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Variation in sound production of the blue catfish, Ictalurus furcatus.

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VARIATION IN SOUND PRODUCTION OF THE BLUE CATFISH, *ICTALURUS*

FURCATUS

A Thesis submitted in partial fulfillment of the requirements for the degree of Master of Science at Virginia Commonwealth University.

by

ZACHARY N. GHAHRAMANI B.S., Virginia Commonwealth University, 2007 M.S., Virginia Commonwealth University, 2010

Major Director: MICHAEL L. FINE, Ph.D. Professor, Department of Biology

Virginia Commonwealth University Richmond, Virginia August 2010

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Table of Contents

List of Tables

List of Figures

Abstract

VARIATION IN SOUND PRODUCTION OF THE BLUE CATFISH, *ICTALURUS FURCATUS*

By Zachary N. Ghahramani, M.S.

A thesis submitted in partial fulfillment of the requirements for the degree of Master of Science in Biology at Virginia Commonwealth University.

Virginia Commonwealth University, 2010

Major Director: Michael L. Fine, Ph.D. Professor, Department of Biology

The blue catfish, *Ictalurus furcatus*, is an invasive species introduced to Virginia in 1974 and is the largest catfish in the United States. Like other Ictalurids, they are capable of producing disturbance calls via stridulation of the pectoral spine. These sounds can be made in air and water, and catfish can be preyed upon by both aerial and underwater predators. I characterized these putative distress calls by recording them in air and in the fish's natural habitat. Sounds exhibited a wide variation in acoustic parameters relative to fish ontogeny: larger fish produced higher amplitude sounds with lower frequency bands. Sweep and pulse duration increased with

fish size, but pulse rate and the number of pulses per sweep decreased. Sounds were more robust in water with a 1400 fold increase in sound pressure compared to air. Frequency response was much more peaked underwater with a considerable amount of high frequency absorption. These sounds appear to be better adapted to water, suggesting that their use in air may be inconsequential.

Introduction

Animals have evolved a diverse array of behavioral adaptations for defending themselves and their resources. Defensive and offensive behavior often begins with visual, acoustical or olfactory signals before physical interactions occur (Ladich and Myrberg 2006). Production of these signals represents an evolutionarily economic method for solving disputes over resources otherwise decided at much higher costs such as injury or death. Among fishes, numerous species have been observed to emit sounds in these agonistic contexts (Ladich and Myrberg 2006). While much work has been done on the mechanisms and functional significance of sound production in other vertebrates such as amphibians and birds, there is a relative deficit in detailed descriptions of sound production and communication in fishes.

The majority of fish communicate through visual and chemical means although some use sound and electrical signals. Ladich and Myrberg (2006) suggest that environmental constraints such as light limitation in turbid waters or during dusk, night, and dawn may have decreased the usefulness of visual signals and increased the efficiency of the acoustical communication channel. According to Ladich and Fine (2006), fishes have evolved the largest diversity of sound-generating mechanisms among vertebrates. This diversity is uncommon for most vertebrates, which usually generate sounds using a single sonic organ: the larynx in amphibians and mammals and the syrinx in birds. Since there is no definitive classification of sounds or sound-generating mechanisms in fish, Ladich and Fine (2006) suggest a classification based on morphological structures which have evolved exclusively for acoustical signaling. The two major

groups of sound-producing structures are the swimbladder (and the sonic muscles that insert upon it), and the pectoral group comprised of pectoral rubbing, pectoral tendon plucking, and pectoral girdle vibrations. These sound-producing adaptations have been described in numerous families of catfish (order Siluriformes). Stridulation sounds are often found in species possessing pectoral spines. Conversely, swim bladder sounds (generally) dominate in taxa with weak pectoral girdles, thin spines, and reduced or lacking bony scutes (Fine and Ladich 2003).

