

An ensonified bubble curtain blocks 4 species of invasive carp in a laboratory flume but also deters other fish, while sound alone is less effective overall and does not target carp

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1 **An ensonified bubble curtain blocks 4 species of invasive carp in a laboratory flume but**
2 **also deters other fish, while sound alone is less effective overall and does not target carp**

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11 **Abstract** Four species of invasive carp from Asia are advancing up the Mississippi River
12 through its locks and dams and threatening to damage to its ecosystems. It has been
13 hypothesized that sensory stimuli could be projected into locks to block the movement of these
14 carp. Sound has garnered attention because carp are hearing specialists, so they might be
15 targetable. A recent study demonstrated that when a broadband cyclic sound was projected into
16 an air curtain to create an ensonified bubble curtain (EBC), it was especially effective at blocking
17 bighead and common carp and less effective at blocking a native species that lacked hearing
18 specializations, while sound alone was generally less effective. However, whether an EBC
19 might be similarly and uniquely effective at blocking all species of carp, and what its effects
20 might be on other fishes in general, has not yet been addressed. To answer these questions, this
21 study examined the responses of 10 species of fishes including 4 carps, 2 native hearing
22 specialists, and 4 native non-specialists in a darkened laboratory flume while either a cyclic
23 sound was played on its own or projected into an air curtain. The EBC blocked all 4 carps 92-
24 97% of the time without habituation, but 5 native fish were also partially blocked. In contrast,
25 sound alone only blocked 2 carps and affected the other fishes in ways not related to their
26 hearing abilities. An EBC appears well suited to blocking carp invasions, especially if native
27 fish movement is a secondary concern.

28

29 **Keywords** Bioacoustic Fish Fence; BAFF; carp; native fish; grass carp; silver carp
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32 Introduction

33

34 In the 1970's, four species of carp from Asia were introduced into sewage and aquaculture ponds
35 in the southern United States from which they escaped into the Mississippi River (Kolar et al.
36 2007; Chapman and Hoff 2011; Reeves 2019). These species joined the common carp (*Cyprinus*
37 *carpio*) which had been introduced from Europe a century before and now dominates many lake
38 and river ecosystems worldwide (Sorensen and Bajer 2011). The "Asian" carps are currently
39 breeding and moving away from their site of introduction, threatening ecosystems in the upper
40 reaches and tributaries of the Mississippi River as well as the Laurentian Great Lakes (ACRCC
41 2021). In most regions, the silver carp (*Hypophthalmichthys molitrix*) is of greatest concern
42 because it is a highly efficient planktivore (Dong and Li 1994; Claus and Sorensen 2019) and
43 jumps when startled (Stell et al. 2020). Its congener, the bighead carp (*H. nobilis*), is also
44 considered a serious threat because it often grows to a large size (~40 kg; Kolar et al. 2007) and
45 hybridizes with silver carp (Lamer et al. 2010). In addition to the bigheaded carps (i.e. the silver
46 and bighead carps), concerns are growing about the grass carp (*Ctenopharyngodon idella*), which
47 feeds on plants and is now breeding in some tributaries of Lake Erie (Cudmore and Mandrak
48 2004; Embke et al. 2016). Further, in the southern United States, the black carp
49 (*Mylopharyngodon piceus*) threatens its mollusks (Nico and Jelks 2011). Finally, the common
50 carp remains a concern because although well established, management efforts continue to
51 remove it from waterbodies which managers do not wish them to re-invade (Sorensen and Bajer
52 2011). All of these carps exhibit migratory behaviors (deGrandcahamp et al. 2008; Harris et al.
53 2021; Banet et al. 2021) which, in the Mississippi River and its tributaries, results in their
54 swimming through locks and dams to invade upstream habitats. Accordingly, locks and dams
55 are being considered as pinch-points in rivers to block invasive carps by performing various
56 actions including adding carp deterrent systems (ACRCC 2021; Zielinski and Sorensen 2021).

57 An especially promising option to stop the invasion of carp is to place deterrent systems
58 in the navigation locks of locks and dams, especially locks and dams with spillway gates that
59 rarely open and are thus not routinely passable so fish must pass through their locks (Zielinski et
60 al. 2018; Zielinski and Sorensen 2021). Several types of deterrent systems are being considered
61 for use in locks (Noatch and Suski 2012), but those which use nonphysical, or sensory stimuli,
62 are favored. This is because nonphysical systems are relatively simpler and less expensive to

63 install and run, do not pose a hazard to human health, and have the potential to target particular
64 species because different fish species have different sensory capabilities (Fay and Tavolga 2012).
65 Sound is of special interest because it is relatively easy to project and carp, like other
66 ostariophysan fishes, have an exceptional sense of hearing because they possess a type of hearing
67 specialization known as Weberian ossicles (Popper and Carlson 1998). A Weberian apparatus
68 can extend the hearing range of fish up to ~1000 hz and increase their sensitivity by several fold
69 (Popper and Carlson 1998; Putland and Mensinger 2019). While the effects of various sounds
70 have been tested on about a dozen species of fish and found to have promise, a wide range of
71 deterrence efficiencies have also been described; however, these tests have used a variety of
72 testing apparatuses, experimental protocols, and sound signals, so conclusions about their true
73 potential remain elusive (Zielinski and Sorensen 2017; Murchy et al. 2016; Putland and
74 Mensinger 2019). Nevertheless, habituation, the phenomenon in which animals learn to ignore
75 biologically-irrelevant stimuli and become less responsive to them with repeated exposure, has
76 emerged as a concern (Zielinski and Sorensen 2017; Dennis and Sorensen 2020a). In sum, it
77 remains an open question whether fish with hearing specializations including carps are more
78 deterred by sound than species that lack specializations and why.

79 Because of the variability and often low level of responsiveness of fish to sound, studies
80 are now testing sound in conjunction with other sensory stimuli to produce multi-modal cues that
81 take advantage of all of their properties. One of the best studied of these are ensonified bubble
82 curtains (EBCs), a type of stimulus in which sound is projected into an air bubble stream (i.e. air
83 curtain) to focus and enhance sound fields while often causing its bubbles to resonate (Brevik
84 and Kristiansen 2002; Leighton 2012; Dennis et al. 2019). In addition, bubble curtains can be
85 aversive in their own right because they have their own acoustic, physical, and visual properties
86 which can be felt and heard by fish acoustico-lateralis system as well as visualized (Zielinski et
87 al. 2014; Zielinski and Sorensen 2016). A commercial version of an EBC is available and
88 known as a bioacoustic fish fence (BAFF) (<https://www.fgs.world>) and has been tested a few
89 times with some success. Welton et al. (2002) found that young, downstream-migrating Atlantic
90 salmon (*Salmo salar*) were deterred by a BAFF by 66-79% in a small stream with the highest
91 efficiencies being observed at night. A similar finding without a day-night effect was noted for
92 downstream-migrating Chinook salmon smolts (*Oncorhynchus tshawytscha*) in a large river,
93 although this BAFF was illuminated and no day-night effect was noted (Perry et al. 2014). In a

94 raceway test, Taylor et al. (2005) found that bighead carp were repelled up to 95% of the time by
95 a BAFF but no other fish was tested, nor was sound alone. Later, in a field test, a variety of
96 fishes (including some carps) were captured and transplanted downstream of an illuminated
97 BAFF and it was seen to reduce the upstream recapture of many species, including silver carp,
98 suggesting this system can work in the field, but not how well, or why (Ruebush et al. 2012).
99 Finally, in a laboratory test of an EBC, we found that common carp and bighead carp were
100 nearly completely blocked by an EBC in a darkened lab flume (blockage efficiencies of 97% and
101 99% respectively) while largemouth bass (*Micropterus salmoides*), which lack hearing
102 specializations, were blocked to a lesser (86%) extent (Dennis et al. 2019). We also found that
103 an EBC worked more effectively than sound or air alone and that a cyclic broadband sound was
104 especially effective. In sum, while these studies suggest that EBCs have promise to block carp
105 and might even be able to target them, this type of stimulus has only been tested on a few species
106 including two carps so conclusions about its broad applicability for field implementation cannot
107 be drawn.

