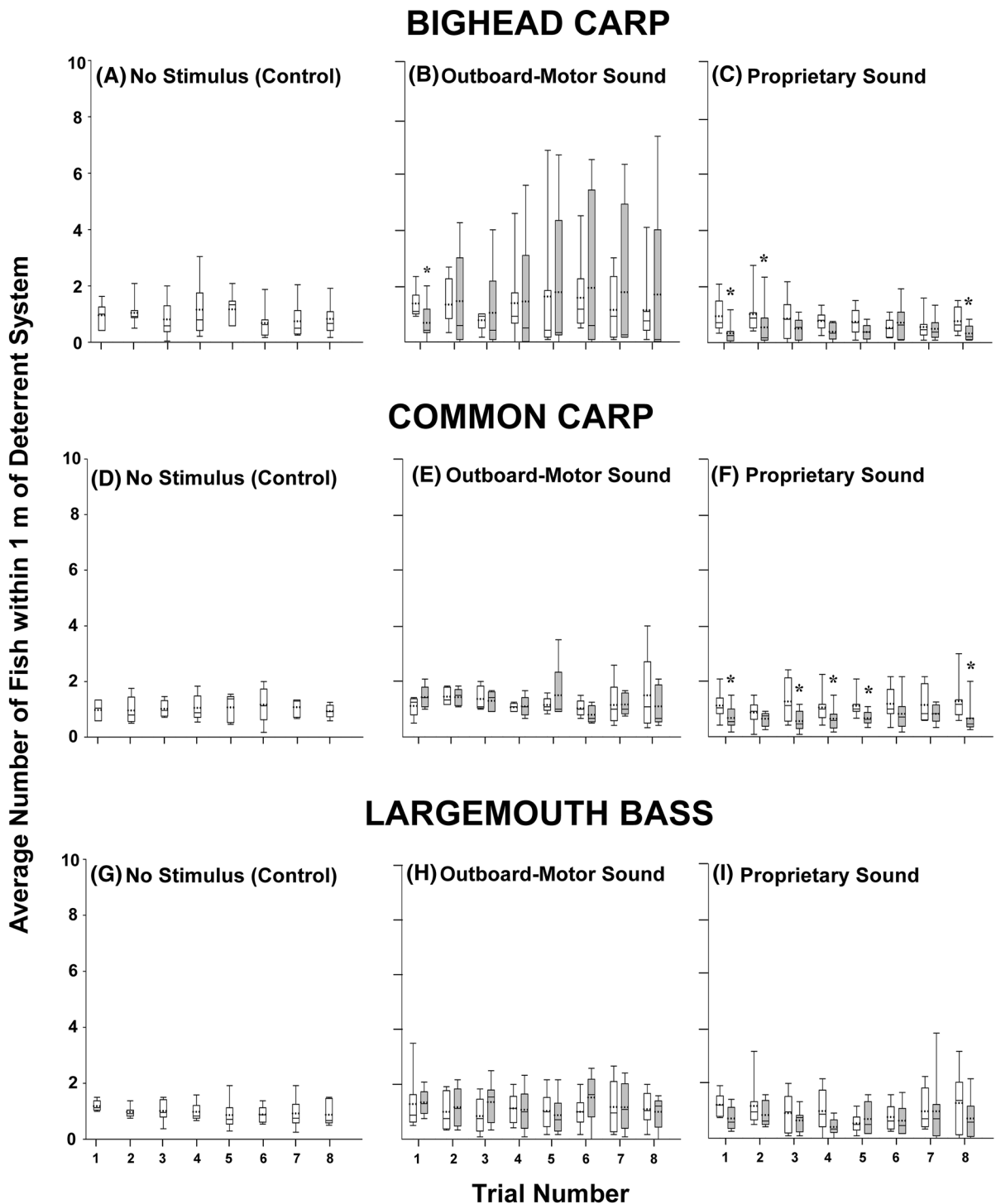
Fig. 6 Passage rates of largemouth bass (i.e., number of passages per 6 min pre-test or test period) to 5 sound stimuli across time: **a** no stimulus (control); **b** outboard-motor sound; **c** proprietary sound; **d** air curtain; **e** outboard-motor sound coupled with the air curtain; and **f** the proprietary sound coupled with the air curtain. Box and whisker plots in each panel show lower bound, 25th percentile, median (solid line), mean (dotted line), 75th percentile, and upper bound values for passage rates during pre-test periods (white bars) and test periods (gray bars)