Fishes often produce sounds in disturbance situations when caught, prodded, or handheld. Disturbance sounds are uttered not only in anthropogenic contexts, but toward piscine predators as well. The longspine squirrelfish, *Holocentrus rufus,* and the related soldierfish, *Myripristis berndti,* emitted grunts and staccato sounds against moray eels (order Anguilliformes, family Muraenidae) introduced into their territories (Winn et al. 1964; Salmon 1967). The atlantic cod, *Gadus morhua,* was also observed producing grunts toward a conger eel and click sounds in the presence of seals or human divers (Brawn 1961; Vester et al. 2004). Myrberg (1981) found that serranids produced drumbeats when sharks approached. Besides these interspecific agonistic situations, numerous fishes produce sounds during aggressive intraspecific encounters while competing for resources. Competitive feeding has been observed to evoke low levels of aggression, while competing for mates and space tends to induce higher levels of aggression (Ladich and Myberg 2006). Despite these observations, there are few studies that demonstrate the clear functional significance of these disturbance sounds.

The functional significance of sound production against heterospecifics, especially predators, can be derived from existing knowledge of other taxa. Fishes may utilize sounds to deter or attract predators or alarm conspecifics (Ladich and Myrberg 2006). There is no evidence, however, that predators were startled or retreated when distress calls were emitted. For

example, stridulation sounds emitted by a doradid catfish did not prevent it from being preyed upon by a piranha (Markl 1968). Disturbance calls could also have an alarm function by warning conspecifics and thus helping them to seek protection and survive. This could increase the inclusive fitness of the sender, if protected conspecifics are closely related to the sender or could represent altruistic behavior (Ladich and Myrberg 2006). Disturbance calls could also function as a way to attract additional predators; thus, disrupting the predation event and providing an opportunity for the prey to escape. This notion is supported by evidence of alarm substances in fish and distress calls in birds (Högstedt 1983; Matthis et al. 1995; Chivers et al. 1996). Bradbury and Vehrencamp (1998) observed that birds and mammals produce alarm calls that signal conspecifics and heterospecifics. The functional significance of disturbance calls is still largely unproven and requires further inquiry.

Stridulation sounds have been described in several families of catfish that possess only pectoral mechanisms. Pruzsinszky and Ladich (1998) presented the first evidence of sex-specific vocalization in catfishes by observing the reproductive behavior of *Corydoras paleatus*. Kaatz and Lobel (1999) observed that *Corydoras* catfishes produce sounds in four behavioral contexts, and their acoustic activity is low for non-reproductive fishes and significantly higher for the same individuals when they are reproductive. Heyd and Pfeiffer (2000) observed that bagrids, mochokids, doradids, and aspredinidids produce stridulation sounds by abducting and adducting their spines. In the same study, the families Ariidae, Pimelodidae, Callichthyidae, and Loricariidae all produce sounds by means of abduction only. Mahajan (1963) found that the Indian catfish, *Sisor rhabdophorus,* not only stridulates with its pectoral spines but dorsal spine as well. Rigley and Muir (1979) and Fine et al. (1996, 1997) described sounds emitted by the

ictalurids *Ameiurus nebulosus* and *Ictalurus punctatus*, respectively. The blue catfish, *Ictalurus furcatus,* produces stridulation sounds in air and water but the sounds have not been described.

Sound generation by means of the pectoral spine involves a series of intricate anatomical interactions. Stridulation sounds produced by *I. punctatus* consisted of "a rapid series of pulses produced by rubbing a ridged process on the first pectoral spine against the rough surface of a groove in the pectoral girdle during fin abduction" (Fine et al. 1997). The fused pectoral girdle functions as an unspecialized acoustic radiator excited into motion by contact with the ridges on the dorsal process (Fine et al. 1997). Fine and Ladich (2003) give a general description of sounds emitted by fishes possessing pectoral spines: "stridulation sounds occur in groups of short, wideband pulses produced during a fin sweep. Energy in the pulses occurs at frequencies of about 100-8,000 Hz and above, and commonly most of the energy is concentrated between 1,000 and 4,000 Hz. Energy is not necessarily equal within this range and often occurs in multiple bands, making it difficult to characterize a dominant or central frequency." The high frequency content of pectoral sounds is mainly above the hearing abilities of many fish predators, e.g. cichlids, and can only be perceived by hearing specialists. In pimelodid catfish two different types of acoustic signals – low-frequency sounds and high-frequency sounds – may be an adaptation to the hearing abilities of predators (Ladich and Myrberg 2006).