108 The overarching goal of this study was to determine if EBCs are a better option to control
109 invasive carps than sound alone and if either option can target carps without significantly
110 affecting native fishes. We asked two questions. First, does a cyclic broadband sound
111 effectively block all four species of carp without affecting other fishes including native hearing
112 specialists? Second, does this sound block carps more effectively than sound alone, and if so,
113 what effects might it have on native fishes, including hearing specialists? To answer these
114 questions, we tested the responses of 4 species of invasive carp, as well as 2 native fish species
115 with hearing specializations and 4 without hearing specializations, to sound alone and an EBC in
116 the darkened laboratory flume with protocols we have used previously (Dennis et al. 2019;
117 Dennis and Sorensen 2020b).

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120 **Materials and methods**

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122 Experimental Design

123

124 Experiments proceed in a stepwise fashion, following established approaches (Dennis et al 2019;
125 Dennis and Sorensen 2020b). First, we selected native species of interest as well as species of
126 invasive carp that we could obtain from local hatcheries (see below). Second, we brought these
127 fish into the laboratory where they were held in large aquaria (see below). Third, these fish were
128 then tested following established protocols (Dennis et al. 2019) in a 8-m darkened laboratory
129 flume as groups of 10 to one of three stimuli: 1) no stimulus (“no-treatment control” to determine
130 their basal level of activity); 2) a cyclic sound (the same sound tested by Dennis et al. 2019; see
131 below); or 3) this cyclic sound coupled with air to create an EBC (also the same as Dennis et al.
132 2019; see below). After a 1-h pre-test/acclimation period, these groups of fish were tested 8
133 times (each testing period was considered a trial), each of which had two sets of 6-min periods, a
134 6-min pre-test with no stimulus, followed by a 6-min test period with a stimulus. Trials were
135 separated by a 10-min period with no stimulus to permit recovery. The flume was designed so a
136 stimulus could be played on either side with side being selected at random by coin-toss for each
137 experimental trial. Each experiment took a total of 238 min. Fish position was recorded during
138 the pre-test and test-periods (test number) using overhead cameras (confirming crossing if/as
139 necessary using underwater cameras), then analyzed by quantifying the number of times fish
140 crossed the midline where the deterrent system was located (i.e., passage rate) for each pre-test
141 or test period. Because we had a disease problem with our bighead carp, we used the data
142 collected by Dennis et al. (2019) for this species although it was re-analyzed as our analysis
143 differed slightly. Fish were only tested once so all fish were naive and we could address
144 habituation with clarity.

145

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147 Fish

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149 In addition to the four species of carp that we could obtain from local hatcheries, we selected a
150 variety of 6 native fishes based on availability, taxonomic variety, ecology, and whether or not
151 they had hearing specializations (Table 1). Fish were sexually immature and ranged in size from
152 about 90-200 mm in total length (TL). Channel catfish (*Ictalurus punctatus*) and lake sturgeon
153 (*Acipenser fulvescens*) were obtained from the Genoa National Fish Hatchery (Genoa, WI,
154 USA) while bluegill sunfish, (*Lepomis macrochirus*), largemouth bass, golden shiners

155 (*Notemigonus crysoleucas*), common carp, rainbow trout (*Oncorhynchus mykiss*), grass carp,
156 bighead carp, and silver carp were obtained from Osage Catfisheries (Osage Beach, MO, USA).
157 All fish were shipped to the University of Minnesota and placed into inflow-through 1000L
158 circular tanks prior to testing for at least 3 months supplied with well water on a 16:8 L:D
159 photoperiod. Bluegill sunfish, channel catfish, largemouth bass, golden shiners, common carp,
160 rainbow trout, and grass carp were fed 2.5 mm floating pellets (Skretting USA, Tooele, UT,
161 USA). Silver carp and bighead carp were fed a mixture of Spirulina and Chlorella algae (Claus
162 and Sorensen 2017; Nuts.com, NJ, USA). Lake sturgeon were fed brine shrimp (Hikari, Japan).
163 Procedures were approved by the University of Minnesota Institutional Animal Care and Use
164 Committee (Protocol: 1712-35381A) and all necessary federal and state permits were obtained.

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166

167 Laboratory Flume

168

169 Experiments were performed in the same custom-built indoor elliptical flume (8 m long x 1 m
170 wide channel, 1.0 m wall height) employed by Dennis et al. (2019) who provides a detailed
171 description so only an overview is provided here for context. Briefly, the flume was constructed
172 of fiberglass and its floor and walls (inside and out) lined with concrete pavers with foam pads to
173 reduce sound reverberation. Sound/air sources which were positioned on its bottom at the mid-
174 line of each of its long sides. The flume was located in a dark and quiet room and illuminated
175 with 6 overhead infrared illumination systems (840 nm, < 1-lux; VT-IR1, Vitek, Valencia, CA).
176 Low-light cameras were also positioned overhead so fish position could be observed at a remote
177 location. Several underwater cameras were also placed in the flume so that crossings through the
178 bubble curtain could be confirmed when needed. Well water (18°C) was supplied to the flume
179 until 1-h before the experiments started, when it was turned off except for the bighead carp trials
180 for which a slow flow was maintained as we found they stopped swimming in stagnant water.
181 Water depth was maintained at 0.3 m.

182

183

184

185

186 Stimuli

187

188 We used the same speakers, sound, and EBC set-up as that employed by Dennis et al (2019) who
189 provides detailed descriptions of all three so only an overview is provided here for context.

190 Briefly, the sound system was comprised of two sets of two speakers (FGS MkII 15-100; Fish
191 Guidance System Ltd.; Southampton, UK), which were positioned equidistant from each other at
192 the center of each of the long sides of the flume alongside two fine porous pipes (AD100T;
193 Pentair AES; Apopka, FL). For EBC experiments the porous pipes were supplied with air at a
194 rate of 1.2 L s^{-1} to create a fine bubble stream via blowers located in another room while sound
195 settings were left as is. Our test sound contained frequencies between 20-2000 hz which cycled
196 (Sound 7, Fish Guidance Systems) and was played at a volume to create a sound field of ~150-
197 160 db at 1000 hz (ref $1 \mu\text{Pa}$) at the source (Fig. 1; see Dennis et al. 2019 for detail). Sound
198 pressure and particle acceleration levels for both the sound and EBC were mapped using a C15
199 hydrophone (Cetacean Research, Seattle, WA) as well as an accelerometer (TASCAM US-
200 12mkII; TEAC, Montebello, CA). Dennis et al. (2019) provide initial descriptions of this sound
201 and the EBC including spectrograms and elaborate here by showing sound maps for sound
202 pressure (SPL_{RMS}) at three selected frequencies within the carps' hearing range: 500-600hz,
203 1000-1100hz, and 1500-1600hz. These maps appear to show much sharper sound pressure
204 gradients near the stimulus for the EBC than sound alone, especially for the higher frequencies,
205 but that maximum sound pressures were similar (Fig. 1).

