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Pectoral sound generation in the blue catfish *Ictalurus furcatus*

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1 Developmental variation in sound production in water and air in the blue catfish *Ictalurus*
2 *furcatus*

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15 **Summary**

16 Blue catfish *Ictalurus furcatus* Lesueur, the largest catfish in North America, produces
17 pectoral stridulation sounds (distress calls) when attacked and held. They have both fish
18 and bird predators, and the frequency spectrum of their sounds is better matched to
19 hearing of birds than to that of unspecialized fish predators with low frequency hearing. It
20 is unclear whether their sounds evolved to function in air or water. We categorized the
21 calls and how they change with fish size in air and water and compared developmental
22 changes in call parameters with stridulation motions captured with a high-speed camera.
23 Stridulation sounds consist of a variable series of pulses produced during abduction of the
24 pectoral spine. Pulses are caused by quick rapid spine rotations (jerks) of the pectoral
25 spine that do not change with fish size although larger individuals generate longer, higher
26 amplitude pulses with lower peak frequencies. There are longer pauses between jerks,
27 and therefore fewer jerks and fewer pulses in larger fish that take longer to abduct their
28 spines and therefore produce a longer series of pulses per abduction sweep. Sounds
29 couple more effectively to water (1400 times greater pressure in Pascals at 1m), are more
30 sharply tuned and have lower peak frequencies than in air. Blue catfish stridulation
31 sounds appear to be specialized to produce under-water signals although most of the
32 sound spectrum includes frequencies matched to catfish hearing but largely above the
33 hearing range of unspecialized fishes.

34 Key Words: sound production, bioacoustics, distress sounds, Ictaluridae, predator-prey,
35 pectoral spine, anti-predator adaptation

36

37 **Introduction**

38 Catfishes are one of the most successful groups of fishes with over 3,000 species
39 (Ferraris, 2007). They have highly modified pectoral spines that can be bound, locked
40 and rubbed to produce stridulation sounds (Fine and Ladich, 2003). A number of species
41 produce sounds in disturbance, courtship and agonistic situations (Abu-Gideiri and Nasr,
42 1973; Heyd and Pfeiffer, 2000; Kaatz et al., 2010; Lechner et al., 2010; Papes and Ladich,
43 2011; Pfeiffer and Eisenberg, 1965; Pruzinszky and Ladich, 1998). Additionally, many
44 species produce sounds with extrinsic muscles that cause rapid swimbladder vibration
45 (Kaatz and Stewart, 2012; Ladich, 2001). North American freshwater catfishes form a
46 single family, the Ictaluridae and produce stridulation sounds but do not possess
47 swimbladder muscles. Despite their importance in natural systems, fisheries and
48 aquaculture (Irwin et al., 1999; Michaletz and Travnichek, 2011), little work has been
49 devoted to acoustic communication or sound production in this family. A single study
50 found stridulatory sounds in agonistic behavior in the brown bullhead *Ameiurus*
51 *nebulosus* Lesueur (Rigley and Muir, 1979), and hand-held sounds and the morphological
52 basis of sound production have been described in domesticated (Fine et al., 1996; Fine et
53 al., 1997) and wild (Vance, 2000) channel catfish, *Ictalurus punctatus* Rafinesque. These
54 sounds are produced when catfish are held, and they have been interpreted as distress
55 calls since pectoral stridulation motions were observed when channel catfish were
56 captured tail-first in the mouth of a largemouth bass but were not produced before the
57 catfish was attacked (Bosher et al., 2006). Additionally, largemouth bass avoid channel
58 catfish in preference to bluegill sunfish and goldfish in a choice situation (Sismour et al.,
59 2013), supporting Forbes' dangerous prey hypothesis (Forbes, 1989) .

60 The pectoral spine base of catfishes has derived dorsal, anterior and ventral
61 processes not found in other fish taxa (Fine et al., 1997; Hubbs and Hibbard, 1951; Kaatz
62 et al., 2010). These processes mate with complimentary structures on the pectoral girdle
63 and control specialized functions including stridulation. The medial surface of the dorsal
64 process in channel catfish has a ridged profile that rubs against a rough but featureless
65 surface on the cleithrum (Fine et al., 1997). Each forward sweep (abduction) of the spine
66 produces a series of pulses (Fine et al., 1997). Based on the logic of cricket stridulation,
67 Fine et al. (1997) posited that contact of individual ridges would be responsible for pulse

68 generation although they stated there would be insufficient time for a ridge to make, lose
69 and re-contact the cleithrum between pulses. In work with mochokid catfishes using a
70 high-speed camera, Parmentier et al. (2010) established that pulses are generated by a
71 series of quick rotation movements or “jerks” of the pectoral spine separated by pauses.
72 They described the mechanism of sound generation as similar to a railroad break
73 (Parmentier et al., 2010). More recent work in the blue catfish, *Ictalurus furcatus*,
74 (Mohajer et al. submitted) has modified this interpretation, demonstrating jerks generate
75 sound by a stick-slip mechanism as in spiny lobsters (Patek, 2001; Patek, 2002) in which
76 the jerk transfers energy from the dorsal-process ridges to the cleithrum of the fused
77 pectoral girdle (Fine et al., 1997; Shaefer, 1984), which in turn excites the girdle to
78 radiate one sound pulse for each jerk. Multiple ridges likely make contact during each
79 pulse, but the number has not been established.

80 Blue catfish have both aquatic and aerial predators (Duvall, 2007) and produce
81 stridulation sounds in both media. Sympatric underwater predators are likely to have
82 unspecialized auditory systems capable of perceiving low frequencies (Ladich and Fay,
83 2013), and aerial predators such as birds hear higher frequencies (Dooling, 1982) and will
84 be better tuned to catfish stridulation sounds. On the other hand, catfishes have bony
85 connections (Weberian ossicles) between the swimbladder and the ears and are sensitive
86 to higher frequencies (Ladich and Fay, 2013) that would be useful in intraspecific
87 communication. Therefore, the primary goal of this study was to compare acoustic
88 properties of blue catfish stridulation sounds in air and water and to determine how
89 sounds change with fish size. High-speed photography synchronized with sound
90 production was also used to describe developmental changes in sound-generating pectoral
91 motions.

92

93 **Results**

94 Blue catfish recorded in air ranged in length and weight from 12.5 cm TL and 11.6 g to
95 52.5 cm TL and 1327 g. Twenty-five of 27 fish (93%) produced sounds in air, and the
96 two silent fish had severe skin lesions. Twenty of these fish were recorded in air with the
97 high-speed camera synchronized to sound allowing us to correlate developmental
98 changes in motion with changes in sound production. These fish were recorded outside

99 the sound-proof booth, and these recordings were not included in regressions of sound
100 parameters. Video recordings from individuals that produced regular pulses, designated
101 pulsers, were utilized in this study (See Mohajer et al., submitted). Finally ten additional
102 fish ranging in size from 16 cm TL and 20.5 g to 32.5 cm TL and 218 g were recorded in
103 shallow water in the James River.