The family Ictaluridae is found from Southern Canada through North America and down to Guatemala (Nelson 2006). Ictalurid pectoral spines are enlarged fin rays that serve three purposes: swimming and movement, defense against predators, and sound production. Since they do not have sonic muscles associated with the swim bladder, ictalurids rely on the pectoral spine as their sole sound-producing mechanism (Fine, et al. 1997). The channel catfish, *Ictalurus punctatus*, even exhibits a preference for the right or left fin in sound production, which suggests

a striking anatomical resemblance to the human preference between two equally developed limbs (Fine, et al. 1996). By completely abducting the pectoral fin, the spine becomes locked into the fossa of the pectoral girdle and can resist all linear forces (Fine and Ladich 2003). The extended spine increases the effective size of the fish, making predation more difficult by other aerial or aquatic organisms, particularly the largemouth bass (Bosher et al. 2006). The locked spine is also dangerous to predators and handlers, as the spines can easily penetrate skin and other soft internal tissues.

This study focuses on sounds generated by the pectoral spines of the blue catfish *Ictalurus furcatus,* the largest catfish in the United States (Graham 1999). This species was introduced to Virginia in 1974 and may be replacing fish populations in the tributaries of the Chesapeake Bay. Fish biologists at Virginia Commonwealth University and the Virginia Department of Game and Inland Fisheries estimate that blue catfish compose up to 80% of the biomass in parts of the James River (unpublished). They are native to the Mississippi, Missouri, and Ohio River basins, and occupy Gulf Coast streams from Alabama south into Mexico, northern Guatemala (Glodek 1980), and Belize (Greenfield and Thomerson 1997). They frequent open waters of large reservoirs and backwaters of flowing rivers where water turbidity is high and the substrate varies from gravel-sand to silt-mud (Burr and Warren 1986). Blue catfish are opportunistic and consume a variety of animal life including fishes, immature aquatic insects, crayfish, fingernail clams, and freshwater mussels (Brown and Dendy 1961; Chandler 1998; Minckley 1962; Perry 1969). Growth is rapid, especially when on a piscivorous diet. Factors such as increased growing season, warmer water, and more diverse forage base contribute to faster growth in southern regions (Graham 1999). The tendency to live in habitats difficult to observe explains why details are lacking on its biology and life history.

Blue catfish can be attacked by both aquatic and aerial predators, and are capable of producing stridulation sounds in both air and water that contain wide frequency bands. Underwater predators are more likely to be auditory generalists capable of perceiving only low frequencies, and aerial predators such as birds can hear higher frequencies. Are these putative distress calls better suited for air, water, or equally some take on both? This study aims to address this question by describing the acoustic properties of stridulation sounds produced by *I. furcatus* and how these sounds change with development; a vital step in investigating functional significance.

Materials and Methods

Ictalurus furcatus were sampled from tidal fresh water regions of the James River around Richmond, VA by electro-shocking. They were allowed to recover for 48-72 hours in 70 gallon tanks in the aquatics lab. To eliminate ectoparasites and minimize bacterial contamination, the fish were treated with a 10 mg/L dose of potassium permanganate for seven minutes prior to placement in tanks. Protocols were approved by the VCU Animal Care and Use Committee (IACUC #AD20216).