206

207

208 Statistical Analysis

209

210 Similar to Dennis et al. (2019) and Dennis and Sorensen (2020a), we used a step-wise approach
211 to analyze our results which was based on generalized linear mixed models (GLMM). Ten
212 models were used in total, one for each species. This approach used custom-built matrices to
213 facilitate comparisons between species and their responses to stimuli and was more powerful and
214 direct than a 3-way ANOVA (Dr. G. Oelhart, Statistical Consulting Center, University of
215 Minnesota< Minneapolis, MN). In particular, these matrices allowed us to directly compare
216 passage rates between control and test conditions for each experiment (species) as well as to

217 calculate overall blockage efficiencies. Once we had determined whether responses to stimuli
218 were significant, we then examined habituation using ANOVAs, before next examining
219 differences between stimuli, species and then groups of species (ex. the carps). These steps are
220 outlined below.

221 For our first step, we examined changes in passage rates using a custom design matrix for
222 each set of experiments written in R and entered into each GLMM. In each GLMM, “fish group
223 number” (test group) was used as a random effect to account for repeated measurements taken
224 from that group of fish. Passage rate data for the pre-test and test periods were transformed to fit
225 a Poisson distribution because these are count data. Assumptions of normality for each GLMM
226 (e.g. that residuals are randomly and normally distributed) were checked visually using a plot of
227 the deviance residuals versus fitted values to test for random distribution of residuals, while
228 over-dispersion was tested by examining the variance of the residuals (McCullagh and Nelder
229 1989). If the variance of the residuals was greater than 2, we corrected for this hyper-variability
230 by dividing our test statistic by the square root of the dispersion parameter (McCullagh and
231 Nelder 1989) and calculating new p-values for each comparison in that GLMM (this was only
232 necessary for silver and bighead carp). Raw passage rate counts were used as the response
233 variable in the GLMM because our fish moved as individuals in darkness (i.e. fish were not
234 observed to be schooling) and initial evaluations showed that all passage rates were described
235 well by log-linear fits (Tables S1- S10). To determine whether each particular stimulus altered
236 the passage rate of each species, we used a GLMM to compare the log-linear passage rates
237 calculated for each control experiment for that species (N=160 control periods) with the matched
238 log-linear passage rate calculated for when the stimulus was being tested (N = 80 test periods)
239 ($P < 0.05$). In addition, if significance was observed, we compared individual test values with
240 their control values using the GLMM while correcting for multiple comparisons using
241 Bonferroni function ($p < 0.05$). Finally, mean blockage efficiencies for each species and
242 stimulus were calculated by dividing each test’s calculated passage rate for each experiment by
243 the calculated mean passage rate noted during the matched no-treatment control experiment,
244 subtracting the resulting value from 1, and then multiplying that by 100 to get a percent. Mean
245 blockage efficiencies were then calculated.

246 For our second step, we tested for changes in passage rate (habituation) over time for
247 each experiment (species). To accomplish this, we subtracted the each test passage rate value

248 from its matched pre-test value in experiment, divided that by the pre-test value and multiplied
249 by 100 to derive a set of 8 passage rates for each experiment. Trends in these values were then
250 evaluated using a separate 1-way repeated measures ANOVA (SAS Institute Inc., Cary, NC,
251 USA) for each species and stimulus type, with trial number (1-8) being the main effect, and fish
252 group number (1-10) as a random effect. If a decrease was described ($p < 0.05$), habituation was
253 noted.

254 Next, for our third step, we determined whether coupling sound with air to make an EBC
255 made it more effective. Mean blockage efficiencies were calculated for each species and
256 stimulus-type, and these values compared by performing a series of Bonferroni-corrected z-tests
257 ($p < 0.05$, $n = 10$). For a fourth step, we sought to determine which fish species were most
258 responsive to each stimulus. To accomplish this, we performed two series of Bonferroni-
259 corrected z-tests ($p < 0.05$, corrected for multiple comparisons). The first compared the blockage
260 efficiencies of sound among the ten tested species ($N = 45$ comparisons), and the second
261 compared the blockage efficiencies of sound coupled with air among the ten tested species ($N =$
262 45 comparisons). Finally, to determine if hearing ability (specializations) affected fish
263 responsiveness, mean blockage efficiencies were compiled by fish type (i.e. carp, native hearing
264 specialists, native non-hearing specialists) for sound alone and the EBC, and then compared
265 using paired t-tests. These a priori analyses were performed using JMP Pro 13. (SAS Institute
266 Inc., Cary NC, USA) with Bonferroni corrections ($P < 0.05$).

267

268

269 **Results**

270

271 *Does a cyclic broadband sound effectively block all four species of carp without affecting other*
272 *fishes, including native hearing specialists?*

273

274 No-treatment control experiments showed that fish passage rates for all 10 species were
275 relatively constant (Fig. 2, 3) and described by log-linear relationships (Supplemental Tables S1-
276 S10). GLMM analysis next showed that the passage rates of all 10 species were affected by
277 sound ($p < 0.05$), with 9 species showing a decrease and channel catfish showing an increase
278 (Figs. 2, 3; Table 2, 3). Habituation was noted in three species: the largemouth bass, silver carp,

279 and grass carp (29 - 42% decreases in blockage rate with time; $p < 0.05$; Table 2). The overall
280 mean blockage efficiency for all fish was only $44 \pm 37\%$ (mean \pm SD).

281 Examining the carps, we noted a high level of variability in the efficacy of sound at
282 blocking the 4 carp species (Fig. 4). While bighead carp and common carp were both effectively
283 blocked by sound ($86 \pm 48\%$, $83 \pm 27\%$ respectively) and without habituation (Figs. 2B, 2H;
284 Table 3), silver and grass carp were only weakly affected ($31 \pm 12\%$; $21 \pm 9\%$ respectively) with
285 habituation being noted in both instances ($p < 0.05$) (Figs. 2E, 2K; Table 3). Silver carp and grass
286 carp were blocked less than the bighead and common carp ($p < 0.05$), which also did not differ
287 from each other (Table 2), but to the same extent as largemouth bass, a native non-hearing
288 specialist (see below). Taken as whole, the carp were not more affected by sound more than any
289 other group of fish including native hearing non-specialists ($p > 0.05$; Table 4).

290 Responses of native hearing specialists also varied between species. Thus, while golden
291 shiners were blocked moderately effectively ($77 \pm 27\%$) and without habituation (Fig. 2N; Table
292 2), channel catfish were strongly attracted ($p < 0.05$; Fig. 3B), also without habituation ($p > 0.05$;
293 Table 2). Native hearing specialists were not affected by sound more than non-hearing
294 specialists when considered as a group ($p > 0.05$; Table 4)

295 Finally, responses of native non-hearing specialists were found to be moderate and less
296 variable and not to differ from each other. Thus, while bluegill sunfish were blocked with
297 moderately effectively by sound alone ($60 \pm 24\%$; Fig. 3H) without habituation, so were lake
298 sturgeon ($47 \pm 24\%$; Fig. 3N), rainbow trout ($45 \pm 27\%$; Fig. 3K), and largemouth bass ($34 \pm$
299 27%) which also showed habituation ($p < 0.05$) (Fig. 3E; Table 2).

