

RESEARCH ARTICLE

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

Zachary N. Ghahramani*, Yasha Mohajer and Michael L. Fine[‡]**ABSTRACT**

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

KEY WORDS: Acoustic communication, Bioacoustics, Distress sounds, Ictaluridae, Predator–prey, Pectoral spine, Anti-predator adaptation

INTRODUCTION

Catfishes are one of the most successful groups of fishes, with over 3000 species (Ferraris, 2007). They have highly modified pectoral spines that can be bound, locked and rubbed to produce stridulation sounds (Fine and Ladich, 2003). A number of species produce sounds in disturbance, courtship and agonistic situations (Abu-Gideiri and Nasr, 1973; Heyd and Pfeiffer, 2000; Kaatz et al., 2010; Lechner et al., 2010; Papes and Ladich, 2011; Pfeiffer and Eisenberg, 1965; Pruzsinszky and Ladich, 1998). Additionally, many species produce sounds with extrinsic muscles that cause rapid swimbladder vibration (Kaatz and Stewart, 2012; Ladich, 2001). North American freshwater catfishes form a single family, the Ictaluridae, and produce stridulation sounds but do not possess swimbladder muscles. Despite their importance in natural systems,

fisheries and aquaculture (Irwin et al., 1999; Michaletz and Travnichek, 2011), little work has been devoted to acoustic communication or sound production in this family. A single study found stridulatory sounds in agonistic behavior in the brown bullhead, *Ameiurus nebulosus* (Rigley and Muir, 1979), and ‘hand-held’ sounds and the morphological basis of sound production have been described in domesticated (Fine et al., 1996; Fine et al., 1997) and wild (Vance, 2000) channel catfish, *Ictalurus punctatus*. These sounds are produced when catfish are held, and they have been interpreted as distress calls as pectoral stridulation motions were observed when channel catfish were captured tail-first in the mouth of a largemouth bass but were not produced before the catfish was attacked (Bosher et al., 2006). Additionally, largemouth bass avoid channel catfish in preference to bluegill sunfish and goldfish in a choice situation (Sismour et al., 2013), supporting Forbes’ dangerous prey hypothesis (Forbes, 1989).

The pectoral spine base of catfishes has derived dorsal, anterior and ventral processes not found in other fish taxa (Fine et al., 1997; Hubbs and Hibbard, 1951; Kaatz et al., 2010). These processes mate with complementary structures on the pectoral girdle and control specialized functions including stridulation. The medial surface of the dorsal process in channel catfish has a ridged profile that rubs against a rough but featureless surface on the cleithrum (Fine et al., 1997). Each forward sweep (abduction) of the spine produces a series of pulses (Fine et al., 1997). Based on the logic of cricket stridulation, Fine et al. (Fine et al., 1997) posited that contact of individual ridges would be responsible for pulse generation although they stated there would be insufficient time for a ridge to make, lose and re-contact the cleithrum between pulses. In work with mochokid catfishes using a high-speed camera, Parmentier et al. (Parmentier et al., 2010) established that pulses are generated by a series of quick rotation movements or ‘jerks’ of the pectoral spine separated by pauses. They described the mechanism of sound generation as similar to a railroad break (Parmentier et al., 2010). More recent work in the blue catfish, *Ictalurus furcatus* Lesueur (Mohajer et al., in press), has modified this interpretation, demonstrating jerks generate sound by a stick–slip mechanism as in spiny lobsters (Patek, 2001; Patek, 2002), in which the jerk transfers energy from the dorsal-process ridges to the cleithrum of the fused pectoral girdle (Fine et al., 1997; Schaefer, 1984), which in turn excites the girdle to radiate one sound pulse for each jerk. Multiple ridges likely make contact during each pulse, but the number has not been established.

Blue catfish have both aquatic and aerial predators (Duvall, 2007) and produce stridulation sounds in both media. Sympatric underwater predators are likely to have unspecialized auditory systems capable of perceiving low frequencies (Ladich and Fay, 2013), and aerial predators such as birds hear higher frequencies (Dooling, 1982) and will be better tuned to catfish stridulation sounds. However, catfishes have bony connections (Weberian ossicles) between the swimbladder and the ears, and are sensitive to

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higher frequencies (Ladich and Fay, 2013) that would be useful in intraspecific communication. Therefore, the primary goal of this study was to compare acoustic properties of blue catfish stridulation sounds in air and water and to determine how sounds change with fish size. High-speed photography synchronized with sound production was also used to describe developmental changes in sound-generating pectoral motions.

RESULTS

Blue catfish recorded in air ranged in length and mass from 12.5 cm total length (TL) and 11.6 g to 52.5 cm TL and 1327 g. Twenty-five of 27 fish (93%) produced sounds in air, and the two silent fish had severe skin lesions. Twenty of these fish were recorded in air with the high-speed camera synchronized to sound, allowing us to correlate developmental changes in motion with changes in sound production. These fish were recorded outside the sound-proof booth, and these recordings were not included in regressions of sound parameters. Video recordings from individuals that produced regular pulses, designated ‘pulsers’, were utilized in this study (see Mohajer et al., in press). Finally, 10 additional fish ranging in size from 16 cm TL and 20.5 g to 32.5 cm TL and 218 g were recorded in shallow water in the James River.