test periods, was also observed for bighead carp when the outboard-motor sound was coupled with the air curtain (Supplemental Tables 1, 2). Similarly, bighead carp passage rates during the experiment in which the proprietary sound was coupled with the air curtain showed a treatment effect but no effect of test-number (Supplemental Table 2) with significant reductions in passage rates again being noted at all 8 test periods ($p < 0.05$; Fig. 4f) resulting in an overall blockage efficiency of $97 \pm 13\%$ (Table 1). Paired t-tests on bighead carp blockage efficiencies showed that the coupled outboard-motor sound and air curtain stimulus was more effective than the air curtain alone ($p < 0.05$) but not the sound alone ($p > 0.05$; Table 1;

over the course of eight consecutive periods (i.e., test numbers). Asterisks denote differences between pre-test and test passage rates for that specific test period ($p < 0.05$ [corrected for multiple comparisons]). Eight trials each consisting of 10 naïve largemouth bass were used for each sound stimulus. In each trial, a naïve group of largemouth bass were exposed to 8 consecutive matched sets of pre-test and test periods ($N = 128$ observations)

Supplemental Table 5). Similarly, the blockage efficiency observed for bighead carp exposed to the proprietary sound coupled with an air curtain was more effective than either the proprietary sound alone or the air curtain alone ($p < 0.05$; Table 1; Supplemental Table 5). There was no difference between the blockage efficiencies of the two complex sounds when they were coupled with the air curtain ($p > 0.05$; Table 1; Supplemental Table 5).

Common carp When common carp were exposed to the air curtain, we measured a treatment effect but no test-number effect (Supplemental Table 2) with reductions in passage rates observed during all 8 test periods ($p < 0.05$; Fig. 5d), resulting in an overall



blockage efficiency of $64 \pm 25\%$ (Table 1). When common carp were tested with the outboard-motor sound coupled to the air curtain, both a treatment

effect and a test-number effect was detected (Supplemental Table 2) with reductions in passage rates being noted at all 8 test periods ($p < 0.05$; Fig. 5e), resulting

◀ **Fig. 7** The number of fish located within 1 m of the deterrent system during pre-test periods (white bars) and test periods (gray bars) for bighead carp, common carp and largemouth bass. Panels **a–c** show results from bighead carp exposed to either no stimulus (**a**), the outboard-motor sound (**b**) or the proprietary sound (**c**). Panels **d–f** show the number of common carp within 1 m of the deterrent system when exposed to either no stimulus (**d**), the outboard-motor sound (**e**) or the proprietary sound (**f**). Panels **g–i** show results from largemouth bass during exposure to either no stimulus (**g**), the outboard-motor sound (**h**) or the proprietary sound (**i**). Box and whisker plots in each panel show lower bound, 25th percentile, median (solid line), mean (dotted line), 75th percentile, and upper bound values. Asterisks denote significant differences between pre-test and test passage rates observed for that specific test period ($p < 0.05$ [corrected for multiple comparisons]). Eight trials each consisting of 10 naive fish of the same species were used for each sound stimulus. In each trial, a naïve group of fish were exposed to 8 consecutive matched sets of pre-test and test periods ($N = 128$ observations)

in an overall blockage efficiency of $88 \pm 19\%$ (Table 1). Follow-up tests on both pre-test and test periods showed no change in common carp passage rates following repeated exposure to the outboard-motor sound coupled with the air curtain (Supplemental Tables 1, 2). Further, when common carp were tested with the proprietary sound coupled with the air curtain, a treatment effect but no test-number effect was observed (Supplemental Table 2) with reductions in passage rates again being noted at all 8 test periods ($p < 0.05$; Fig. 5f), resulting in an overall blockage efficiency of $100 \pm 1\%$ (Table 1). Paired t-tests on common carp blockage efficiencies showed that when the outboard-motor sound was coupled to the air curtain it was more effective than either the sound alone or the air curtain alone ($p < 0.05$; Table 1, Supplemental Table 5). A similar result was noted for the proprietary sound when coupled with the air curtain ($p < 0.05$; Table 1, Supplemental Table 5). The proprietary sound when coupled with the air curtain had a greater blockage efficiency than the outboard-motor sound coupled with the air curtain ($p < 0.05$; Table 1, Supplemental Table 5).