Sounds were recorded in air and water. In-air sound recordings were made in an IAC Controlled Acoustical Environments sound-proof booth. Catfish were picked up by hand and held behind the pectoral fins. Stridulation sounds were recorded using a Zoom Corporation (Tokyo, Japan) H4 portable digital recorder. Each fish was held 10 cm away from the microphone. This method avoids reflection and resonance problems usually associated with aquaria (Akamatsu et al. 2002). Sounds from several individuals were also recorded at 20 cm to examine short distance propagation. In-water recordings were made at the VCU Rice Center dock at distances of 0.5 and 1 m with two HTI-94-SSQ hydrophones. The fish and hydrophones were held approximately halfway between the surface and bottom of the water, which varied between 0.75 and 1 m in depth. Several of these fish were then recorded in air providing sounds from individuals in both media. Signals recorded in air on the dock had acceptable signal-tonoise ratios.

Sounds were sampled at 44.1 kHz (16 bit resolution), and the acoustic parameters (sweep duration, pulse duration, number of pulses per sweep, number of pulses per second, center frequency, peak frequency, and amplitude) were analyzed using Raven Pro v1.3. Sound parameters were regressed against fish total length. A catfish pectoral stridulation sound sweep is defined as a series of pulses produced during abduction of either the right or left pectoral spine (Vance 2000). Eight sweeps per individual were analyzed unless fewer were produced. Data for each fish 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 µPa 500 Hz calibration tone (produced using a Tektronix CFG250 2 MHz Function Generator and played through a Grass AM7 Audio Monitor) was recorded. In-water, calibration utilized a 14 mV RMS tone measured with a Gould 450 Oscilloscope and converted to dB re: 1 µPa (131 dB) using the hydrophone sensitivity calibration (-168.2 dB re: 1V/µPa). 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 the amplitude calibration constant is equal to the true (known) amplitude of the test signal divided by the RMS amplitude measured by Raven. To compare acoustic pressure in air and water, decibel levels were converted to Pascals. Source levels at 1 m were available from underwater recordings. For in-air recordings, sound pressure levels recorded at 10 cm were converted to levels at 1 m by assuming spherical spreading using the formula 20 log r (Mann 2006), resulting in a decrease of 20 dB.

All statistical analyses were performed using GraphPad Prism 5. Sound parameters were scaled against fish total length using linear regression. A paired t-test was used to compare average SPL attenuation during short distance propagation in air and water in the same fish. Parameters in air and water were compared using analysis of covariance with fish total length as

the covariate (ANCOVA). When describing distribution of various acoustic parameters, the mean and standard deviation were reported, and when comparing means the mean and standard error were reported.

Results

Description of sounds in air

Blue catfish utilize their pectoral fins during normal locomotion and hovering and therefore generally carry them forward in an abducted position. Stridulation occurs during abduction, and blue catfish first adduct their pectoral fins silently. Adduction is then followed by a forward sweep (abduction) during which stridulation occurs. Stridulation sweeps vary from 71 to 355 ms (mean \pm SD, 136.5 \pm 47.1) and contain a series of between 5 to 24 pulses (11 \pm 3.6) (Fig. 1, Table 1) with somewhat different temporal patterns in inter-pulse interval and amplitude (Fig. 2). Fish can speed up or slow down at different points in the abduction sweep. Pulse amplitude often varies by 10 dB or more within a sweep and tends to be low in early pulses, and increase in the middle of the sweep before decreasing toward the end. Pulse repetition rate varied from 23 to 156 pulses per second (88.1 ± 33.9) . Sweeps can be made by either left or right fins individually or by a series of alternating lefts and rights in rapid succession. Higher pulse repetition rates stem from successive sweeps produced by both fins. Individual pulses varied from 1 to 15 ms (5.2 ± 2.4) in duration.