104 **Sounds in air**

105 Blue catfish hold their pectoral fins in a forward abducted position at rest.
106 Stridulation occurs during abduction, and therefore blue catfish first adduct their pectoral
107 fins silently before producing a stridulatory-abduction sweep. Sweeps can be made by
108 either left or right pectoral spines individually or by a series of alternating lefts and rights
109 in rapid succession, and higher pulse repetition rates resulted from successive sweeps
110 produced by both fins. Sweep sound duration varied from 71 to 355 ms (mean \pm SD,
111 136.5 ± 47.1) and contained 5 to 24 pulses (11 ± 3.6) (Fig. 1, Table 1) with various
112 temporal patterns in inter-pulse interval and amplitude in both water and air (Fig. 2).
113 Patterns were not stereotyped, and pulse repetition rate increased and decreased at
114 different points in a sweep. Pulse amplitude often varied by 10 dB or more within a
115 sweep and tended to be low in initial pulses, increase in the middle of the sweep and
116 decrease toward the end. Pulse repetition rate varied from 23 to 156 pulses per second
117 (88.1 ± 33.9).

118 Individual pulses varied from 1 to 15 ms (5.2 ± 2.4) in duration and started with a
119 low-amplitude half-cycle that could be positive or negative (though generally positive
120 with a fish facing the microphone). Amplitude rapidly reached a peak (typically the next
121 full cycle) followed by an exponential decay to background levels before the next pulse
122 (Fig. 1). Sonograms indicate a series of wide-band pulses with weak energy at 20 kHz.
123 The frequency spectra indicate a clear peak frequency, which varied from 312 to 2379 Hz
124 (1127.5 ± 348.2) (Fig. 1), and the peak frequency was close to the center frequency
125 calculated by Raven (Table 1). Typical spectra (Fig. 1, bottom) had most energy in the
126 first peak although there were often several additional peaks about 10 dB down from the
127 first one. At higher frequencies the spectrum flattened out and slowly decreased but
128 continued above background levels. The similarity between center frequency and peak
129 frequency indicated that the sound energy is symmetrical about the peak frequency

130 despite the asymmetry in frequency response, which included considerably higher
131 frequencies. The pulses were impulsive (rapid rise time) and suggested a combination of
132 a forced response and resonance. Peaks occurred at odd multiples (third, fifth and
133 seventh) of the first peak in the example shown (Fig. 1). The first peak was at 882 Hz
134 with subsequent peaks at 2485, 4501 and 6121 Hz. Three, five and seven times 882
135 would yield 2646, 4410 and 6174 respectively.

136 Peak amplitude within a sweep varied from 51 to 81 dB re: 20 μ Pa at 10 cm (62.1
137 ± 5.9) and decreased an average (mean \pm SE) of 3.6 ± 0.18 dB by 20 cm (paired $t_3 = 14.8$,
138 $p = 0.0015$), indicating that the walls of the sound-proof booth were channeling the
139 signal. Presuming spherical spreading and a loss of 6 dB per distance doubled (6 dB/DD
140 or a decay of $20 \log r$), the source level would be 20 dB less than the values measured at
141 10 cm and would therefore vary from 31 to 61 dB at 1 m. Ranges in pulses within a
142 sweep varied by as little as 2 to as much as 17 dB in different individuals (6.9 ± 3.3).

143 **Changes in acoustic parameters with fish size: air**

144 Sound pressure level at 10 cm increased linearly from 51 to 81 dB re: 20 μ Pa with TL (r^2
145 $= 0.5379$, $p < 0.0001$, Fig. 3). Amplitude range in dB within individuals did not vary with
146 fish size ($r^2 = 0.045$, $p = 0.307$). Both center frequency and peak frequency declined from
147 about 2 kHz to about 500 Hz with TL ($r^2 = 0.3705$, $p = 0.0012$ and $r^2 = 0.4122$, $p =$
148 0.0005 , respectively) (Fig. 3).

149 Developmental changes in patterning of stridulation sounds were supported by
150 high-speed photography of spine motion. Sweep sound duration increased linearly from
151 71 to 355 ms with TL ($r^2 = 0.487$, $p = 0.0001$), which corresponded with increases in fin
152 sweep duration measured with the camera, ranging from 60 to 350 ms ($r^2 = 0.523$, $p =$
153 0.0075). Abduction rotation varied from 12 to 40° and did not change with TL ($r^2 =$
154 0.027 , $p = 0.628$). Each pulse was generated by a rapid jerk motion. Jerks were of short
155 duration, 1-2 ms over rotations of mostly 2-3°, and jerk rotation and duration did not
156 change with TL (jerk duration $r^2 = 0.059$, $p = 0.498$; jerk rotation $r^2 = 0.0146$, $p = 0.739$).
157 Sound pulses were considerably longer than jerk durations and increased linearly with TL
158 ($r^2 = 0.6799$, $p = < 0.0001$, Fig. 4). Therefore once excited, the pectoral girdle continued
159 to vibrate despite a stationary spine. The number of sound pulses per sweep decreased
160 from 24 to 5 with TL ($r^2 = 0.193$, $p = 0.028$), as did the number of photographed jerks,

161 which decreased from 19-5 ($r^2 = 0.621$, $p = 0.0005$). Pulse rate decreased from 156 to 23
162 pulses per second with TL ($r^2 = 0.6528$, $p = <0.0001$, Fig. 4), which was determined
163 largely by increased pauses between jerks in larger fish; pauses increased from 5 to 18 ms
164 ($r^2 = 0.6373$, $p = 0.0056$).

165

166 **Description of sounds in water**

167 Underwater stridulation sounds had a somewhat similar pulsatile appearance on
168 sonograms and oscillograms (Fig. 5) although there were differences in waveform,
169 amplitude and frequency spectra. Stridulation sounds were more robust underwater and
170 varied between 122 and 145 dB re: 1 μ Pa at 1 m (131.4 ± 5.4). Frequency spectra from a
171 stridulation sound recorded at 0.5 m indicated most energy in a narrower band between
172 127 and 3878 Hz, with a peak at 854 Hz (Fig. 5). Levels dropped about 60 dB between
173 854 and 3875 Hz. High frequencies were strongly diminished in water as reflected in the
174 waveform, which looks “cleaner” without higher frequency energy present in air (Fig. 1,
175 5). Attenuation between 0.5 and 1 m averaged 9 dB (Paired $t_9 = 12.42$, $p < 0.0001$),
176 indicating excess attenuation above cylindrical (3 dB per distance doubled, DD) and even
177 spherical spreading (6 dB/DD) despite the shallow depth of no more than 1 m. Spectra
178 from the same stridulation pulses indicated environmental filtering with a 10 dB decrease
179 in peak energy and highest frequencies reaching background levels by 4 kHz or less (Fig.
180 6). The spectrum at 0.5 m is relatively smooth exhibiting a gradual decrease between
181 peak energy and high frequency drop-off (Fig. 6). However by 1 m the spectrum was
182 considerably more variable, exhibiting several regions with increased and decreased
183 energy levels. A Q_{10dB} value (peak frequency/bandwidth 10 dB down from the peak)
184 indicated a decrease from 1.02 to 0.85 reflecting a flatter spectrum at the greater distance.
185 Comparison at different frequencies (measurements at 100 Hz intervals) indicated energy
186 levels below 1 kHz were generally 10-15 dB greater at 0.5 than 1 m (Fig. 7). At higher
187 frequencies data were highly variable. An approximate midpoint between the peaks and
188 valleys above 1 kHz would indicate a decrease of about 6 dB above and 12.5 dB below 1
189 kHz.