Largemouth bass When largemouth bass were exposed to the air curtain, we measured both a treatment effect and a test-number effect (Supplemental Table 2) with significant reductions in passage rates observed for all 8 test-periods ($p < 0.05$; Fig. 6d), resulting in an overall blockage efficiency of $68 \pm 23\%$ (Table 1). A small, but significant, reduction in largemouth bass passage rates (i.e.

sensitization) was noted with repeated exposure to the air curtain during the pre-test periods but not test periods (Supplemental Tables 1, 2). Similarly, when the outboard-motor sound was coupled with the air curtain, both a treatment and test-number effect were measured (Supplemental Table 2) with reductions in passage rates being noted at all test periods except number 7 ($p < 0.05$; Fig. 6e), resulting in an overall blockage efficiency of $71 \pm 34\%$ (Table 1). Again, a small reduction in pre-test passage rates, but not test passage rates, were observed following repeated exposure to the outboard-motor sound coupled with the air curtain (Supplemental Tables 1, 2). When largemouth bass were tested with the proprietary sound coupled with the air curtain both a treatment and a test-number effect (Supplemental Table 2) were observed with reductions in passage rates again being noted at all test periods except number 7 ($p < 0.05$; Fig. 6f) resulting in an overall blockage efficiency of $87 \pm 24\%$ (Table 1). Pre-test passage rates declined following repeated exposure to the proprietary sound coupled with the air curtain with no change observed for test passage rates (Supplemental Tables 1, 2). Paired t-tests on largemouth bass blockage efficiencies showed that when the outboard-motor sound was coupled with the air curtain, it was more effective than the outboard-motor sound alone ($p < 0.05$) but not the air curtain alone ($p > 0.05$; Table 1; Supplemental Table 5). Similarly, when the proprietary sound was coupled with the air curtain, it was more effective than either the proprietary sound alone or the air curtain alone ($p < 0.05$; Table 1; Supplemental Table 5). The blockage efficiency of the proprietary sound coupled with the air curtain was greater than that of the outboard-motor sound coupled with the air curtain ($p < 0.05$; Table 1; Supplementary Table 5).

Discussion

Our study clearly demonstrated that the tendency of complex sound to block both bighead and common carp movements is strongly enhanced by coupling it with an air curtain. Additionally, we show the effects of complex sounds can be both species- and sound-specific: a proprietary sound was more effective than an outboard-motor sound at deterring bighead and common carps, but not largemouth bass in which hearing is less sensitive than the carps. The different

effects of each sound stimulus including the air curtain on all three fish species demonstrate that the actions of acoustic deterrents are complex, species-specific and likely multimodal suggesting that even more targeted sets of deterrent stimuli could be developed once understood. Given the strong responses seen to the proprietary sound when coupled with the air curtain, the urgency of addressing the bigheaded carp invasion, and that a commercial version of this system is available; it seems reasonable to field-test a BAFF system at a lock and dam where wild bigheaded carps are found. A field test is extremely important as both biotic (e.g., fish size, fish motivation) and abiotic factors (e.g., water depth, temperature, background noise) will likely affect ultimate deterrent efficiency.

Aside from the practical importance of identifying a carp deterrent system that can be tested in the field, our most important finding was that coupling air curtains with complex sound greatly improves its ability to block invasive carps without apparent habituation. Remarkably, we observed relative blockage efficiencies of approximately 98% for bighead carp and nearly 100% for the common carp to the coupled proprietary sound and air curtain system. These high blockage rates are similar to the over 95% values reported by both Taylor et al. (2005) in a hatchery raceway and Ruebush et al. (2012) in a small creek for the BAFF. Notably, it does not appear that the effects of the air curtain is a unique synergism to just the proprietary sound because the air curtain also improved the effectiveness of the outboard-motor sound. Similarly, Zielinski et al. (2014) showed that playing the sound of a strong air curtain in the vicinity of a weak air curtain greatly enhanced the blockage rate of common carp relative to a weak air curtain or sound alone, leading them to suggest that multiple sensory cues maybe involved in deterrence. Although the reason(s) why the sound coupled with an air curtain worked so well is unclear, our sound mapping suggested that steeper gradients for sound pressure and particle acceleration at higher frequencies (1500 and 2000 Hz), which are within the hearing range of carps (but not largemouth bass) could be partially responsible. This observation of enhanced sound gradients is consistent with mathematical calculations showing that air bubble mixtures alter sound speed in such a way as to both intensify sound capture within air curtains while creating sharp sound gradients in their immediate vicinity (Domenico 1982). Because