Individual pulses are somewhat variable but generally start with a low-amplitude halfcycle that can be positive or negative (though generally positive with a fish facing the microphone). Amplitude rapidly reaches a peak (typically the next cycle) followed by an exponential decay (Fig. 1). Sonograms indicate a series of wide-band pulses, and energy can reach 20 kHz. The frequency spectra indicate a clear peak frequency, which varied from 312 to 2379 Hz (1127.5 \pm 348.2) (Fig. 1), which is close to the center frequency calculated by Raven (Table 1). Typical spectra (Fig. 1, bottom) indicate most energy is in the first peak although there are often several peaks that tend to be about 10 dB down from the first one, after which the call pulse has lost about 20 dB but still continued above background levels, which decreased to about 30 dB above 10 kHz. Sound amplitude varied from 51 to 81 dB re: 20 μ Pa at 10 cm (62.1 \pm 5.9) and decreased an average (mean \pm SE) of 3.6 \pm 0.1768 dB by 20 cm (t3 = 14.8, p = 0.0015, Fig. 3), indicating that the walls of the sound-proof booth interfered with spherical spreading at this distance. 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 vary from 31 to 61 dB. Ranges in pulses within a sweep varied by as little as 2 to as much as 17 dB across fish (6.9 ± 3.3) .

Description of sounds in water

Stridulation sounds recorded in water have a similar appearance on sonograms and oscillograms (Fig. 4); although there are a number of quantitative differences between air and water. Stridulation sounds are more robust underwater and vary between 122 and 145 dB re: 1 μ Pa at 1 m (131.4 \pm 5.4). Frequency spectra from a stridulation sound recorded at 0.5 m indicated most energy in a single band between 127 and 3878 Hz, with a peak at 854 Hz (Fig. 6). Levels dropped about 60 dB between 854 and 3875 kHz. The loss of high frequencies in water is reflected in the waveform, which looks "cleaner" without higher frequency vibrations (Fig. 1, 4). Attenuation between 0.5 and 1 m averaged 9 dB ($t_9 = 12.42$, $p = 0.0001$, Fig. 5), indicating excess attenuation above cylindrical (3 dB/DD) and even spherical spreading (6 dB/DD). Spectra from the same stridulation pulses indicate environmental filtering with a 10 dB decrease in peak energy (Fig. 6).

An attempt at comparing sound levels in air and water was attempted by converting source levels to Pascals (Pa) and comparing them. The conversion required dividing the Pa measured at 10 cm by 10, equivalent to a 20 dB decrease. Pressure in air at 10 cm averaged (mean \pm SE) 0.0032 \pm 0.0005 Pa compared to 4.5104 \pm 1.0229 Pa in water, indicating a 1410 fold greater pressure at 1 m in water compared to air. The trend in the spectrum at 0.5 m is relatively smooth exhibiting a gradual decrease between peak energy and high frequency dropoff (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_{10dB}) indicated a decrease from 1.02 to 0.85 suggesting that the spectrum flattened out at the greater distance. Comparison at different frequencies indicates energy levels were generally 10-15 dB greater at 0.5 than 1 m below 1 kHz. 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 (Fig. 7). Pressure levels in water averaged 4.5104 ± 1.0229 Pa, indicating that stridulation vibrations coupled more efficiently into water. Other differences between sounds in the two media were compared by scaling various parameters to fish total length (see below).

Changes in acoustic parameters with fish size: air

Blue catfish ranged in length and weight from 12.5 cm TL and 11.6 g to 52.5 cm TL and 1327.4 g. Twenty-five of 27 fish (93%) produced sounds in air, and the two silent fish had severe skin lesions. Sound pressure level at 10 cm re: 20 µPa varied from 51 to 81 dB and increased by 21 dB with TL ($r^2 = 0.5379$, p = <0.0001, Fig. 8).

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. 8). Fin sweeps varied from 71 to 355 ms in duration and increased with TL (r^2 = 0.4866, p = 0.0001, Fig. 9). Pulse duration ranged between 1 and 15 ms and increased linearly with TL ($r^2 = 0.6799$, p = <0.0001, Fig. 9). The number of pulses per sweep ranged from 5 to 24 and decreased significantly with total length (r^2 = 0.1927, p = 0.0282, Fig. 9). Pulse rate ranged from 23 to 156 pps and decreased with total length (r^2 = 0.6528, p = <0.0001, Fig. 9). Pulse duration increased linearly with sweep duration (r^2 = 0.5386, p = <0.0001, Fig. 10). Pulse rate was inversely related to sweep duration $(r^2 = 0.4086, p = 0.0006, Fig. 10)$ and to pulse duration $(r^2 = 0.5555, p = 0.0001, Fig. 10)$.