190 An attempt at comparing sound levels in air and water by converting source levels
191 to Pascals (Pa). The conversion required dividing the Pa measured at 10 cm by 10,

192 equivalent to a 20 dB decrease to calculate pressure at 1 m. Extrapolated pressure in air at
193 1 m averaged (mean \pm SE) 0.0032 ± 0.0005 Pa compared to 4.5104 ± 1.0229 Pa in water,
194 indicating a 1410 fold greater pressure in water than air. Greater long-distance
195 propagation therefore indicates that stridulation sounds coupled more efficiently into
196 water than to air.

197

198 **Changes in acoustic parameters with fish size: water**

199 Sounds in water came from a smaller number of individuals with a smaller size range
200 than those recorded in air. Yet size trends for sound parameters were generally similar
201 with fish size (Fig. 4, Table 2). Although some regressions had slopes or intercepts that
202 were significant between air and water (Table 2), many data points overlapped so that not
203 all differences may be meaningful biologically. Sound pressure level at 1 m increased
204 from about 128 to 153 dB re: 1 μ Pa with TL ($r^2 = 0.8204$, $p = 0.0003$, Fig. 3); correlations
205 were higher and slopes were greater in water than in air (Table 2) suggesting that larger
206 fish with larger pectoral girdles become increasingly effective at radiating sounds into
207 water. Decibel levels in air and water are not directly comparable, but we have already
208 provided evidence that the signal is considerably more robust in water.

209 Sweep duration increased from 47 to 216 ms in water ($r^2 = 0.4794$, $p = 0.0265$)
210 and overlapped considerably with values in air (Fig. 4); adjusted means for a 25 cm TL
211 individual were similar (107 ms in air and 111 ms in water). Pulses per sweep varied
212 over two fold in different individuals and overlapped with values in air. There was not a
213 significant size effect in pulses per sweep in water unlike in air, but comparisons over the
214 same size range indicate little change to 30 cm in air with the decrease depending on
215 larger individuals. Pulses per second decreased more sharply in water than air, but
216 adjusted means were quite similar (115 in air and 122 in water). Pulse duration changed
217 non-significantly from 3 to 7 ms in water ($p = 0.0896$), and durations were shorter in air
218 with adjusted means of 3.3 ms in air and 4.3 ms in water, a 27% difference. Unlike in air
219 peak and center frequency did not vary with fish size in water, and values were lower
220 than in air (Table 2): adjusted means of 939 Hz in water and 1331 Hz in air.

221

222 **Discussion**

223 Blue catfish stridulation sounds consist of a series of pulses produced during
224 abduction of the pectoral spine and remaining rays. Unlike channel catfish, which tend to
225 have their pectoral fins adducted as the default position (and thus in the ready position for
226 stridulation), the blue catfish carries them in a more forward position and adducts them
227 silently before producing the sonic abduction. There are numerous catfishes that produce
228 both adduction and abduction stridulation pulses (Heyd and Pfeiffer, 2000; Ladich,
229 1997), and it is possible that the blue catfish represents an intermediate stage in
230 transformation from abduction only sounds to stridulating in both directions. Fine et al
231 video recorded one adduction sound out of 256 in channel catfish (Fine et al., 1996)
232 indicating that there is no mechanical impediment to producing adduction sounds, which
233 would require amended neural commands.

234 High-speed videos reveal that individual pulses are produced during a series of
235 quick jerk movements, invisible to the human eye, during abduction (Parmentier et al.,
236 2010; Mohajer et al. submitted) when ridges on the underside of the dorsal process rub
237 against a groove in the cleithrum (Fine et al., 1997). Sounds are produced by a slip-stick
238 mechanism when abduction force exceeds static friction from the two rubbing surfaces
239 (Patek, 2001) causing a quick forward motion, the jerk (Parmentier et al., 2010). The jerk
240 in turn transfers energy to the pectoral girdle, the sound radiator (Fine et al., 1997).
241 Stridulatory abduction motions are several times longer than the preceding adductions
242 because of pauses, and pauses with no spine movement comprise 86% of abduction time
243 (Mohajer et al. submitted). The pauses, in fact, determine the temporal pattern of the
244 sounds (Mohajer et al., submitted), which is quite variable and changes developmentally.
245 Larger fish produce louder calls at lower frequencies owing to a more massive pectoral
246 girdle (Duvall, 2007) that would have a lower natural frequency. Both sweep duration
247 and pulse duration increase with fish TL, and high-speed camera data indicate that time
248 to abduct the spine increases in larger individuals, whose muscles are longer and should
249 take longer to contract (Connaughton et al., 2000; Wainwright and Barton, 2005; Miano
250 et al., 2013). The number of jerks and pulses per sweep as well as pulse rate decrease
251 with fish size. However, jerk duration does not change although sound pulses (jerk
252 sounds) increase in duration with fish size. Therefore jerks in larger fish excite the more
253 massive pectoral girdle to vibrate for a longer period before amplitude decay, and pauses

254 between jerks become longer in larger individuals accommodating the longer sound
255 pulse. Longer pauses likely result from a change in neural output.

256 Many acoustic parameters in water showed similar developmental trends found in
257 recordings in air. Some of the differences likely result from the smaller range in fish size
258 in the water samples. Amplitude will be discussed below. Other notable differences are
259 pulse duration, which is shorter in water and peak, center and upper frequencies, which
260 decrease in water. Sharpness of tuning increases in water. Many of these differences
261 parallel findings on Atlantic croaker recorded in both media (Fine et al., 2004). Peak
262 frequency in croaker sounds does not differ between air and water because it is
263 determined by sonic muscle contraction-relaxation time, which is not affected by acoustic
264 loading. Croaker sounds in water are more sharply tuned (higher Q) and damp more
265 quickly than in air, similar to the more sharply tuned frequency spectrum and shorter
266 pulses in the blue catfish. In air where the system is less tuned, the broader response at
267 lower frequencies appears to excite other modes at higher frequencies. With increased
268 loading in water the catfish spectrum decreases from > 20 kHz to about 4 kHz, and the
269 peak-frequency tuned mode apparently does not excite higher modes in water. Parallels
270 are noteworthy since the different radiators, the pectoral girdle in catfishes and the
271 swimbladder in Atlantic croaker, appear to be affected similarly in both media.