particle acceleration is a vector, fishes can also use it to perform oriented movements away from the coupled system, something likely not possible with sound pressure, which is scalar (Zielinski and Sorensen 2017). The humpback whale (*Megaptera novaeanglae*) may also exploit these properties of air bubbles when they herd and capture fishes while emitting sounds into the bubble nets they create (Leighton et al. 2004). It is highly likely that both air bubble size and flow rate (see Domenico 1982; Zielinski et al. 2014) impact sound intensity and frequency within (and near) the coupled air curtain system, and should be optimized to improve function and design of these coupled systems in the field. These possibilities all warrant explicit exploration. The great increase in efficiencies associated with adding an air curtain to complex sound suggests that the additional engineering costs associated with deploying such systems in the field are likely warranted.

Our second most important finding was that different types of complex sounds deterred fishes to different extents; fishes can seemingly perceive discriminate complex sound signals. The cyclic, proprietary sound performed better (though not always significantly better) than a continuous, outboard-motor sound even though the two signals contained similar frequencies and were played at the same amplitude (see Figs. 2, 3). While the difference in blockage and deterrence efficiencies between these two complex sounds was not always large, it was especially apparent for the common carp for which the proprietary sound was nearly twice as effective as the outboard-motor sound at blocking passage. Also notable was our finding that the proprietary sound kept a greater number of common carp and bighead carp away from the deterrent. Why this proprietary sound decreased the number of carps observed near the speaker system is presently not known, but this response would likely be advantageous at navigation locks where boat traffic will complicate the operations and effectiveness of these deterrent systems by creating flows and sound-shadows that fishes could use. The difference in the relative responsiveness of common carp and bighead carp to the outboard-motor sound compared to the proprietary sound likely reflects a species-specific cognitive attribute, rather than a physiological constraint, as bighead carp often seem to be more responsive behaviorally to complex sounds even though they have similar hearing

capabilities (Murchy et al. 2016; Zielinski and Sorensen 2017; Vetter et al. 2018). Additionally, others have noted that fishes tend to be more behaviorally responsive to abrupt sounds (Schwarz and Greer 1984; Engås et al. 1995; Hawkins et al. 2014) which may help explain why the cyclic, proprietary sound was more effective than the continuous, outboard-motor sound. However, some differences in the sound spectrum of the two sounds were also evident with the outboard-motor sound having a bias towards higher frequencies. Without specific paired tests of different complex sounds that only differ in specific frequencies and/or temporal patterns, possible reasons for differences in their efficacies must be considered speculative at this time. What is most important about our study is that we observed differences between different complex sound signals in their ability to block and deter invasive carps, not what may (or may not) be responsible for these differences. Further study on how and why different complex sound signals alter the swimming behavior of different fish species will be challenging because they are best conducted in the field but are clearly warranted. It may be possible that even more deterrent complex sounds could be identified.

Our results also confirm previous work showing that air curtains on their own can serve as relatively efficient deterrents for carps (Zielinski et al. 2014; Zielinski and Sorensen 2015, 2016). By testing different-sized bubbles and lighting conditions, Zielinski et al. (2014) showed that their efficacy in blocking common carp passage is attributable to a combination of sound and hydrodynamic cues although definitive experiments remain to be performed. Presumably, commercially available technologies, such as the BAFF, which has been under development for decades, have optimized techniques to produce specific types of complex sound and air bubble sizes that most reliably and effectively couple sound with an air curtain in the field. Of course, our observation that the air curtain was also modestly effective at blocking largemouth bass, speaks to the likelihood that attributes other than sound are involved in how fishes respond to these stimuli. While we only tested air curtains in near darkness, it is possible that as observed by others (e.g., Patrick et al. 1985), air curtains systems might be more effective when combined with lights allowing fishes to see the deterrent system. In fact, the BAFF system typically

uses lights (Ruebush et al. 2012). Three notable properties of air curtains (and thus air curtain coupled systems) that must be considered in implementation are that air production can be costly, air curtain efficiency drops with water depth and flow (because air bubbles coalesce), and that air curtains are likely to be more effective if slanted in a way to guide (vs. block) fishes (Welton et al. 2002; Perry et al. 2014; Zielinski and Sorensen 2016). These attributes all warrant field testing.