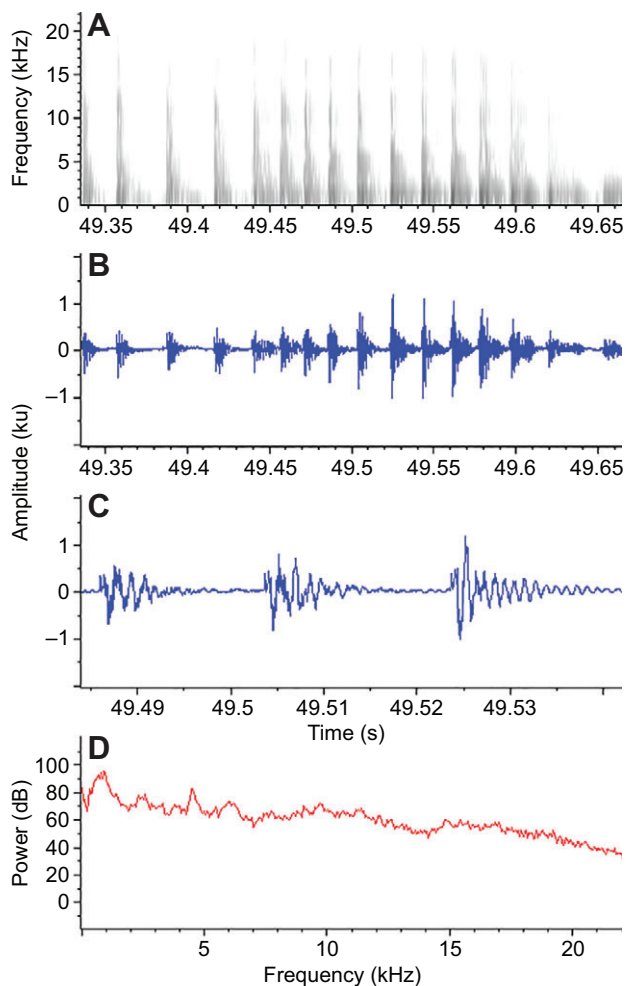


Fig. 1. Sounds made by a blue catfish in air. A spectrogram (A) and oscillogram (B) showing pulse pattern, an expanded oscillogram illustrating pulse waveform (C) and a power spectrum (D) from a 49.5 cm total length (TL), 1089 g blue catfish. Hann window, 3171 samples, 20 Hz bandwidth with 50% overlap.

Sounds in air

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

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

Table 1. Acoustic parameters of stridulation sounds of blue catfish in air and water

	Mean \pm 1 s.d.	Range
Parameter (in air)		
Sweep duration (ms)	136.5 ± 47.1	71–355
Pulses per sweep	11 ± 3.6	5–24
Pulse rate (s^{-1})	88.1 ± 33.9	23–156
Pulse duration (ms)	5.2 ± 2.4	1–15
SPL re. 20 μ Pa at 10 cm (dB)	62.1 ± 5.9	51–81
dB range (within sweeps)	6.9 ± 3.3	2–17
Center frequency (Hz)	1130.4 ± 345.9	409–2702
Peak frequency (Hz)	1127.5 ± 348.2	312–2379
Parameter (in water)		
Sweep duration (ms)	93.8 ± 44.8	47–216
Pulses per sweep	11.7 ± 2.7	7–23
Pulse rate (s^{-1})	141.6 ± 46.8	66–188
Pulse duration (ms)	4 ± 0.9	3–7
SPL re. 1 μ Pa at 0.5 m (dB)	140.2 ± 6.3	128–153
SPL re. 1 μ Pa at 1 m (dB)	131.4 ± 5.4	122–145
dB range within sweeps re. 1 μ Pa at 0.5 m (dB)	6.1 ± 3.1	2–11
dB range within sweeps re. 1 μ Pa at 1 m (dB)	8 ± 2.6	4–13
Center frequency at 0.5 m (Hz)	1090.4 ± 438.8	775–3338
Center frequency at 1 m (Hz)	1197.8 ± 436.1	744–3889
Peak frequency at 0.5 m (Hz)	1106.9 ± 492	732–3889
Peak frequency at 1 m (Hz)	1300.8 ± 529.6	759–3892

$N=25$ in air and $N=10$ in water. SPL, sound pressure level.

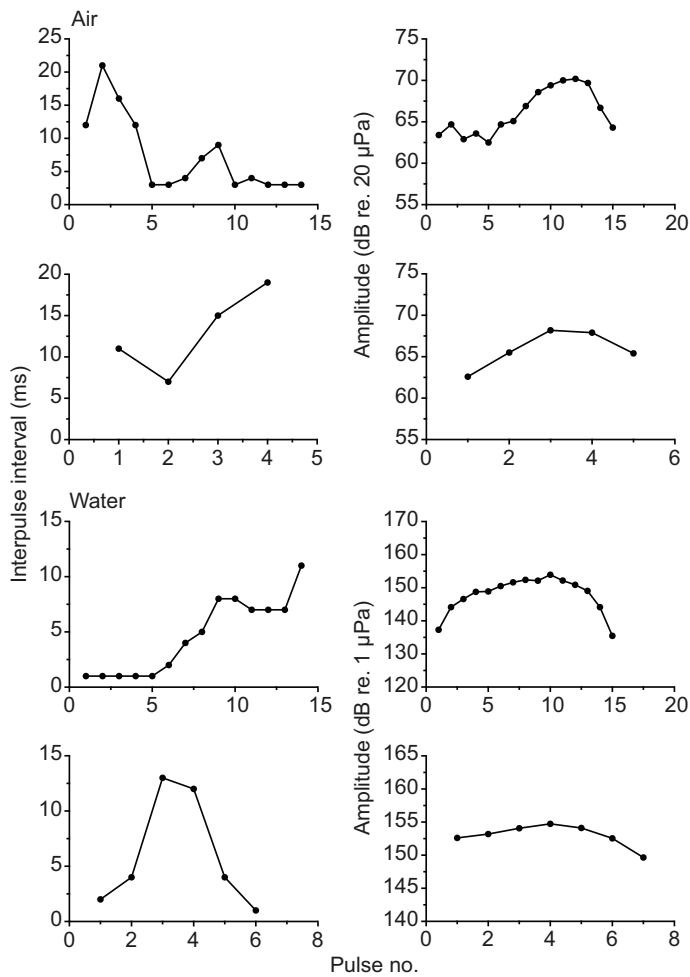


Fig. 2. Representative patterns of inter-pulse interval and amplitude in individual stridulation sweeps. Data are from two blue catfish recorded in air (top) and two recorded in water (bottom).

impulsive (rapid rise time) and suggested a combination of a forced response and resonance. Peaks occurred at odd multiples (third, fifth and seventh) of the first peak in the example shown (Fig. 1D). The first peak was at 882 Hz with subsequent peaks at 2485, 4501 and 6121 Hz. Three, five and seven times 882 would yield 2646, 4410 and 6174, respectively.