272 The acoustic properties of channel catfish sounds from domesticated stocks (Fine
273 et al., 1996; Fine et al., 1997) share similarities to those of blue catfish, and unpublished
274 work on scaling of acoustic parameters to channel catfish size show similar trends to this
275 current findings in blue catfish. There are a few marked differences between the two
276 species. Channel catfish sounds came from domesticated fish that have smaller spines
277 and pectoral girdles than wild individuals (Fine et al., 2014). The frequency spectrum of
278 channel catfish sounds tend to separate into several bands, whereas blue catfish spectra
279 are more continuous for unknown reasons related to the structure of the pectoral girdle.
280 Channel catfish sounds tend to be more variable, and many individuals failed to make
281 sounds when held. Over 90% of blue catfish and 100% of fish without skin lesions
282 sampled in this study stridulated, suggesting that the calls may serve a more important
283 role in the life history of wild blue catfish. Sounds in blue catfish may be used for
284 intraspecific communication (currently unknown) and likely have an as yet undefined

285 role in avoiding predation. In an experiment with large juveniles (> 40 cm TL) utilizing
286 an intruder blue catfish introduced to a resident, stridulation sounds were not heard
287 (Morgan, 2014). Additionally, diel underwater recordings were made in the tidal fresh-
288 water James River in a location where blue catfish are plentiful (monthly recordings for
289 10 minutes per hour over 24 hours). These included spring and summer months when
290 mating would be expected, but no catfish sounds were heard (Morgan, 2014). It is
291 premature to conclude that blue catfish do not make sounds during courtship and
292 agonistic behavior since reproduction could be restricted to specific areas, and larger
293 adults could potentially stridulate in agonistic conditions. At this point however, evidence
294 only points to an anti-predator function.

295 In addition to fish predators blue catfish are commonly consumed by aerial
296 predators such as bald eagles and ospreys (Duvall, 2007). Blue catfish are also
297 cannibalized by their own species (Chandler, 1998; Schlosser et al., 2011), and catfish
298 have specialized hearing sensitive at low-thresholds and high frequencies (Ladich, 1999;
299 Ladich and Fay 2013; Lechner et al., 2010; Papes and Ladich, 2011). Most fish predators
300 that consume them would be less well tuned to the frequency spectrum of the blue catfish
301 sounds than would bird predators (Dooling, 1982). This question of tuning brings up the
302 question of whether the sounds evolved primarily for underwater or aerial use. The data
303 demonstrate that the frequency spectrum is considerably sharper and the sound pressure
304 in Pascals is about 1400 times greater at a meter underwater than in air. Sound pressure
305 level in air averaged 62 dB re: 20 uPa at 10 cm, equivalent to 42 dB at 1 m, a low level
306 particularly in small fish. In water however, the source level was 131.4 dB re: 1 μ Pa, and
307 the oyster toadfish, *Opsanus tau*, often considered a “loud” fish for instance, produces a
308 sound pressure level of 130 dB (Barimo and Fine, 1998) albeit using a swimbladder
309 mechanism.

310 Fine et al. demonstrated that the pectoral girdle is the primary acoustic radiator of
311 channel catfish sounds (Fine et al., 1997). This coupled with increasing pectoral girdle
312 dimensions with fish size (Duvall, 2007) explains the decreasing peak frequency in larger
313 fish. Given the high acoustic impedance of water over air (Urlick, 1975), girdle vibrations
314 will couple more successfully into water and be audible at a much greater distance than in
315 air. Even by 1 m however, environmental filtering changed the spectrum of the catfish

316 sound compared to 0.5 m, albeit in a shallow site. Low frequency attenuation is likely due
317 extinction of long wavelength sound in shallow water (Urick, 1975; Fine and Lenhardt,
318 1983; Mann, 2006), and higher frequencies exhibit a series of peaks and troughs
319 suggesting constructive and destructive interference from reflections from water
320 boundaries. The wide-frequency band of stridulation pulses therefore provides
321 redundancy ensuring that the call will likely be recognizable with distance (Fine and
322 Lenhardt, 1983; Sisneros et al., 2004). Blue catfish are more common in deeper water
323 where the call will suffer less environmental filtering. We suggest that stridulation sounds
324 in blue catfish have evolved primarily for use in water and await experiments on the
325 reactions of predators to these sounds.

326

327 **Materials and Methods**

328 *Ictalurus furcatus* were collected by electroshocking from tidal fresh-water regions of the
329 James River near the Rice Center of Virginia Commonwealth University (VADGIF
330 permit number 0444631). They were allowed to recover for 48-72 hours in 280 L aquaria
331 before recording. Protocols were approved by the VCU Animal Care and Use Committee
332 (IACUC #AD20216).

333 Sounds were recorded in air and water. In-air sound recordings were made in a
334 soundproof booth (IAC Controlled Acoustical Environments, Bronx, New York). Catfish
335 were held by hand behind the pectoral fins and placed head-first 10 cm from the internal
336 microphone of a Zoom Corporation (Tokyo, Japan) H4 portable digital recorder. This
337 method avoids reflection and resonance problems associated with aquaria (Akamatsu *et*
338 *al.*, 2002; Parmentier *et al.*, 2014). Sounds from several individuals were also recorded 20
339 cm from the microphone to examine short distance propagation. In-water recordings were
340 made from a shallow wing of the dock at the VCU Rice Center in the tidal fresh-water
341 James River. This part of the dock is close to water level and allowed us to hold the fish
342 in the water at a known distance from two HTI-94-SSQ hydrophones (High Tech Inc.,
343 Long Beach, Mississippi), one at 0.5 and the other 1 m from the fish. The fish and
344 hydrophones were positioned approximately halfway between the surface and bottom of
345 the water, which varied between 0.75 and 1 m in depth. Blue catfish are present at this
346 depth although they occur more commonly in deeper water. We note that these acoustic

347 conditions avoid reflection and resonance problems inherent in small tanks (Akamatsu et
348 al., 2002; Parmentier et al., 2014)

349 Sounds were sampled at 44.1 kHz (16 bit resolution), and the acoustic parameters
350 (sweep duration, pulse duration, number of pulses per sweep, number of pulses per
351 second, peak frequency, center frequency, and amplitude) were analyzed using Raven Pro
352 v1.3. Sound parameters were regressed against fish total length (TL). A catfish pectoral
353 stridulation sound sweep is defined as a series of pulses produced during abduction of
354 either the right or left pectoral spine. Sounds from eight pectoral sweeps per individual
355 were analyzed unless fewer were produced, and parameters were averaged and treated as
356 an N of 1.