300

301

302

303 *Does the cyclic sound block carps more effectively than sound alone and if so, what effects might*
304 *it have on native fishes, including hearing specialists?*

305

306 GLMM analysis for each of the 10 species exposed to the EBC showed that the passage rates of
307 all 10 species decreased dramatically when exposed to this multi-modal stimulus ($p < 0.05$; Figs.
308 2, 3). Notably, habituation was not observed for any species (Table 4). Taken as a whole, the
309 mean blockage efficiency for all 10 species to the EBC was $82 \pm 23\%$, nearly twice that of the

310 sound. Increases in blockage were noted for all 10 species, which on average differed by 11%
311 ($P < 0.05$) (Fig. 4).

312 Mean blockage efficiencies for all 4 carp were consistently high ($94 \pm 29\%$) for the EBC
313 and while the silver carp was blocked more efficiently than the other 3 carp species ($p < 0.05$;
314 Table 3), the difference was small (2%) and the other carp species did not differ from each other
315 ($p > 0.05$). While silver carp were blocked $97 \pm 36\%$ of the time (Fig. 2F), bighead carp were
316 blocked $92\% \pm 42\%$ of the time (Fig. 2C), grass carp $95 \pm 24\%$ of the time (Fig. 2L), and
317 common carp $95 \pm 42\%$ of the time (Fig. 2I). When the carp were analyzed as a group the carps
318 were blocked more than the native non-hearing specialists ($p < 0.05$), but not the native hearing
319 specialists ($p > 0.05$) (Table 5).

320 Both of the native hearing specialists were also blocked more efficiently by the EBC than
321 sound alone (36% increase; $p < 0.05$). While golden shiners were blocked with high efficiency by
322 sound ($89 \pm 27\%$; $p < 0.05$) and without habituation (Fig. 2P; Table 2), channel catfish were
323 weakly repelled ($P < 0.05$; Fig. 3C) without habituation ($p > 0.05$; Table 3). Notably, this species
324 had been attracted by the sound alone (41%, see above).

325 Finally, responses of the native non-hearing specialists were relatively strong ($P < 0.05$)
326 and did not differ from each other ($p > 0.05$), or golden shiners, a hearing specialist (Table 3).
327 Thus, while bluegill sunfish were moderately blocked ($p < 0.05$) by the EBC ($83\% \pm 30\%$)
328 without habituation (Fig. 3I), so were lake sturgeon ($84\% \pm 39\%$) (Fig. 3P), rainbow trout (81%
329 $\pm 39\%$) (Fig. 3P), and largemouth bass ($88 \pm 48\%$) (Fig. 3I, Table 3).

330

331

332 **Discussion**

333

334 Our laboratory study clearly demonstrated that ensonified bubble curtains (EBCs) are a highly
335 effective way to block the movement of 4 species of invasive carp presently found in North
336 America. However, while the effects of an EBC on all 4 tested carps were substantial (92 - 97%
337 blockage), and carp did not habituate to it, we also found that the EBC partially blocked many
338 native fishes, including some lacking hearing specializations. In contrast, the sound projected
339 into the EBC was much less effective when tested on its own for all 10 fish species, especially

340 the silver and grass carp, which were blocked less than 50% of the time and habituated.
341 Remarkably, no relationship was noted between whether species had hearing specializations or
342 not and how strongly they were responded by the sound alone. In contrast, responses to the EBC
343 were seen to be weakly carp-specific. We conclude that EBCs offer genuine and unique promise
344 to block invasive carps in rivers, including the highly invasive grass and silver carps, although
345 their effects on the movement of native fishes will need to be addressed.

346 Our most important finding was that the EBC we tested functions as a singularly effective
347 fish deterrent for fish, and carp in particular. All 4 species of the carp we tested, including the
348 silver and grass carp, were nearly completely blocked and without habituation. However,
349 although carps as a group were more affected the EBC, 5 of the other 6 native species we tested
350 were also strongly effected with blockage efficiencies in the 81-89% range. Thus, although the
351 EBC did not target carps very effectively, it did show promise in that regard. We expect the
352 EBC to have similar effects on other carp including the black carp. Importantly, our results
353 appear replicable; the results of this study are nearly identical to those previously described for
354 both the common carp (95% vs 99%, a hearing specialist, and largemouth bass, a non-hearing
355 specialist (88% vs. 87%) (Dennis et al. 2019). The reasons for the EBC's high level of overall
356 efficacy likely relate to its multi-modal nature with sound playing an important role (see below).
357 Our finding of extremely high blockage efficiencies are also similar to those noted by a
358 commercial BAFF tests for carp. Taylor et al. (2005) noted an approximate 90% block of
359 bighead carp in a hatchery raceway. Additionally, Ruebush et al. (2012) noted similarly high
360 blockage rates (seemingly over 95%) for wild transplanted silver carp in a small creek using an
361 illuminated BAFF under natural conditions although they, like us, noted that a number of native
362 species were also seemingly affected. In any case, the EBCs appear to present new opportunities
363 for reliably controlling carp passage.

364 Our second most important finding was that the sound we tested, and which Dennis et al.
365 (2019) had previous found more effective than another broadband sound, was consistently less
366 effective than the EBC for all 10 species of fish while having little effect on two carps and being
367 plagued by habituation. Especially notable was the fact the nether silver nor grass carps were
368 strongly affected by sound alone. The blockage efficiencies we noted for common carp and
369 largemouth bass were also very similar to those seen previously for sound (83% vs 79%; 34% vs
370 50%; Dennis et al. 2019). Indeed, our study may be the first study to show such a high level of

371 repeatability, suggesting that the high level of variation between species is biologically relevant.
372 Especially intriguing was our observation that the channel catfish was strongly attracted to the
373 sound, perhaps reflecting the fact that this species uses a stridulatory sound that might resemble
374 the cyclic sound to communicate (Fine et al. 1995). Also interesting and relevant was the fact
375 that silver and grass carp quickly habituated to this sound after showing a few strong responses.
376 In both cases, we were testing small, young fish that were very active; perhaps these fish were
377 innately more motivated to stay active to find food than to avoid a sound of little apparent
378 significance. Notably, we were able to repeat the silver carp results on a small scale with few
379 unused fish (Fig S1) and all fish were healthy. Although we were the first to test responses of
380 grass carp to sound, others have tested much older/ larger silver carp. While Vetter et al. (2015)
381 noted consistent aversion in a well-lit tank that may have permitted visual learning, Zielinski and
382 Sorensen (2017) tested silver carp in darkness and observed rapid habituation as noted here.
383 Habituation, the tendency of animals to learn to ignore biologically irrelevant stimuli (Rankin et
384 al. 2007) once again appears to be a challenge when testing sound alone (Dennis and Sorensen
385 2020b), at least to the synthetic sounds being employed. We do not believe that there is anything
386 unusual about the broadband cyclic sound we tested because while Dennis et al. (2019) showed it
387 to be more effective than the broadband outboard-motor sound, the difference was not great or
388 qualitatively different. Together, the results of our studies and others (Putland and Messinger
389 2019) describe responses to sound varying by species and testing scenario, calling into question
390 the value of sound on its own to block carps in rivers.