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

Changes in acoustic parameters with fish size: air

Sound pressure level (SPL) at 10 cm increased linearly from 51 to 81 dB re. 20 μ Pa with TL ($r^2=0.5379$, $P<0.0001$, Fig. 3). Amplitude range in dB within individuals did not vary with fish size ($r^2=0.045$, $P=0.307$). Both center frequency and peak frequency declined from about 2 kHz to about 500 Hz with TL ($r^2=0.3705$, $P=0.0012$ and $r^2=0.4122$, $P=0.0005$, respectively) (Fig. 4).

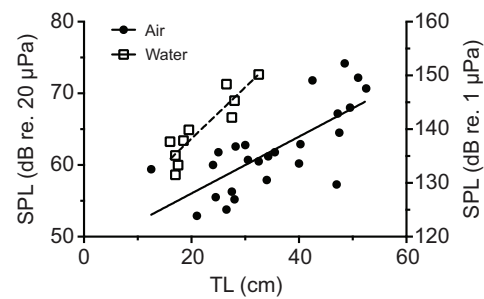


Fig. 3. Relationship of sound pressure level to total length in blue catfish. Data were recorded in air (dB re. 20 μ Pa at 10 cm) and water (dB re. 1 μ Pa at 1 m). SPL, sound pressure level.

Developmental changes in patterning of stridulation sounds were supported by high-speed photography of spine motion. Sweep sound duration increased linearly from 71 to 355 ms with TL ($r^2=0.487$, $P=0.0001$), which corresponded with increases in fin sweep duration measured with the camera, ranging from 60 to 350 ms ($r^2=0.523$, $P=0.0075$). Abduction rotation varied from 12 to 40 deg and did not change with TL ($r^2=0.027$, $P=0.628$). Each pulse was generated by a rapid jerk motion. Jerks were of short duration, 1–2 ms over rotations of mostly 2–3 deg, and jerk rotation and duration did not change with TL (jerk duration $r^2=0.059$, $P=0.498$; jerk rotation $r^2=0.0146$, $P=0.739$). Sound pulses were considerably longer than jerk durations and increased linearly with TL ($r^2=0.6799$, $P<0.0001$, Fig. 4). Therefore, once excited, the pectoral girdle continued to vibrate despite a stationary spine. The number of sound pulses per sweep decreased from 24 to 5 with TL ($r^2=0.193$, $P=0.028$), as did the number of photographed jerks, which decreased from 19 to 5 ($r^2=0.621$, $P=0.0005$). Pulse rate decreased from 156 to 23 pulses s^{-1} with TL ($r^2=0.6528$, $P<0.0001$, Fig. 4), which was determined largely by increased pauses between jerks in larger fish; pauses increased from 5 to 18 ms ($r^2=0.6373$, $P=0.0056$).

Sounds in water

Underwater stridulation sounds had a somewhat similar pulsatile appearance on sonograms and oscillograms (Fig. 5) although there were differences in waveform, amplitude and frequency spectra. Stridulation sounds were more robust underwater and varied between 122 and 145 dB re. 1 μ Pa at 1 m (131.4 ± 5.4 dB re. 1 μ Pa). Frequency spectra from a stridulation sound recorded at 0.5 m indicated most energy in a narrower band between 127 and 3878 Hz, with a peak at 854 Hz (Fig. 5). Levels dropped about 60 dB between 854 and 3875 Hz. High frequencies were strongly diminished in water as reflected in the waveform, which looks ‘cleaner’ without the higher frequency energy present in air (Figs 1, 5). Attenuation between 0.5 and 1 m averaged 9 dB (paired $t_9=12.42$, $P<0.0001$), indicating excess attenuation above cylindrical (3 dB/DD) and even spherical spreading (6 dB/DD) despite the shallow depth of no more than 1 m. Spectra from the same stridulation pulses indicated environmental filtering with a 10 dB decrease in peak energy and highest frequencies reaching background levels by 4 kHz or less (Fig. 6). The spectrum at 0.5 m was relatively smooth, exhibiting a gradual decrease between peak energy and high frequency drop-off (Fig. 6). However, by 1 m the spectrum was considerably more variable, exhibiting several regions with increased and decreased energy levels. A Q_{10dB} value (peak frequency/bandwidth 10 dB down from the peak) indicated a decrease from 1.02 to 0.85, reflecting a flatter spectrum at the greater distance. Comparison at