357 Absolute sound pressure was measured in air and water. In air, a 90 dB re: 20 μ Pa
358 500 Hz calibration tone produced using a function generator connected to a speaker was
359 recorded. In-water, calibration utilized a 14 mV RMS tone measured with an oscilloscope
360 and converted to dB re: 1 μ Pa (equivalent to 131 dB) using the hydrophone sensitivity
361 calibration (-168.2 dB re: 1V/ μ Pa). The true amplitude of the stridulation sounds (in
362 absolute pressure units) is equal to the amplitude measured by Raven multiplied by an
363 amplitude calibration constant. The value of this constant is equal to the true (known)
364 amplitude of the test signal divided by the RMS amplitude measured by Raven. Since
365 decibel levels in air and water are not directly comparable, levels from a sample of the
366 fish recorded in air and water were converted to Pascals. Source levels at 1 m were
367 available from underwater recordings, and sound pressure levels recorded at 10 cm in air
368 were decreased by 20 dB to convert them to source levels at 1 m, assuming spherical
369 spreading as described by $20 \log r$ (Fine and Lenhardt, 1983; Mann, 2006; Urick, 1975).

370 Pectoral stridulation motions were recorded with a video camera (Fastcam PCI R-
371 2, Photron, San Diego, CA) synchronized with sounds recorded in air through a
372 triggerbox (NI BNC-2110, National Instruments, Austin, TX). Images were captured at
373 1,000 or 2,000 frames per second. See Mohajer et al. (submitted) for more information.
374 We determined the relationship of spine motion to sound with frame-by-frame analysis
375 (0.5 or 1 ms per frame). Parameters measured were angular rotation and duration of fin
376 sweeps, duration and angular rotation of small micro-movements (jerks), inter-jerk
377 interval (the time from the beginning of one jerk to the next), and pause duration (time

378 when the spine was stationary). Camera data in air were used to compare quantitative
379 aspects of motion with equivalent sound parameters.

380 Statistical analyses were performed using GraphPad Prism 5 (San Diego, CA).
381 Sound parameters were scaled against fish TL using linear regression. A paired t test was
382 used to compare sound attenuation (10 to 20 cm in air and 0.5 to 1 m in water) from
383 recordings of the same individual. Regressions of parameters in air and water were
384 compared using analysis of covariance (ANCOVA) with fish TL as the covariate, and an
385 adjusted mean was calculated for a 25 cm TL fish using regressions from air and water to
386 appreciate differences between the two media. The mean and standard deviation were
387 used to describe acoustic parameters, and the mean and standard error were used when
388 comparing means.

389

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394

395 **AUTHOR CONTRIBUTIONS**

396 Conceived and designed the experiments: ZNG, YM, MLF. Performed the experiments:

397 ZNG, YM. Analyzed the data: ZNG, YM, MLF. Wrote the paper: ZNG, MLF.

398

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402

403 **Competing Interests**

404 No competing interests declared.

405

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530
531 **Figure Legends**

532
533 Fig. 1. Spectrogram (A) and oscillogram (B) showing pulse pattern, expanded
534 oscillogram illustrating pulse waveform (C) and power spectrum (D) from a 49.5 cm TL
535 1089 g blue catfish. Hann window, 3171 samples, 20 Hz bandwidth with 50% overlap.

536
537 Fig. 2. Representative patterns of inter-pulse interval and amplitude in individual
538 stridulation sweeps from two blue catfish recorded in air (top) and two recorded in water
539 (bottom).

540
541 Fig. 3. Relationship of sound pressure level to total length in blue catfish recorded in air
542 (dB re: 20 μ Pa at 10 cm) and water (dB re: 1 μ Pa at 1 m).

543
544 Fig. 4. Relationship of sweep (abduction) sound duration (A), pulses per sweep (B),
545 pulses per second (C), pulse duration (D), peak frequency (E), and center frequency (F)
546 to total length in blue catfish recorded in air and water.

547
548 Fig. 5. Spectrogram (A) and oscillogram (B) illustrating pulse pattern and waveform, and
549 power spectrum (C) recorded underwater from a 28 cm TL 189 g blue catfish 1m from
550 the hydrophone. Hann window, 3171 samples, 20 Hz bandwidth with 50% overlap.

551
552 Fig. 6. Power spectra of the same stridulation sound recorded at 0.5 m (A) and 1 m (B)
553 from a blue catfish, and background noise (C). Hann window, 3171 samples, 20 Hz
554 bandwidth with 50% overlap.

555
556 Fig. 7. Maximum decibel difference at 100 Hz intervals between spectra in Fig. 6
557 recorded at 0.5 and 1 m from the hydrophone.

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565 Table 1. Acoustic parameters of stridulation sounds of blue catfish in air and water. N=25
 566 in air and 10 in water.
 567

Parameter (in air)	Mean ± 1 SD	Range
Sweep duration	136.5 ± 47.1 ms	71-355 ms
Pulses per sweep	11 ± 3.6	5-24
Pulses per second	88.1 ± 33.9	23-156
Pulse duration	5.2 ± 2.4 ms	1-15 ms
Sound pressure level*	62.1 ± 5.9 dB	51-81 dB
dB range (within sweeps)	6.9 ± 3.3 dB	2-17 dB
Center frequency	1130.4 ± 345.9 Hz	409-2702 Hz
Peak frequency	1127.5 ± 348.2 Hz	312-2379 Hz

*re: 20 µPa at 10 cm

Parameter (in water)	Mean ± 1 SD	Range
Sweep duration	93.8 ± 44.8 ms	47-216 ms
Pulses per sweep	11.7 ± 2.7	7-23
Pulses per second	141.6 ± 46.8	66-188
Pulse duration	4 ± 0.9 ms	3-7 ms
Sound pressure level*	140.2 ± 6.3 dB	128-153 dB
Sound pressure level†	131.4 ± 5.4 dB	122-145 dB
dB range within sweeps*	6.1 ± 3.1 dB	2-11 dB
dB range within sweeps†	8 ± 2.6 dB	4-13 dB
Center frequency at 0.5 m	1090.4 ± 438.8 Hz	775-3338 Hz
Center frequency at 1 m	1197.8 ± 436.1 Hz	744-3889 Hz
Peak frequency at 0.5 m	1106.9 ± 492 Hz	732-3889 Hz
Peak frequency at 1 m	1300.8 ± 529.6 Hz	759-3892 Hz