Changes in acoustic parameters with fish size: water

The blue catfish recorded underwater ($N = 10$) ranged in size from 16 cm TL and 20.5 g to 32.5 cm TL and 218 g. Sound pressure level at 1 m varied from about 128 to 153 dB re: 1 μ Pa and increased significantly with TL (r^2 = 0.8204, p = 0.0003, Fig. 11). Neither center nor peak frequency scaled significantly with fish size. Sweep duration varied from 47 to 216 ms and increased significantly with TL (r^2 = 0.4794, p = 0.0265, Fig. 12). Pulse duration ranged between 3 and 7 ms, and the number of pulses per sweep ranged from 7 to 23; neither parameter correlated significantly with TL. Pulse rate decreased significantly from 188 to 66 pps with TL $(r^2 = 0.7223, p = 0.0018, Fig. 12)$. Pulse duration increased significantly with sweep duration (r^2 $= 0.5585$, p = 0.0130, Fig. 13). Pulse rate was inversely related to sweep duration ($r^2 = 0.6908$ p $= 0.0029$, Fig. 13) and pulse duration ($r^2 = 0.6564$, p = 0.0045, Fig. 13).

Comparison of acoustic parameters in air and water

Acoustic parameters in air and water were compared using ANCOVA with fish TL as the covariate (Table 2). The difference between the slopes of SPL was significant ($F_{1, 31} = 6.2951$, p $= 0.01755$) (Fig. 14). The slopes of center frequency and peak frequency did not change (F_{1, 30} = 0.7688, $p = 0.3875$, $F_{1, 30} = 1.01982$, $p = 0.3206$, respectively), but the elevation differences were significant (F_{1, 30} = 13.34, p = 0.0009, F_{1, 30} = 14.67, p = 0.0006, respectively) (Fig. 15) indicating higher frequencies in water. In fact, stridulation pulses sounded more musical in air because of higher frequencies included in the spectra (Fig. 1). Sweep duration slopes ($F_{1, 31} = 1.1399$, p = 0.2939) and elevations ($F_{1, 32}$ = <0.0001, p = 0.9936) did not differ significantly in air and water (Fig. 15) indicating that time to abduct the pectoral fin did not increase pulling against a greater load in water. The difference between slopes of pulse duration did not differ ($F_{1, 31} = 0.4692$, p = 0.4984), but elevations differed significantly ($F_{1, 32} = 5.5907$, p = 0.0243) suggesting that girdle vibrations were prolonged in water (Fig. 15). Slopes and elevations of pulses per sweep did not differ $(F_{1, 31} = 0.7669, p = 0.3879, F_{1, 32} = 0.3687, p = 0.548$, respectively) (Fig. 15). Differences between the slopes of pulses per second were significant $(F_{1, 31} = 8.4812, p = 0.0066)$ (Fig. 15), but this finding may be due to smaller fish in the water sample rather than a biological difference.

Discussion

Catfishes, one of the world's most successful groups of fishes (Irwin et al. 1999), have highly modified pectoral spines that can be bound, locked and used to produce stridulation sounds (Fine and Ladich 2003). Additionally, many tropical species produce sounds with an extrinsic muscle that causes rapid swimbladder movement. North American catfishes form a single family, Ictaluridae, which does not possess swimbladder muscles. Despite their importance in natural systems, fisheries and aquaculture (Irwin et al. 1999), little work has been devoted to acoustic communication or sound production in this family. A single paper demonstrates stridulatory sounds in agonistic behavior in the brown bullhead, *Ameiurus nebulosus* (Rigley and Muir 1979). Sounds and changes in sound parameters with fish size, and the mechanism of sound production have been described in channel catfish, *Ictalurus punctatus* (Fine et al. 1996, 1997, 1999). Channel catfish produce sounds when they are grabbed and held, and these sounds have been interpreted as a distress call that would be produced when held by a predator (Bosher et al. 2006) This study examined sounds in the congeneric blue catfish, *Icalurus furcatus*, a species introduced into Virginia waters that has similar morphology to the channel catfish (Miano 2007) but grows to a much larger size.