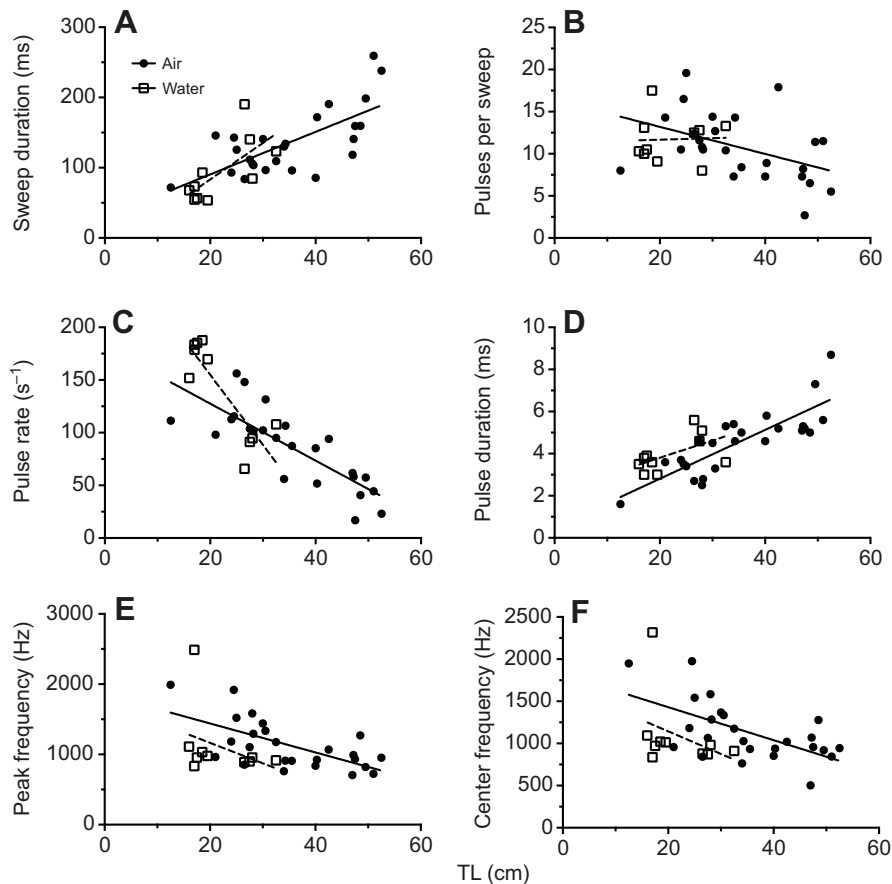


Fig. 4. Acoustic parameters in air and water. Relationship of sweep (abduction) sound duration (A), number of pulses per sweep (B), number of pulses per second (C), pulse duration (D), peak frequency (E) and center frequency (F) to TL in blue catfish recorded in air and water.

different frequencies (measurements at 100 Hz intervals) indicated energy levels below 1 kHz were generally 10–15 dB greater at 0.5 than at 1 m (Fig. 7). At higher frequencies, data were highly variable. An approximate midpoint between the peaks and valleys above 1 kHz would indicate a decrease of about 6 dB above and 12.5 dB below 1 kHz.

We attempted to compare sound levels in air and water by converting source levels to Pa. The conversion required dividing the value in Pa measured at 10 cm by 10, equivalent to a 20 dB decrease, to calculate pressure at 1 m. Extrapolated pressure in air at 1 m averaged (mean \pm s.e.) 0.0032 ± 0.0005 Pa compared with 4.5104 ± 1.0229 Pa in water, indicating a 1410-fold greater pressure in water than in air. Greater long-distance propagation therefore indicates that stridulation sounds coupled more efficiently to water than to air.

Changes in acoustic parameters with fish size: water

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

Sweep duration increased from 47 to 216 ms in water ($r^2=0.4794$, $P=0.0265$) and overlapped considerably with values in air (Fig. 4); adjusted means for a 25 cm TL individual were similar (107 ms in air and 111 ms in water). The number of pulses per sweep varied over 2-fold in different individuals and overlapped with values in air. There was not a significant size effect in the number of pulses per sweep in water, unlike in air, but comparisons over the same size range indicate little change below 30 cm TL values in air, with the decrease depending on larger individuals. Pulse rate decreased more sharply in water than in air, but adjusted means were quite similar (115 s^{-1} in air and 122 s^{-1} in water). Pulse duration changed non-significantly from 3 to 7 ms in water ($P=0.0896$), and durations were shorter in air, with adjusted means of 3.3 ms in air and 4.3 ms in water, a 27% difference. Unlike in air, peak and center frequency did not vary with fish size in water, and values were lower than in air (Table 2): adjusted means were 939 Hz in water and 1331 Hz in air.

DISCUSSION

Blue catfish stridulation sounds consist of a series of pulses produced during abduction of the pectoral spine and remaining rays. Unlike channel catfish, which tend to have their pectoral fins adducted as the default position (and thus in the ready position for stridulation), blue catfish carry their pectoral fins in a more forward position and adduct them silently before producing the sonic abduction. There are numerous catfishes that produce both adduction and abduction stridulation pulses (Heyd and Pfeiffer, 2000; Ladich, 1997), and it is possible that the blue catfish represents an intermediate stage in transformation from abduction-only sounds to stridulating in both directions. Fine et al. video recorded one adduction sound out of 256 in channel catfish (Fine et