391 It is interesting and important to speculate why the EBC is so potent because
392 understanding its actions might lead to more effective and/or better targeted EBCs. By
393 previously showing that the effects of an EBC on three species of fish were greater than elicited
394 by either sound or air alone, Dennis et al. (2019) provided compelling evidence that the EBC is
395 multi-modal. The weak relationship we saw between EBC potency and fish hearing ability in our
396 experiment (at least for carp), also argues that factors in addition to sound pressure are important.
397 Likely, particle motion, which is perceived by all fish with otoliths, plays a role in the actions of
398 the EBC because sturgeon, which are insensitive to pressure component of sound, showed
399 surprisingly robust responses to the EBC in our study. However, while the specific
400 characteristics of the sound used in an EBC may be important, it does not appear to be critical or
401 enabling because Dennis et al. (2019) showed the cyclic sound to be only ~10% more effective

402 than the outboard motor sound, and quantitatively no different. Likely an EBC is effective
403 because it produces a range of sensory fields that are detected by multiple sensory systems as
404 fish encounter the sharp but complex sound pressure, particle motion, and tactile cues associated
405 near EBCs (Leighton 2002; Leighton et al. 2004; Dennis et al. 2019). We speculate that this
406 combination of sensory cues may be perceived as novel and distinctive by fish which then seek
407 to avoid it because it is stress-inducing. Avoidance is easily achievable because walls of bubbles
408 and the sensory fields associated with them can followed (Dominico 1982; Leighton et al. 2004;
409 Dennis et al. 2019). Sound does not act in such a complex manner. The dynamic, turbulent
410 nature of bubble curtains may also reduce habituation. In this way, fish that hear well (i.e. detect
411 sound pressure via hearing specializations) such as carp, will be especially deterred (unless the
412 sound is actually innately relevant to them), but those that do not hear it will still detect the EBC
413 and avoid it. The carps may be strongly deterred because they share a common set of sensory
414 systems and neurological/ cognitive processes in addition to hearing. If true, then the efficacy of
415 EBC might be increased and targeted by varying the nature of the bubble systems (bubble size,
416 flow and structure) and how sound pressure is coupled to it to drive resonance, as well as by
417 adding other stimuli to match sensory perception in carps. Introducing visual cues (see below)
418 into air curtains might be another possible option, as seen at some commercial BAFFs (Perry et
419 al. 2014). These possibilities will require additional study that should pair high-resolution
420 measurement of all sensory fields associated with EBCs, fish sensory physiology, and fish
421 behavior, both in the laboratory and natural world.

422 Our study had some significant strengths and a few weaknesses. We believe it is the
423 largest study of its kind to test acoustic stimuli as deterrents on fish, having tested 10 species to
424 two stimuli and using over 3000 individuals. We tested only naive (and healthy) fish, although
425 all were immature and unmotivated. Importantly, our findings both replicate and compliment
426 those of Dennis et al. (2019), and support field observations with a BAFF (see below).
427 Nevertheless, like all laboratory studies our study has its limitations. In particular, we only
428 tested small sample of the many taxa of fish found in the Mississippi River and only one type of
429 hearing specialization (i.e. the Weberian apparatus in Ostariophysans). Further, we only tested
430 one water depth and set of lighting conditions (darkness) and some experiment suggest that
431 BAFF are more effective in the day (Welton et al. 2002). We also did not test the effects of
432 water flow which would alter EBC structure and acoustics in rivers. More field tests of EBCs

433 that include more variables and both carps as well as native fishes are needed to expand on
434 Ruebush et al. (2012)'s pioneering work. Light should be included because carp are deterred by
435 it and when used to illuminate air curtains, it provides additional orientational cues (Dennis and
436 Sorensen 2020b). These tests should consider measuring sensory fields in detail and evaluating
437 how fish approach and hopefully avoid these fields, or some combination thereof. Efforts
438 probably need to consider effects on migrating native fish and also how possible concerns might
439 be addressed by running BAFFs using different types of bubble systems at times that target carp
440 migrations, or perhaps using traps (or fish ladders) in combination with the air curtain so that
441 native fish can be captured and moved upstream while carp are removed. The economic and
442 environmental damage being wrought by invasive carps and the value of maintaining
443 biodiversity argue that these possibilities are well worth exploring (ACRCC 2021).

444 In conclusion, the results of this study, taken together with those of Dennis et al. (2019)
445 in the laboratory and others in the field (Ruebush et al. 2012), demonstrate that EBCs have great
446 and singular promise to stop invasive carps while carrying some risk of disrupting the movement
447 of native fishes. However, based on the present results, sound on its own would appear to little
448 promise at stopping all species of carps, especially grass and silver carps, or effectively targeting
449 any group. Field and laboratory studies of EBCs are urgently needed to elucidate their actions
450 on wild fish while determining how they work and might be improved.

451

452

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463

464 **Declarations**

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468 **Conflicts of interest/ competing interests:** Not applicable.

469 **Availability of Data and Materials:** Data are available from the authors upon request.

470 **Code availability:** Available from authors upon request

471 **Author contributions.** This research was conceived by Peter Sorensen who also acquired the
472 funding and edited final drafts of the manuscript. Data collection and analysis was performed by
473 Jane Feely who wrote the first drafts of the manuscript.

474 **Ethics approval:** Procedures were approved by the University of Minnesota Institutional
475 Animal Care and Use Committee (Protocol: 1712-35381A).

476

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577 **Figure legends**

578

579 **Fig. 1** Schematic drawing of an overhead view of the elliptical laboratory flume used by this
580 study and by Dennis et al. (2019) as well as Dennis and Sorensen (2020b). Pairs of speakers
581 were placed in mid-channel along with an air injection system. Panels A-F to the right show
582 plan views of sound pressure (RMS) levels in dB (ref 1 μ Pa) at different frequency ranges for
583 sound alone (A, C, F) and the ensonified bubble curtain (EBC) (B, D, G) (see text for details).
584

585 **Fig. 2** Mean passage rates \pm standard deviation (SD) (i.e. number of passages per 6-min pre-test
586 or test period with stimulus) of 5 species of fish with hearing specializations (4 carps and 1
587 native hearing specialist) during control conditions (no stimulus), sound only, and sound coupled
588 with air as an ensonified bubble curtain (EBC) across time. Test number is indicated on the x-
589 axis and differences between individual pre- and test passage rates are shown by an asterisk
590 ($p < 0.05$; see text): (A). Bighead carp - control; (B) Bighead carp - sound only; (C). Bighead carp
591 - EBC; (D). Silver carp - control; (E) Silver carp - sound only; (F). Silver carp - EBC; (G).
592 Common carp - control; (H) Common carp - sound only; (I) Common carp - EBC; (J). Grass
593 carp - control; (K) Grass carp - sound only; (L). Grass carp, - EBC; (M). Golden shiners- control;
594 (N) Golden shiners - sound only; (O). Golden shiners – EBC. Note that scale is different fro
595 silver and grass carp as they were more active.

596

597 **Fig. 3** Mean passage rates \pm standard deviation (SD) (i.e. number of passages per 6-min pre-test
598 or test period with stimulus) of 1 species of native hearing specialist and 4 native non-hearing
599 specialists during control conditions (no stimulus), when tested with sound alone, and sound

600 coupled with air as an ensonified bubble curtain (EBC) across time. Test number is indicated on
601 the x-axis and differences between individual pre- and test passage rates are shown by an asterisk
602 ($p < 0.05$; see text): (A). Channel catfish - control; (B) Channel catfish - sound only; (C). Channel
603 catfish - EBC; (D). Largemouth bass - control; (E) Largemouth bass - sound only; (F).
604 Largemouth bass - EBC; (G). Bluegill sunfish - control; (H) Bluegill sunfish - sound only; (I)
605 Bluegill sunfish - EBC; (J). Rainbow trout- control; (K) Rainbow trout - sound only; (L).
606 Rainbow trout - EBC; (M). Lake sturgeon - control; (N) Lake sturgeon - sound only; (O). Lake
607 sturgeon – EBC.