*re: 1 µPa at 0.5 m

†re: 1 µPa at 1 m

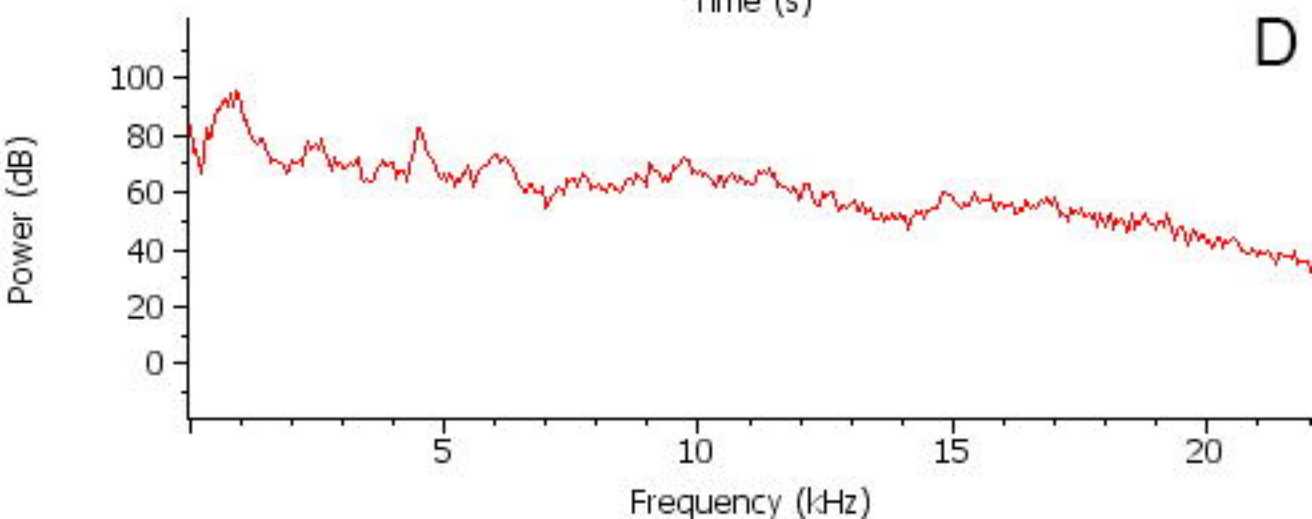
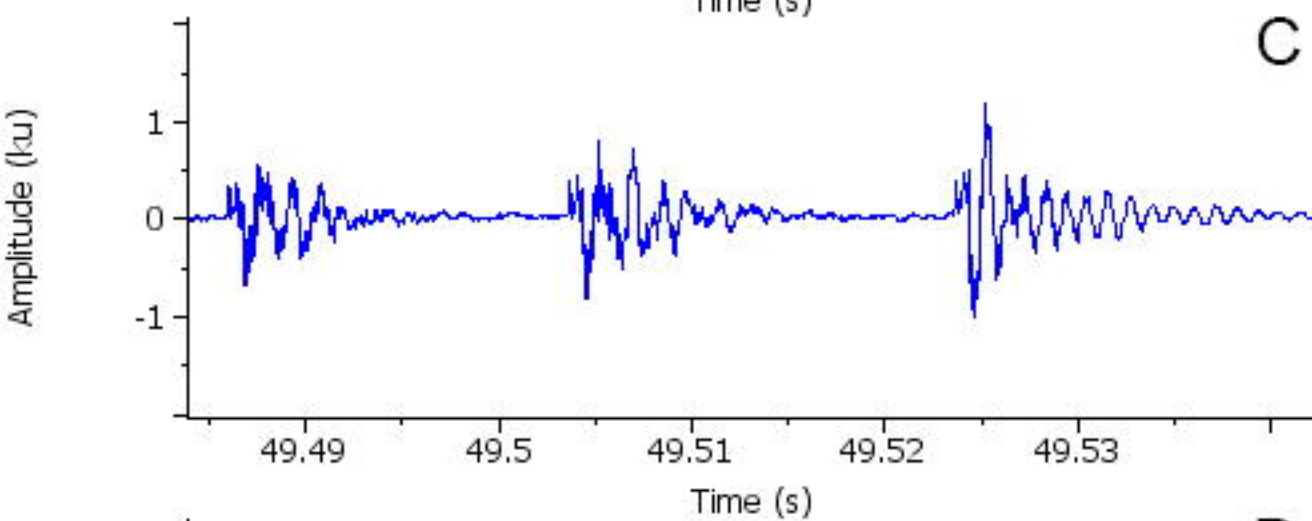
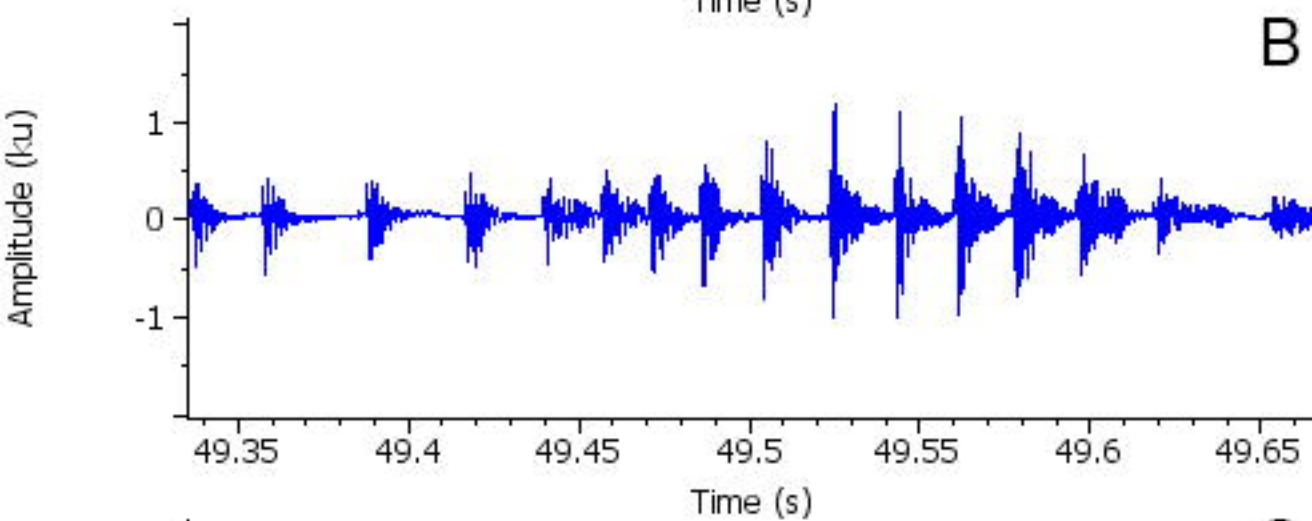
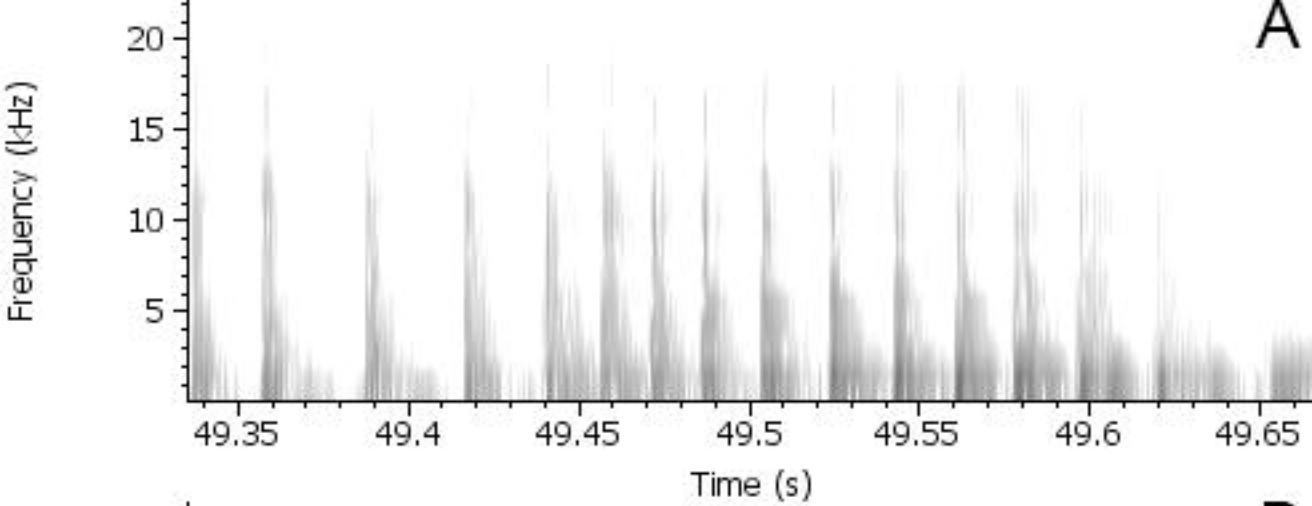
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572 Table 2. Regression equations of acoustic parameters of stridulation sounds against fish total length, coefficients of determination,
 573 analysis of covariance, and adjusted means for a 25 cm TL blue catfish in air and water. SPL, sound pressure level; CF, center
 574 frequency; PF, peak frequency; SD, sweep duration; PD, pulse duration; P/Sw, pulses per sweep; PPS, pulses per second.
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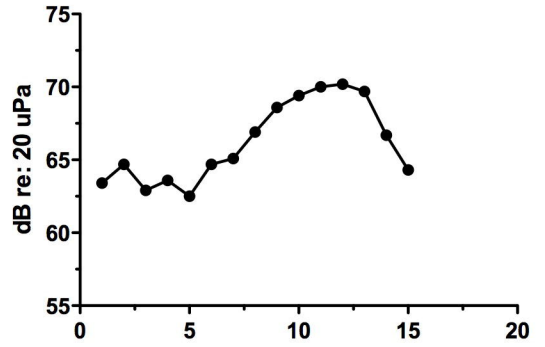
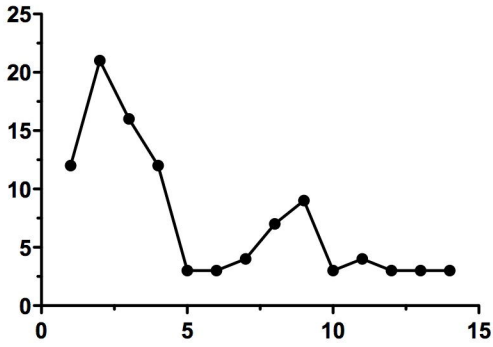
Parameter		Regression equation	r ²	p	Slopes		Intercepts		Adjusted mean
					F	p	F	p	
SPL	air	Y = 48.11 + 0.3963TL	0.5379	< 0.0001	6.2851	0.0176	a	a	58 dB
	water	Y = 119.1 + 0.9560TL	0.8204	0.0003					143 dB
CF	air	Y = 1822 - 19.58TL	0.3705	0.0012	0.7688	0.3875	13.3433	0.0001	1331 Hz
	water	Y = 1680 - 26.79TL	0.1905	0.2402					939 Hz
PF	air	Y = 1853 - 20.62TL	0.4122	0.0018	1.0198	0.3206	14.6729	0.0006	1319 Hz
	water	Y = 1746 - 29.04TL	0.1245	0.2997					936 Hz
SD	air	Y = 29.91 + 3.028TL	0.4866	0.0001	1.1399	0.2939	< 0.0001	0.9936	107 ms
	water	Y = -20.45 + 5.191TL	0.4794	0.0265					111 ms
PD	air	Y = 0.4894 + 0.1160TL	0.6799	< 0.0001	0.4682	0.4984	5.5907	0.0243	3.33 ms
	water	Y = 2.174 + 0.08165TL	0.3179	0.0896					4.25 ms
P/Sw	air	Y = 16.41 - 0.1608TL	0.1927	0.0282	0.7669	0.3879	0.3687	0.548	12.3
	water	Y = 11.32 + 0.01788TL	0.0015	0.9143					11.8
PPS	air	Y = 181.7 - 2.704TL	0.6527	< 0.0001	8.4812	0.0066	a	a	115
	water	Y = 288 - 6.654TL	0.7223	0.0018					122