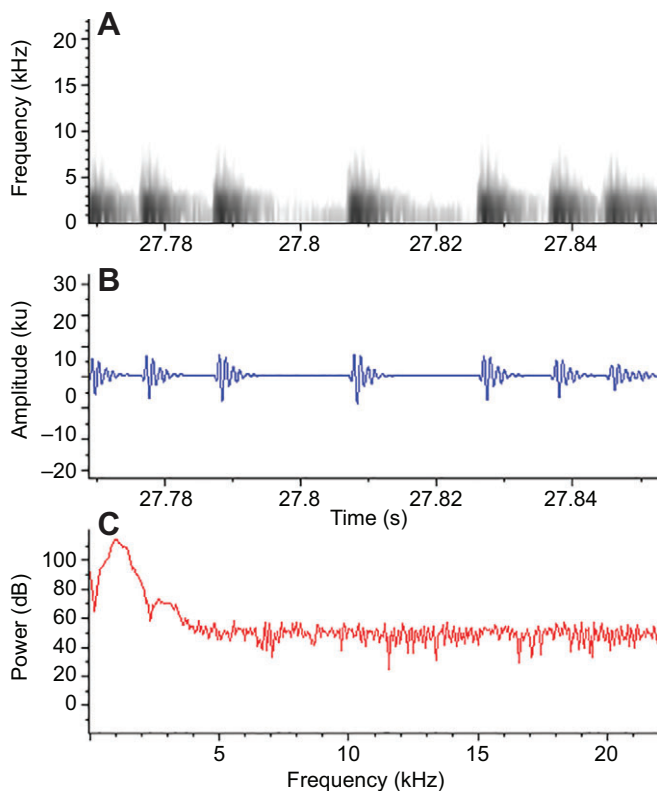


Fig. 5. Sounds made by a blue catfish in water. A spectrogram (A) and oscillogram (B) illustrating pulse pattern and waveform, and a power spectrum (C) recorded underwater from a 28 cm TL, 189 g blue catfish, 1 m from the hydrophone. Hann window, 3171 samples, 20 Hz bandwidth with 50% overlap.

al., 1996), indicating that there is no mechanical impediment to producing adduction sounds, which would require amended neural commands.

High-speed videos reveal that individual pulses are produced during a series of quick jerk movements, invisible to the human eye, during abduction (Parmentier et al., 2010; Mohajer et al., in press) when ridges on the underside of the dorsal process rub against a groove in the cleithrum (Fine et al., 1997). Sounds are produced by a slip-stick mechanism when abduction force exceeds static friction from the two rubbing surfaces (Patek, 2001), causing a quick forward motion, the jerk (Parmentier et al., 2010). The jerk, in turn, transfers energy to the pectoral girdle, the sound radiator (Fine et al., 1997). Stridulatory abduction motions are several times longer than the preceding adductions because of pauses, and pauses with no spine movement comprise 86% of abduction time (Mohajer et al., in press). The pauses, in fact, determine the temporal pattern of the sounds (Mohajer et al., in press), which is quite variable and changes developmentally. Larger fish produce louder calls at lower frequencies owing to a more massive pectoral girdle (Duvall, 2007) that would have a lower natural frequency. Both sweep duration and pulse duration increase with fish TL, and high-speed camera data indicate that time to abduct the spine increases in larger individuals, whose muscles are longer and should take longer to contract (Connaughton et al., 1997; Connaughton et al., 2000; Wainwright and Richard, 1995; Miano et al., 2013). The number of jerks and pulses per sweep as well as pulse rate decrease with fish size. However, jerk duration does not change although sound pulses (jerk sounds) increase in duration with fish size. Therefore, jerks in larger

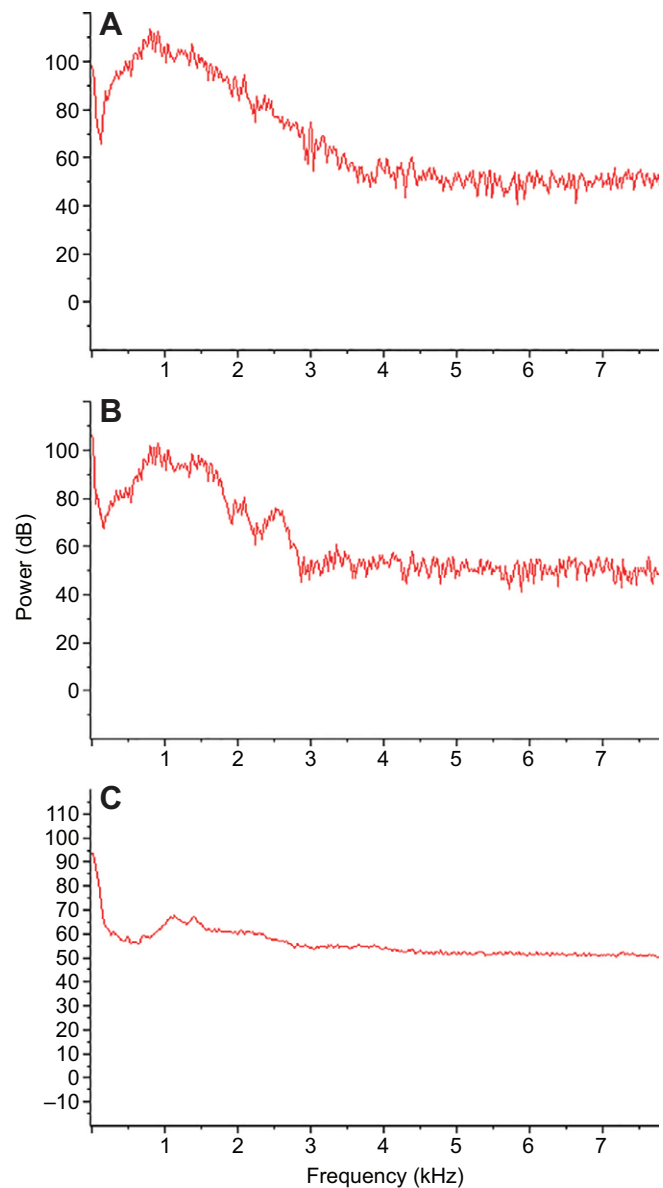


Fig. 6. Spectra from underwater stridulation sounds. Power spectra of the same stridulation sound recorded at 0.5 m (A) and 1 m (B) from a blue catfish, and background noise (C). Hann window, 3171 samples, 20 Hz bandwidth with 50% overlap.

fish excite the more massive pectoral girdle to vibrate for a longer period before amplitude decay, and pauses between jerks become longer in larger individuals, accommodating the longer sound pulse. Longer pauses likely result from a change in neural output.