608

609 **Fig. 4** Mean blockage efficiencies \pm standard deviation (SD) of 10 species of fish to sound alone
610 (light bars) or an ensonified bubble curtain (EBC, dark bars). Rates for each species were
611 compared with each other (see Tables 2 and 3) and between sound and EBC (see text).
612 Differences for the latter ($p < 0.05$) are noted with an asterisk.

613

614 **Table 1** Species tested, their taxonomic group, origin, size, and whether they possess hearing
 615 specializations.

Fish Species	Family	Native or Non-native	Length (mean \pm SD) cm	Weight (mean \pm SD) g	Hearing Specialization (Yes or No)
Bighead carp (BC) (<i>Hypophthalmichthys nobilis</i>)	Cyprinidae	Non-native	142 \pm 15	33.06 \pm 8.48	Yes
Silver carp (SC) (<i>Hypophthalmichthys molitrix</i>)	Cyprinidae	Non-native	85 \pm 11	5.58 \pm 1.55	Yes
Common carp (CC) (<i>Cyprinus carpio</i>)	Cyprinidae	Non-native	110 \pm 19	20.22 \pm 10.59	Yes
Grass carp (GC) (<i>Ctenopharyngodon idella</i>)	Cyprinidae	Non-native	133 \pm 18	24.34 \pm 9.78	Yes
Golden shiners (GS) (<i>Notemigonus crysoleucas</i>)	Cyprinidae	Native	88 \pm 10	6.52 \pm 3.18	Yes
Channel catfish (CH) (<i>Ictalurus punctatus</i>)	Ictaluridae	Native	138 \pm 19	23.62 \pm 8.89	Yes
Largemouth bass (LB) (<i>Micropterus salmoides</i>)	Centrarchidae	Native	124 \pm 23	24.76 \pm 13.54	No
Bluegill sunfish (BS) (<i>Lepomis macrochirus</i>)	Centrarchidae	Native	106 \pm 15	20.75 \pm 10.19	No
Rainbow trout (RT) (<i>Oncorhynchus mykiss</i>)	Salmonidae	Native	130 \pm 13	24.50 \pm 5.24	No
Lake sturgeon (LS) (<i>Acipenser fulvescens</i>)	Acipenseridae	Native	162 \pm 18	12.75 \pm 3.14	No

616

Table 2. Effects of sound alone on the passage rates of 10 species of fish. Species, mean passage rates for the no-treatment control and test periods (calculated from individual trials), mean blockage efficiency (from GLMM), habituation, comparisons between the blockage efficiencies between the 10 species ($p < 0.05$). Mean \pm Standard Deviation (SD).

Species	Mean Passage Rate Control	Mean Passage Rate Sound	Mean Blockage Efficiency	Habituation Measured (Yes or No)	Blocked More Than:	Blocked Less Than:
Bighead Carp (BC)	14 \pm 8	2 \pm 2*	86 \pm 48%	No	GC, SC, CH, LS, RT, LB, BS	N/A
Silver Carp (SC)	30 \pm 20	35 \pm 21*	31 \pm 12%	Yes	CH	BC, CC, GS, BS
Common Carp (CC)	16 \pm 9	3 \pm 4*	83 \pm 27%	No	GC, SC, CH, LS, RT, LB, BS	N/A
Grass Carp (GC)	57 \pm 14	46 \pm 20*	21 \pm 9%	Yes	CH	BC, CC, GS, LS, RT, LB, BS
Golden Shiners (GS)	10 \pm 5	4 \pm 3*	77 \pm 27%	No	GC, SC, CH, LS, RT, LB, BS	N/A
Channel Catfish (CC)	11 \pm 5	19 \pm 7 ⁺	-41 \pm 15%	No	N/A	BC, CC, GC, SC, GS, LS, RT, LB, BS
Largemouth Bass (LB)	11 \pm 10	3 \pm 3*	34 \pm 27%	Yes	CH	BC, CC, GS, BS
Bluegill Sunfish (BS)	8 \pm 3	3 \pm 2*	60 \pm 24%	No	GC, SC, CH, LB	BC, CC, GS
Rainbow Trout (RT)	7 \pm 5	5 \pm 4*	45 \pm 27%	No	GC, CH	BC, CC, GS
Lake Sturgeon (LS)	8 \pm 6	5 \pm 4*	47 \pm 24%	No	GC, SC, CH	BC, CC, GS

*decrease in passage rate vs. control rate measured by GLMM ($P < 0.05$); + significant increase; N/A= no affect

Table 3 Effects of the ensonified bubble curtain (EBC) on passage rates of 10 species of fish. Species, mean passage rates for no-treatment control and test periods (calculated from individual trials), mean blockage efficiency (from GLMM), habituation, comparisons between the blockage efficiencies of the 10 species ($p < 0.05$). Means \pm Standard Deviation (SD).

Species	Mean Passage Rate Control	Mean Passage Rate EBC	Mean Blockage Efficiency	Habituation? (Yes or No)	More Effective Than Sound?	Blocked More Than:	Blocked less Than:
Bighead Carp (BC)	14 \pm 8	1 \pm 0.6*	92 \pm 53%	No	Yes	CH, RT	SC
Silver Carp (SC)	30 \pm 20	1 \pm 3*	97 \pm 36%	No	Yes	BC, CC, GS, BS, LS, RT, LB, GC, CH	N/A
Common Carp (CC)	16 \pm 9	0.9 \pm 1*	95 \pm 42%	No	Yes	CH, GS, LS, RT, LB, BS	SC
Grass Carp (GC)	57 \pm 14	3 \pm 3*	95 \pm 24%	No	Yes	CH, GS, LS, RT, LB, BS	SC
Golden Shiners (GS)	10 \pm 5	1 \pm 0.5*	89 \pm 36%	No	Yes	CH	CC, GC, SC
Channel Catfish (CT)	11 \pm 5	10 \pm 3*	19 \pm 18%	No	Yes	N/A	BC, CC, GC, BS, LS, RT, LB, SC, GC
Largemouth Bass (LB)	11 \pm 10	0.8 \pm 1*	88 \pm 48%	No	Yes	CH	CC, GC, GC
Bluegill Sunfish (BS)	8 \pm 3	2 \pm 2*	83 \pm 30%	No	Yes	CH	CC, GC, SC
Rainbow Trout (RT)	7 \pm 5	1 \pm 2*	81 \pm 39%	No	Yes	CH	CC, GC, SC
Lake Sturgeon (LS)	8 \pm 6	1 \pm 1*	84 \pm 39%	No	Yes	CH	CC, GC, SC

* decrease in passage rate versus no-treatment control measured by GLMM ($P < 0.05$); N/A= not affected

Table 4. Effects of sound alone on different groups of fish (carp, native hearing specialists, native non-hearing specialists). No differences ($P>0.05$) were noted.