^a Because the slopes differed so much, it was not possible to test the intercepts.

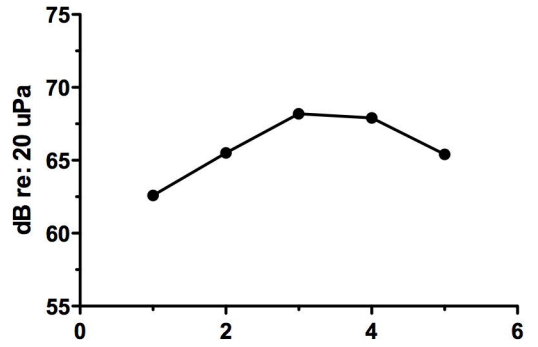
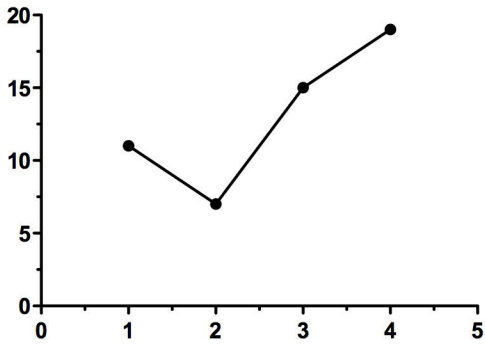
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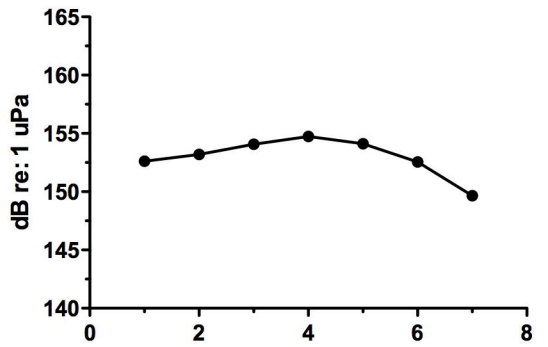
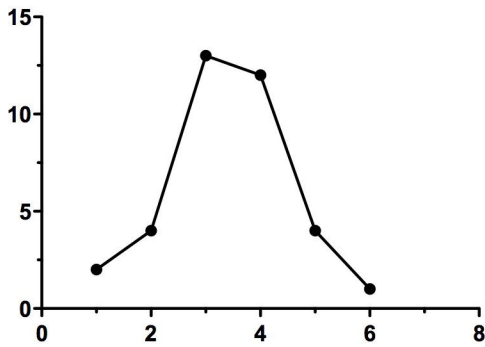
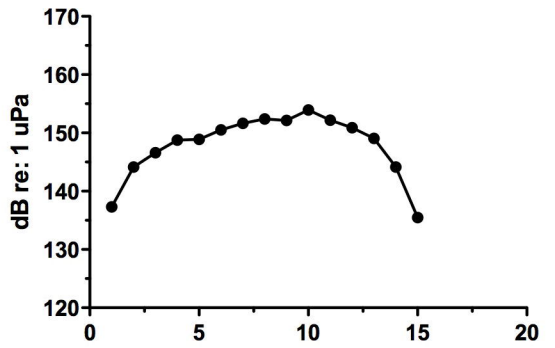
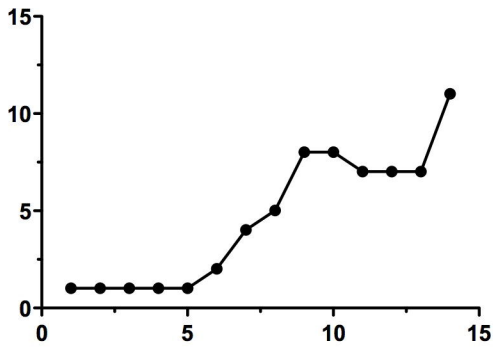
Air