A blue catfish stridulation sound consists of a series of pulses produced during abduction of the pectoral fin and spine (also referred to as a sweep). High speed videos reveal that individual pulses are produced during a series of jerky movements during abduction (Parmentier et al. 2009). Stridulation sounds exhibited a wide variation in acoustic parameters (Table 1) and

change over the course of the fish's life cycle (Fig. 14, 15); larger fish produce louder calls at lower frequencies. Both sweep duration and pulse duration increased with fish total length, demonstrating that a large blue catfish takes longer to abduct its spine during stridulation. The number of pulses per sweep and pulse rate decreased with total length, which may correlate with longer pulses. This could be attributed to wearing of the ridges on the dorsal process of the pectoral spine. Most acoustic parameters showed similar developmental trends in air and water with the exception of center and peak frequency, pulse duration, and number of pulses per sweep; these apparent contradictions could have more to do with the smaller sample size in water than any real differences.

The acoustic properties of channel catfish sounds described by Fine et al. (1997) are similar to those made by the blue catfish, and unpublished work on scaling of acoustic parameters to channel catfish size show similar trends to this paper's findings in blue catfish. There are a few marked differences between the two species which are worth mentioning. Channel catfish sounds tend to be more variable and many individuals do not make sounds at all. Over 90% of blue catfish sampled in this study produced stridulation sounds, suggesting that the calls may serve a more important role in their life history. The frequency responses of channel catfish sounds tend to have discrete peaks and valleys, whereas frequency responses in blue catfish calls are more continuous.

Sounds in blue catfish may be used for intraspecific communication (currently unknown) and/or have an as yet undefined role in avoiding predation. 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 eaten by their own species (Chandler 1998), and catfish are auditory specialists that can hear high frequencies with low thresholds (Popper and Fay 1999). However,

most fish predators likely to consume young blue catfish are likely hearing generalists that will be less well tuned to the frequency spectrum of the blue catfish sounds than bird predators. This question of tuning brings up the question of whether the sounds are evolved primarily for underwater or aerial use. The data demonstrate that the frequency spectrum is considerably sharper and the sound pressure in Pascals is 1400 times greater underwater than in air. Sound pressure level in air averaged 62 dB re: 20 uPa at 10 cm, equivalent to 42 dB at 1 m, which would be a really weak sound, particularly in small fish. In water however, the source level was 131.4 dB re: 1 uPa, a rather high pressure sound. The oyster toadfish, *Opsanus tau,* often considered a "loud" fish for instance, produces a sound pressure level of 130 dB (Barimo and Fine 1998).

Fine et al. (1997) demonstrated that the pectoral girdle is the primary acoustic radiator of channel catfish sounds. This coupled with the fact that in blue catfish, midline pectoral girdle depth increases linearly with total length (Duvall 2007) suggests that the pectoral girdle plays a major role in blue catfish sound production. Given the high acoustic impedance of water over air, it appears that girdle vibrations will be coupled more successfully into water and be audible at a much greater distance than in air. Even by 1 m however, environmental filtering changed the spectrum of the catfish sound. Low frequency changes were likely caused by extinction of long wavelength sound in the shallow water we used for recording (Mann 2006) and higher frequencies exhibited a series of peaks and troughs suggesting constructive and destructive interference from reflections from water boundaries. The wide frequency band of each stridulation pulse therefore acts as a form of redundancy ensuring that the basic characteristics of the call will likely be recognizable with distance. I suspect that the call will be less affected by the environment in deeper water, as blue catfish are found in water below a meter in depth.