Groups Being Compared	Mean Blockage Efficiency	Difference (Prob > t)
Carp vs. Native hearing specialists	55 ± 34% vs. 18 ± 83%	0.6405
Carp vs. Native non-hearing specialists	55 ± 34% vs. 46 ± 11%	0.6552
Carp + Native hearing specialists vs. Native non-hearing specialists	43 ± 49% vs. 46±10.7%	0.8670

Table 5. Effects of the ensonified bubble curtain (EBC) on different groups of fish (carp, native hearing specialists, native non-hearing specialists). Difference is noted at $p < 0.05$.

Groups Being Compared	Mean Blockage Efficiencies	Difference (Prob > t)
Carp vs. Native hearing specialists	95 ± 29% vs. 54 ± 42%	0.4516
Carp vs. Native Non-hearing specialists	95 ± 31% vs. 84 ± 84%	0.0015*
Carp + Native hearing specialists vs. Native non-hearing specialists	81 ± 31% vs. 84 ± 3%	0.8304

*P < 0.05

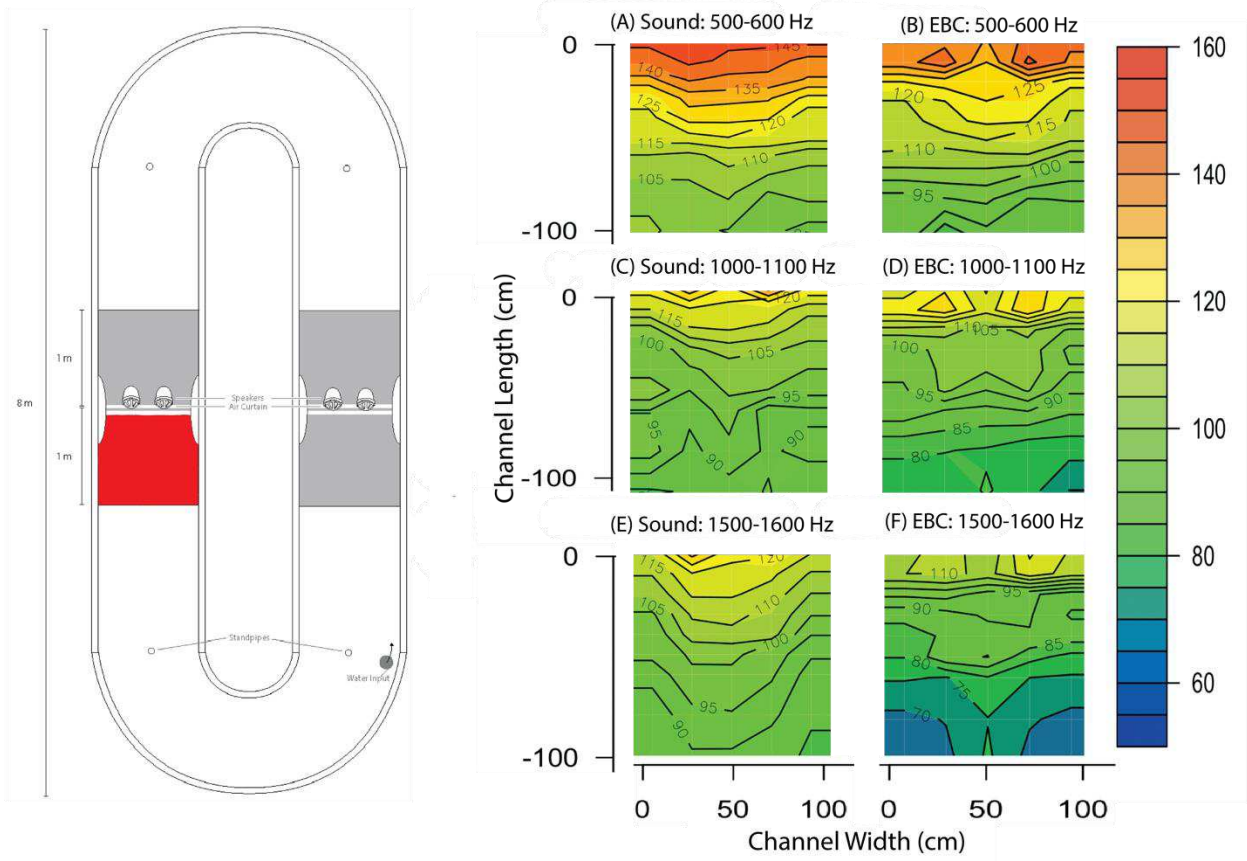


Fig 1

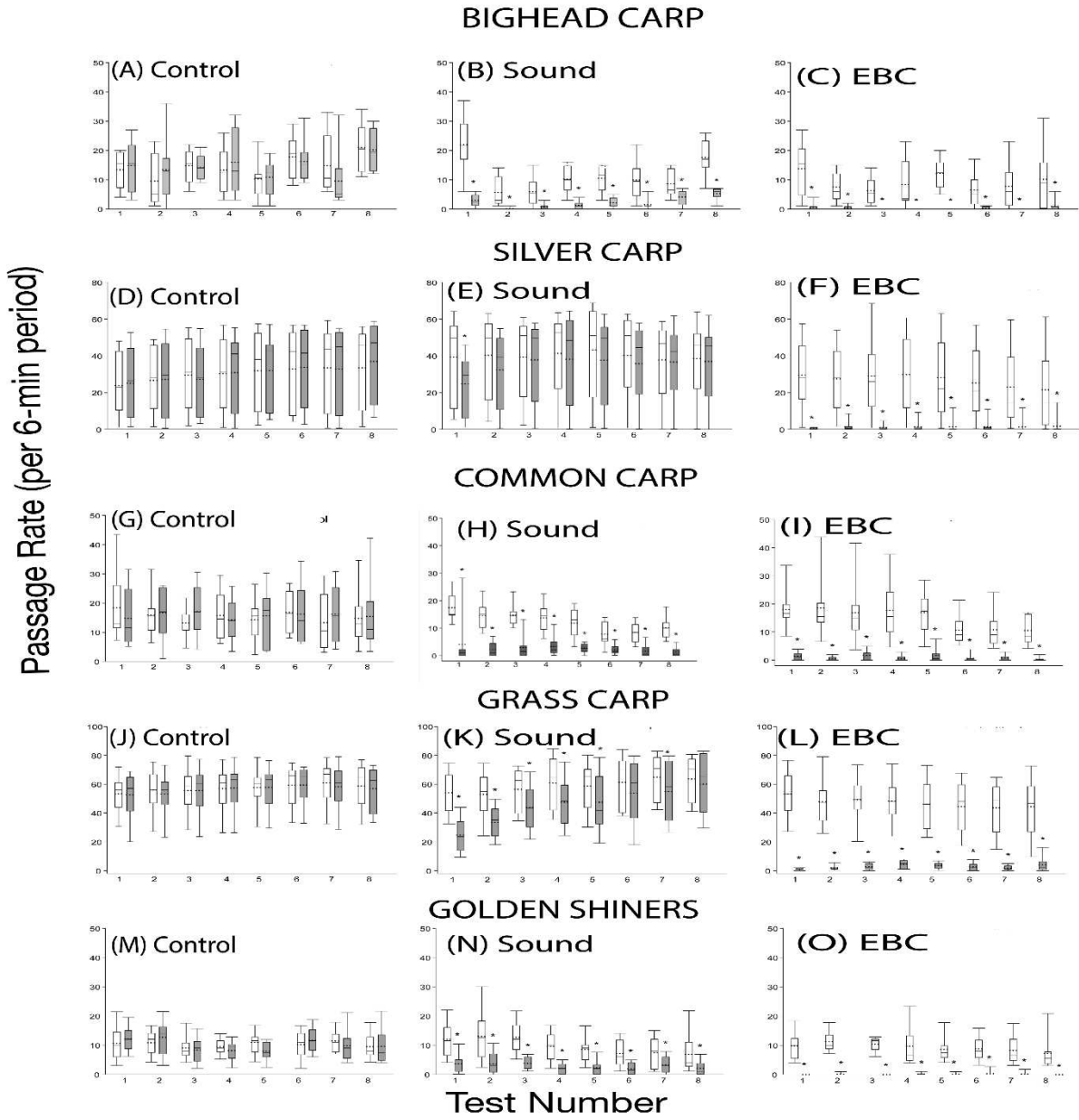
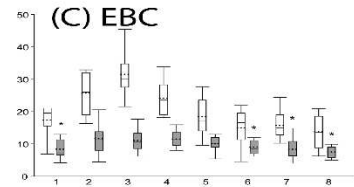
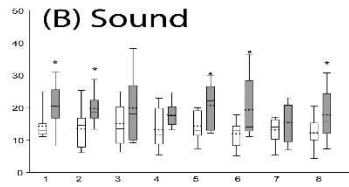
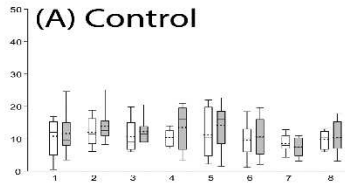