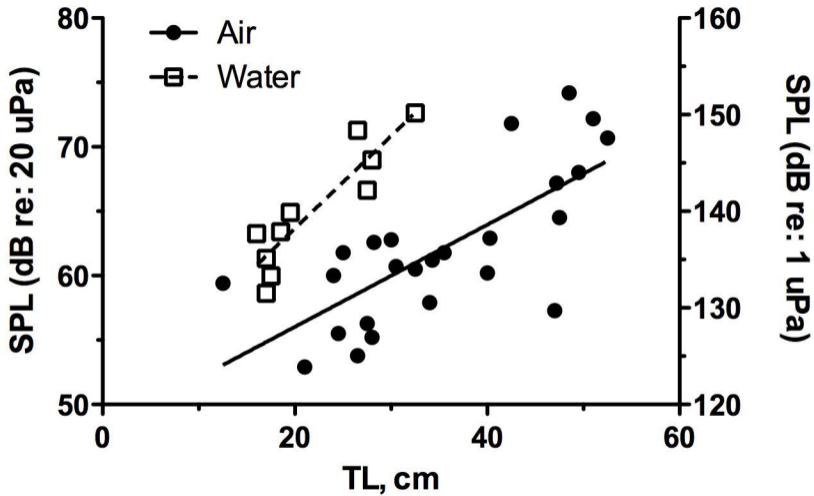
Interpulse interval, ms

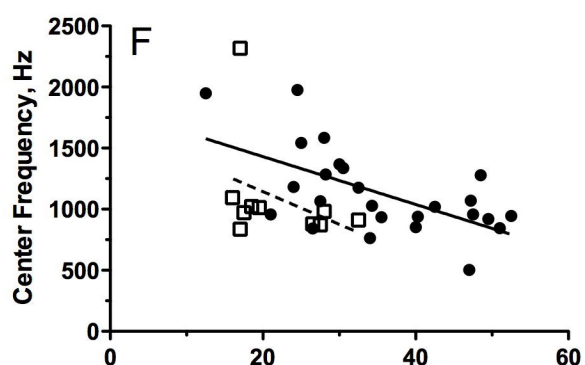
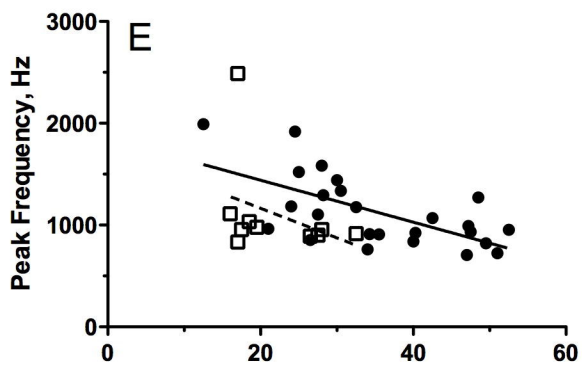
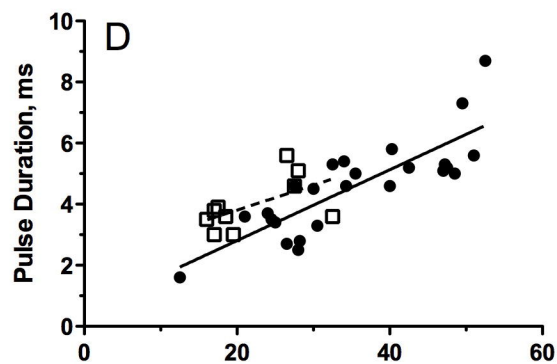
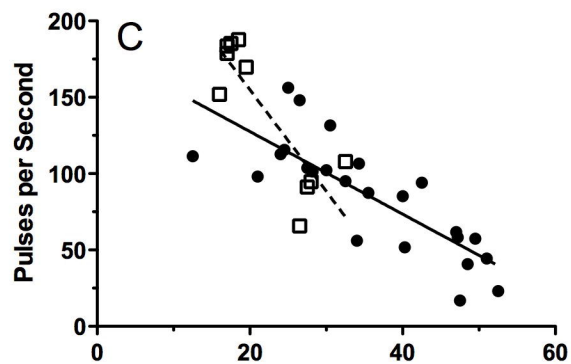
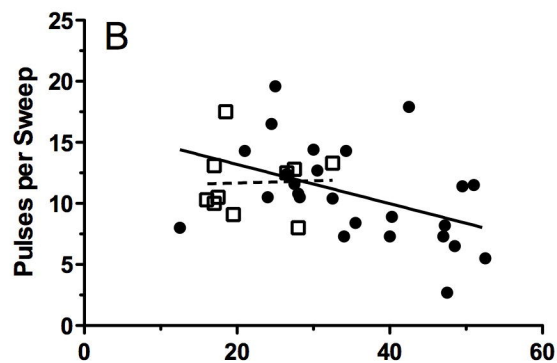
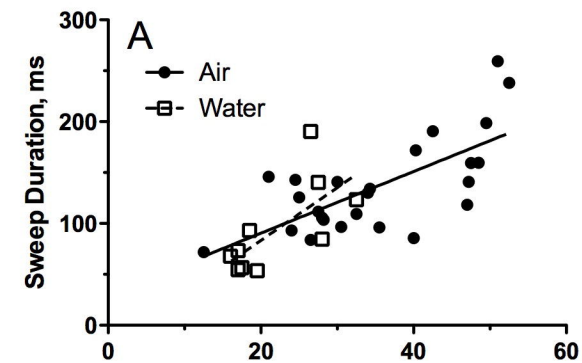


Water



Pulse Number





TL, cm