Figure 1. Spectrogram (top), waveform (center), and power spectra (bottom) of a blue catfish stridulation sound in air, $TL = 49.5$ cm, $W = 1088.5$ g. Note the frequency spectrum indicates peaks at 882 Hz (93 dB), 2485 Hz (79 dB), 4501 Hz (82 dB), 6121 Hz (71 dB).

Figure 2. Representative patterns of inter-pulse interval and amplitude in individual stridulation sweeps from four different blue catfish; two which were recorded in air (top) and two in water (bottom).

Figure 3. Sound pressure level of four blue catfish stridulation sounds recorded at 10 and 20 cm in air.

Figure 4. Waveform (top), spectrogram (center), and power spectra (bottom) of a blue catfish stridulation sound in water recorded at 0.5 m from the fish, $TL = 28$ cm, $W = 187.8$ g.

Figure 5. Sound pressure level of four blue catfish stridulation sounds recorded at 0.5 and 1 m in water.

Figure 6. Power spectra of the same stridulation sound in water at 0.5 m (top) and 1 m (middle) and background noise (bottom) from a stridulating catfish.

Figure 7. Decibel difference with frequency between spectra recorded at 0.5 and 1 m from a stridulating blue catfish.

Figure 8. Relationship of sound pressure level, dB range, center frequency, and peak frequency in air to total length in blue catfish.

Figure 9. Relationship of sweep duration, pulse duration, pulses per sweep, and pulses per second in air to total length in blue catfish.

Figure 10. Relationship of sweep duration to pulse duration and pulses per second, and pulse duration to pulses per sweep and pulses per second in air in blue catfish.

Figure 11. Relationship of sound pressure level, dB range, center frequency, and peak frequency to total length in blue catfish in water. Sounds were recorded 1 m from the stridulating fish.

Figure 12. Relationship of sweep duration, pulse duration, pulses per sweep, and pulses per second to total length in blue catfish in water.

Figure 13. Relationship of sweep duration to pulse duration and pulses per second, and pulse duration to pulses per sweep and pulses per second in blue catfish in water.

Figure 14. Comparison of sound pressure level in air and water to total length in blue catfish.

Figure 15. Comparisons of acoustic parameters in air and water to total length in blue catfish.

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

*re: 1 µPa at 0.5 m

[†]re: 1 µPa at 1 m

Table 2. 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 TL blue catfish in air and water. SPL, sound pressure level; CF, center frequency; PF, peak frequency; SD, sweep duration; PD, pulse duration; P/Sw, pulses per sweep; P/Sec, pulses per second.

					Slopes		Intercepts		
Parameter		Regression equation	r^2	p	F	р	F	p	Adjusted mean
SPL	air	$Y = 48.11 \pm 0.3963$ TL	0.5379	< 0.0001	6.2851	0.0176	a	a	58 dB
	water	$Y = 119.1 \pm 0.9560$ TL	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	0.0005	1.0198	0.3206	14.6729	0.0006	1319 Hz
	water	$Y = 1746 \pm 29.04$ TL	0.1710	0.2686					936 Hz
SD	air	$Y = 29.91 \pm 3.028$ TL	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	$Y = 2.174 \pm 0.08165$ TL	0.3179	0.0896					4.25 ms
P/Sw	air	$Y = 16.41 \pm 0.1608$ TL	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
P/Sec	air	Y = 181.7 ± -2.704TL	0.6527	< 0.0001	8.4812	0.0066	a	a	115
$\overline{}$	water	Y = 288 ± -6.654TL	0.7223	0.0018					122

 $\mathrm{^a}$ Because the slopes differed so much, it was not possible to test whether the intercepts differ significantly.

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Vita

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"To touch the roots of experience / the most basic ingredients / to see the unseen glitter of life / and feel the dirt, grief, anger, and strife / Cherish the certainty of now / it kills you a bit at a time / cradle the inspiration / it'll leave you writhing on the floor."

- Faith No More, 'The Real Thing'