Although our finding that the three fish species we tested responded differently to the five types of sound stimuli was not surprising to us, both the magnitude and nature of the differences we described were. While it not remarkable that bighead carp would be more sensitive to the sound stimuli than the largemouth bass, it was unexpected that the two carp species should respond so differently to the two complex sounds. Especially notable was the sensitivity of largemouth bass to the air curtain, but this might be related to hydrodynamic and/or visual cues. Similar results have been described for the walleye (*Sander vitreus*), a fish native to the Mississippi River basin that also lacks hearing specializations, for which an air curtain reduced escapement from a pond by 44% (Flammang et al. 2014). Although an audiogram for largemouth bass has not been published, the hearing thresholds for the closely related red eye bass (*Micropterus coosae*) and Alabama bass (*Micropterus henshalli*) show these species to be most sensitive to frequencies between 100 and 600 Hz, similar to many native non-ostariophysan fishes (Lovell et al. 2005; Mann et al. 2007; Ladich and Fay 2013). Our study appears to be one of the first to systematically compare responses of different fish species to different sound stimuli and highlights the need for future work. Field work will be especially important because wild fishes may behave differently, and different sets of sensory stimuli are present in the natural world. The success of future applications in the field will depend on developing a good understanding of fish behavior.

Finally, the overall lack of habituation observed in our study, including to the complex sounds coupled with air curtains, is notable and important. In fact, we saw sensitization to the outboard-motor sound in bighead carp and largemouth bass. The basal activity (pre-test passage rates) of largemouth bass decreased with repeated exposure to all five types of sound stimuli, while both pre-test and test movement patterns

for both carp species were remarkably consistent over time. These are seemingly the first observations of behavioral sensitization to sound that we know of in fishes. While it is possible that the sound stimuli we tested were especially resistant to habituation because of their specific attributes, this cannot explain the results for the outboard-motor sound for which we have seen habituation (Zielinski and Sorensen 2017) and it is possible that, by offering fishes a true refuge from sound in the present experiments (as would likely exist in most rivers), we reduced the chance of habituation. Notably, the proprietary sound was also able to deter both carp species and keep them away from the deterrent system. This makes sense because habituation is generally associated with constant exposure regimes (Rankin et al. 2009; Schakner and Blumstein 2013), but this result leads us to question whether even more variable signals might be more effective. Because bigheaded carps are expected to repeatedly challenge locks and dams, along with other fishes that are motivated (e.g., spawning or feeding) to move upstream, both the lack of habituation and indications of sensitization we observed in our study are relevant and warrants further study.

Taken together, the results of our study clearly demonstrate that a proprietary cyclic sound coupled with an air curtain system has special promise to block invasive carps and warrants testing in the field at a navigation lock. An air curtain sound system using the proprietary sound is already commercially available (BAFF) and our data support previous studies suggesting that it is likely to be effective. Nevertheless, while BAFF systems are seemingly well suited to locales that already have many bigheaded carps, and where high rates of blockage are required, sound alone might be adequate for locations where native fishes are of higher concern and/or budgets are limited. Sound also has the advantage of being easier and cheaper to deploy and could be used in deep and fast-flowing waters, where an air curtain coupled with sound may not function as well. Here, the proprietary cyclic sound alone might be best. Lights, as used on the BAFF, also need to be examined, especially because they can make an air curtain more visible. Choices of deterrent type exist and no sensory deterrent system can be expected to be 100% effective, so different combinations (possibly including lights) might be used in different places. While we fully expect that silver carp will respond to the sounds we tested here in similar

way to bighead carp based on past studies (Zielinski and Sorensen 2017), future studies should examine the responses of a broad range of fish species (i.e., invasive and native fishes, fishes with varying hearing sensitivities) to both complex sound and coupled sound and air curtain deterrent systems in natural settings.

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