Many acoustic parameters in water showed similar developmental trends to those found in recordings in air. Some of the differences likely result from the smaller range in fish size in the water samples. Amplitude will be discussed below. Other notable differences are pulse duration, which is shorter in water, and peak, center and upper frequencies, which decrease in water. Sharpness of tuning increases in water. Many of these differences parallel findings from Atlantic croaker recorded in both media (Fine et al., 2004). Peak frequency in croaker sounds does not differ between air and water because it is determined by sonic muscle contraction–relaxation time, which is not affected by acoustic loading. Croaker sounds in water are more sharply tuned (higher Q) and damp more quickly than in air, similar

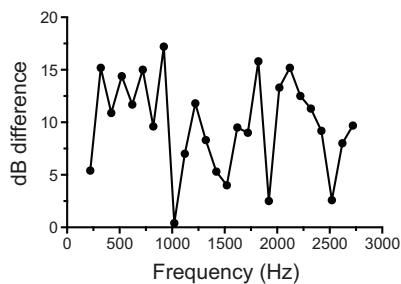


Fig. 7. Comparison of power spectra recorded underwater at 0.5 and 1 m distance. The data show the maximum decibel difference at 100 Hz intervals between spectra in Fig. 6 recorded at 0.5 and 1 m from the hydrophone.

to the more sharply tuned frequency spectrum and shorter pulses in the blue catfish. In air, where the system is less tuned, the broader response at lower frequencies appears to excite other modes at higher frequencies. With increased loading in water, the catfish spectrum decreases from >20 kHz to about 4 kHz, and the peak frequency tuned mode apparently does not excite higher modes in water. Parallels are noteworthy as the different radiators, the pectoral girdle in catfishes and the swimbladder in Atlantic croaker, appear to be affected similarly in the two media.

The acoustic properties of channel catfish sounds from domesticated stocks (Fine et al., 1996; Fine et al., 1997) share similarities with those of blue catfish, and work on the scaling of acoustic parameters to channel catfish size (Fine et al., 1999) shows similar trends to our current findings in blue catfish. There are a few marked differences between the two species. The channel catfish sounds came from domesticated fish, which have smaller spines and pectoral girdles than wild individuals (Fine et al., 2014). The frequency spectrum of channel catfish sounds tends to separate into several bands, whereas blue catfish spectra are more continuous for unknown reasons related to the structure of the pectoral girdle. Channel catfish sounds tend to be more variable, and many individuals failed to make sounds when held. Over 90% of blue catfish and 100% of fish without skin lesions sampled in this study stridulated, suggesting that the calls may serve a more important role in the life history of wild blue catfish. Sounds in blue catfish may

be used for intraspecific communication (currently unknown) and likely have an as yet undefined role in avoiding predation. In an experiment with large juveniles (>40 cm TL) utilizing an intruder blue catfish introduced to a resident, stridulation sounds were not heard (Morgan, 2014). Additionally, diel underwater recordings were made in the tidal freshwater James River in a location where blue catfish are plentiful (monthly recordings for 10 min h⁻¹ over 24 h). These included spring and summer months when mating would be expected, but no catfish sounds were heard (Morgan, 2014). It is premature to conclude that blue catfish do not make sounds during courtship and agonistic behavior as reproduction could be restricted to specific areas, and larger adults could potentially stridulate in agonistic conditions. At this point, however, evidence only points to an anti-predator function.

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

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

Table 2. Regression equations, coefficients of determination, analysis of covariance and adjusted means for sound parameters for blue catfish recorded in air and water

Parameter		Regression equation	r^2	P	Slope		Intercept		Adjusted mean
					F	P	F	P	
SPL	Air	$y=48.11+0.3963TL$	0.5379	<0.0001	6.2851	0.0176	*	*	58 dB
	Water	$y=119.1+0.9560TL$	0.8204	0.0003					143 dB
Center frequency	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
Peak frequency	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
Sweep duration	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
Pulse duration	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
Pulses per sweep	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
Pulse rate	Air	$y=181.7-2.704TL$	0.6527	<0.0001	8.4812	0.0066	*	*	115 s ⁻¹
	Water	$y=288-6.654TL$	0.7223	0.0018					122 s ⁻¹

Regression equations of acoustic parameters of stridulation sounds against fish total length, coefficients of determination, analysis of covariance and adjusted means for a 25 cm total length (TL) blue catfish in air and water.

SPL, sound pressure level.

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

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

MATERIALS AND METHODS

Ictalurus furcatus were collected by electroshocking from tidal freshwater regions of the James River near the Rice Center of Virginia Commonwealth University (VCU; VADGIF permit number 0444631). They were allowed to recover for 48–72 h in 280 l aquaria before recordings were made. Protocols were approved by the VCU Animal Care and Use Committee (IACUC no. AD20216).

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

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

Absolute sound pressure was measured in air and water. In air, a 90 dB re. 20 μ Pa 500 Hz calibration tone produced using a function generator connected to a speaker was recorded. In water, calibration utilized a 14 mV RMS tone measured with an oscilloscope and converted to dB re. 1 μ Pa (equivalent to 131 dB) using the hydrophone sensitivity calibration (−168.2 dB re. 1 V μ Pa^{−1}). The true amplitude of the stridulation sounds (in absolute pressure units) is equal to the amplitude measured by Raven multiplied by an amplitude calibration constant. The value of this constant is equal to the true (known) amplitude of the test signal divided by the RMS amplitude measured by Raven. As decibel levels in air and water are not directly comparable, levels from a sample of the fish recorded in air and water were converted to Pa. Source levels at 1 m were available from underwater recordings, and SPLs recorded at 10 cm in air were decreased by 20 dB to convert them to source levels at 1 m, assuming spherical spreading as described by 20 log r (Fine and Lenhardt, 1983; Mann, 2006; Urlick, 1975).