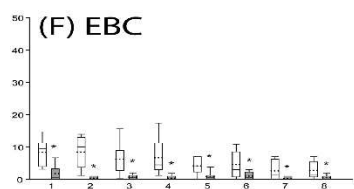
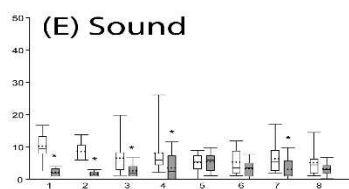
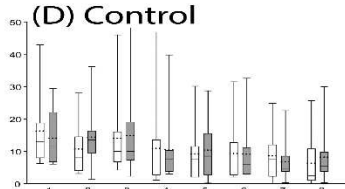
Fig. 2

Passage Rate (per 6-min period)

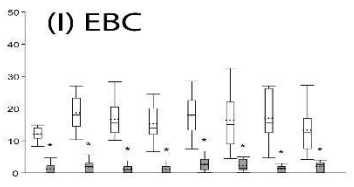
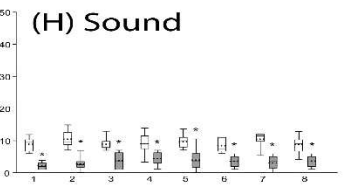
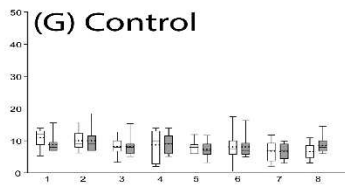
CHANNEL CATFISH



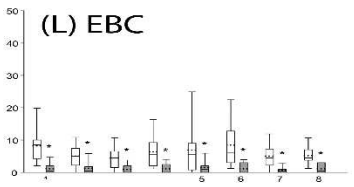
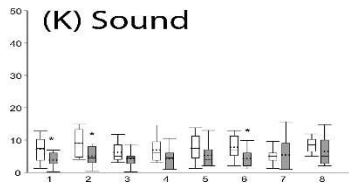
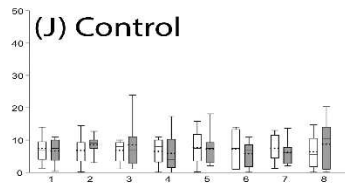
LARGEMOUTH BASS



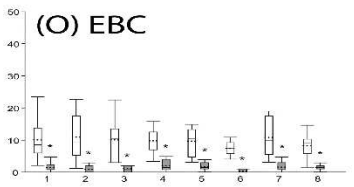
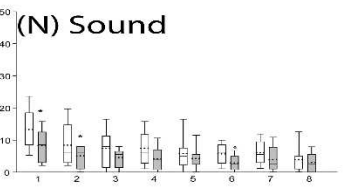
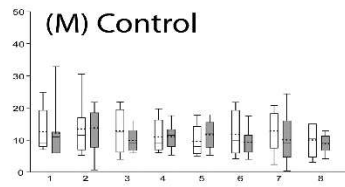
BLUEGILL SUNFISH



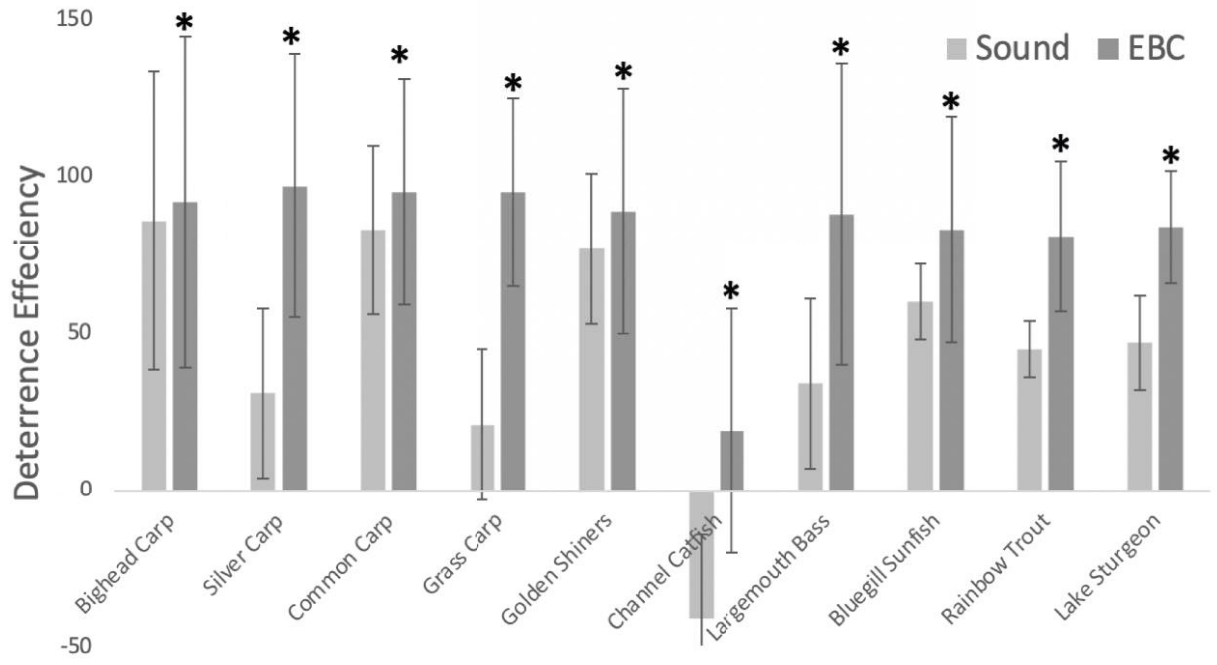
RAINBOW TROUT



LAKE STURGEON



Test Number



Supplementary Files

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- [FeelyandSorensenAugust82021Supplementaryinfo.pdf](#)