Pectoral stridulation motions were recorded with a video camera (Fastcam PCI R-2, Photron, San Diego, CA, USA) synchronized with sounds recorded

in air through a triggerbox (NI BNC-2110, National Instruments, Austin, TX, USA). Images were captured at 1000 or 2000 frames s^{−1}. See Mohajer et al. (Mohajer et al., in press) for more information. We determined the relationship of spine motion to sound with frame-by-frame analysis (0.5 or 1 ms per frame). Parameters measured were angular rotation and duration of fin sweeps, duration and angular rotation of small micro-movements (jerks), inter-jerk interval (the time from the beginning of one jerk to the next) and pause duration (the time when the spine was stationary). Camera data in air were used to compare quantitative aspects of motion with equivalent sound parameters.

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

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Competing interests

The authors declare no competing financial interests.

Author contributions

Z.N.G., Y.M. and M.L.F. conceived and designed the experiments; Z.N.G. and Y.M. performed the experiments; Z.N.G., Y.M. and M.L.F. analyzed the data; Z.N.G. and M.L.F. wrote the paper.

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References

- Abu-Gideiri, Y. B. and Nasr, D. H. (1973). Sound production by *Synodontis schall* (Bloch-Schneider). *Hydrobiologia* **43**, 415–428.
- Akamatsu, T., Okumura, T., Novarini, N. and Yan, H. Y. (2002). Empirical refinements applicable to the recording of fish sounds in small tanks. *J. Acoust. Soc. Am.* **112**, 3073–3082.
- Barimo, J. F. and Fine, M. L. (1998). Relationship of swim-bladder shape to the directionality pattern of underwater sound in the oyster toadfish. *Can. J. Zool.* **76**, 134–143.
- Bosher, B. T., Newton, S. H. and Fine, M. L. (2006). The spines of the channel catfish, *Ictalurus punctatus*, as an anti-predator adaptation: an experimental study. *Ethology* **112**, 188–195.
- Chandler, L. F. (1998). Trophic ecology of native and introduced catfishes in the tidal James River, Virginia. Master's thesis, Virginia Commonwealth University, Richmond, VA, USA.
- Connaughton, M. A., Fine, M. L. and Taylor, M. H. (1997). The effects of seasonal hypertrophy and atrophy on fiber morphology, metabolic substrate concentration and sound characteristics of the weakfish sonic muscle. *J. Exp. Biol.* **200**, 2449–2457.
- Connaughton, M. A., Taylor, M. H. and Fine, M. L. (2000). Effects of fish size and temperature on weakfish disturbance calls: implications for the mechanism of sound generation. *J. Exp. Biol.* **203**, 1503–1512.
- Dooling, R. J. (1982). Auditory perception in birds. In *Acoustic Communication in Birds* (ed. D. E. Kroodsma, E. H. Miller and H. Ouellet), pp. 95–130. New York, NY: Academic Press.
- Duvall, A. D. (2007). A comparison of the pectoral spines in Virginia catfishes. Master's thesis, Virginia Commonwealth University, USA.
- Ferraris, C. (2007). Checklist of catfishes, recent and fossil (Osteichthyes: Siluriformes) and catalogue of siluriform primacy types. *Zootaxa* **1418**, 1–628.
- Fine, M. L. and Ladich, F. (2003). Sound production, spine locking and related adaptations. In *Catfishes* (ed. B. G. Kapoor et al.), pp. 248–290. Enfield, NH: Science Publishers, Inc.
- Fine, M. L. and Lenhardt, M. L. (1983). Shallow-water propagation of the toadfish mating call. *Comp. Biochem. Physiol.* **76A**, 225–231.
- Fine, M. L., McElroy, D., Rafi, J., King, C. B., Loesser, K. E. and Newton, S. (1996). Lateralization of pectoral stridulation sound production in the channel catfish. *Physiol. Behav.* **60**, 753–757.
- Fine, M. L., Friel, J. P., McElroy, D., King, C. B., Loesser, K. E. and Newton, S. (1997). Pectoral spine locking and sound production in the channel catfish (*Ictalurus punctatus*). *Copeia* **1997**, 777–790.

- Fine, M. L., King, C. B., Friel, J. P., Loesser, K. E. and Newton, S. (1999). Sound production and locking of the pectoral spine of the channel catfish. *Amer. Fish Soc. Symp.* **24**, 105-114.
- Fine, M. L., Schrinel, J. and Cameron, T. M. (2004). The effect of loading on disturbance sounds of the Atlantic croaker *Micropogonius undulatus*: air versus water. *J. Acoust. Soc. Am.* **116**, 1271-1275.
- Fine, M. L., Lahiri, S., Sullivan, A. D. H., Mayo, M., Newton, S. H. and Sismour, E. N. (2014). Reduction of the pectoral spine and girdle in domesticated Channel catfish is likely caused by changes in selection pressure. *Evolution* **68**, 2102-2107.
- Forbes, L. S. (1989). Prey defenses and predator handling behavior: the dangerous prey hypothesis. *Oikos* **55**, 155-158.
- Heyd, A. and Pfeiffer, W. (2000). Über die lauterzeugung der welse (Siluroidei, Ostariophysi, Teleostei) und ihre zusammenhang mit der phylogeneese und der schreckreaktion. *Rev. Suisse Zool.* **107**, 165-211.
- Hubbs, C. L. and Hibbard, C. W. (1951). *Ictalurus lambda*, a new catfish, based on a pectoral spine from the lower Pliocene of Kansas. *Copeia* **1951**, 8-14.
- Irwin, E. R., Hubert, W. A., Rabeni, C. F., Schramm, H. L. and Coon, T. (1999). Catfish 2000. In *Proceedings of the International Ictalurid Symposium*. Bethesda, MD: American Fisheries Society Symposium 24.
- Kaatz, I. and Stewart, D. J. (2012). Bioacoustic variation of swimbladder disturbance sounds in neotropical doradoid catfishes (Siluriformes: Doradidae, Auchenipteridae): potential morphological correlates. *Curr. Zool.* **58**, 171-188.
- Kaatz, I. M., Stewart, D. J., Rice, A. N. and Lobel, P. S. (2010). Differences in pectoral fin spine morphology between vocal and silent clades of catfishes (order Siluriformes): ecomorphological implications. *Curr. Zool.* **56**, 73-89.
- Ladich, F. (1997). Comparative analysis of swimbladder (drumming) and pectoral (stridulation) sounds in three families of catfishes. *Bioacoustics* **8**, 185-208.
- Ladich, F. (1999). Did auditory sensitivity and vocalization evolve independently in otophysan fishes? *Brain Behav. Evol.* **53**, 288-304.
- Ladich, F. (2001). Sound-generating and -detecting motor system in catfish: design of swimbladder muscles in doradids and pimelodids. *Anat. Rec.* **263**, 297-306.
- Ladich, F. and Fay, R. R. (2013). Auditory evoked potential audiometry in fish. *Rev. Fish Biol. Fish.* **23**, 317-364.
- Lechner, W., Wysocki, L. E. and Ladich, F. (2010). Ontogenetic development of auditory sensitivity and sound production in the squeaker catfish *Synodontis schoutedeni*. *BMC Biol.* **8**, 10.
- Mann, D. A. (2006). Propagation of fish sounds. In *Communication in Fishes*, Vol. 1 (ed. F. Ladich et al.), pp. 107-120. Enfield, NH: Science Publishers.
- Miano, J. P., Loesser-Casey, K. E. and Fine, M. L. (2013). Description and scaling of pectoral muscles in ictalurid catfishes. *J. Morphol.* **274**, 467-477.
- Michaletz, P. H. and Travnicek, V. H. (2011). *Conservation, Ecology and Management of Catfish: the Second International Symposium*. Bethesda, MD: American Fisheries Society Symposium 77.
- Mohajer, Y., Ghahramani, Z. and Fine, M. L. (in press). Pectoral sound generation in the blue catfish *Ictalurus furcatus*. *J. Comp. Physiol. A*.
- Morgan, L. D. (2014). A passive acoustic and experimental study of juvenile blue catfish, *Ictalurus furcatus* agonistic behavior in the tidal freshwater James River. Master's thesis, Virginia Commonwealth University, Richmond, VA, USA.
- Papes, S. and Ladich, F. (2011). Effects of temperature on sound production and auditory abilities in the striped Raphael catfish *Platydoras armatulus* (Family Doradidae). *PLoS ONE* **6**, e26479.
- Parmentier, E., Fabri, G., Kaatz, I., Decloux, N., Planes, S. and Vandewalle, P. (2010). Functional study of the pectoral spine stridulation mechanism in different mochokid catfishes. *J. Exp. Biol.* **213**, 1107-1114.
- Parmentier, E., Tock, J., Falguière, J. C. and Beauchaud, M. (2014). Sound production in *Sciaenops ocellatus*: preliminary study for the development of acoustic cues in aquaculture. *Aquaculture* **432**, 204-211.
- Patek, S. N. (2001). Spiny lobsters stick and slip to make sound. *Nature* **411**, 153-154.
- Patek, S. N. (2002). Squeaking with a sliding joint: mechanics and motor control of sound production in palinurid lobsters. *J. Exp. Biol.* **205**, 2375-2385.
- Pfeiffer, W. and Eisenberg, J. F. (1965). Die lauterzeugung der dornwelse (Doradidae) und der fiederbartwelse (Mochokidae). *Z. Morphol. Oekol. Tiere* **54**, 669-679.
- Pruzsinszky, I. and Ladich, F. (1998). Sound production and reproductive behavior of the armoured catfish *Corydoras paleatus* (Callichthyidae). *Environ. Biol. Fishes* **53**, 183-191.
- Rigley, L. and Muir, J. (1979). The role of sound production by the brown bullhead *Ictalurus nebulosus*. *Proc. Pennsylv. Acad. Sci.* **53**, 132-134.
- Schloesser, R. W., Fabrizio, M. C., Latour, R. J., Garman, G. C., Greenlee, B., Groves, M. and Gartland, J. (2011). Ecological role of blue catfish in Chesapeake Bay communities and implications for management. *Am. Fish. Soc. Symp.* **77**, 369-382.
- Schaefer, S. A. (1984). Mechanical strength of the pectoral spine/girdle complex in Pterygoplichthys (Loricaridae: Siluroidei). *Copeia* **1984**, 1005-1008.
- Sismour, E. N., Nellis, S. C., Newton, S. H., Mays, D. and Fine, M. L. (2013). An experimental study of consumption of channel catfish *Ictalurus punctatus* by largemouth bass *Micropterus salmoides* when alternate prey are available. *Copeia* **2013**, 277-283.
- Sisneros, J. A., Forlano, P. M., Deitcher, D. L. and Bass, A. H. (2004). Steroid-dependent auditory plasticity leads to adaptive coupling of sender and receiver. *Science* **305**, 404-407.
- Urlick, R. J. (1975). *Principles of Underwater Sound*. New York, NY: McGraw-Hill.
- Vance, T. L. (2000). Variability in stridulatory sound production in the channel catfish, *Ictalurus punctatus*. *Bios* **71**, 79-84.
- Wainwright, P. and Richard, B. (1995). Scaling the feeding mechanism of the largemouth bass (*Micropterus salmoides*): motor pattern. *J. Exp. Biol.* **198**, 1161-1171.