

RESEARCH ARTICLE

Distress sounds of thorny catfishes emitted underwater and in air: characteristics and potential significance

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ABSTRACT

Thorny catfishes produce stridulation (SR) sounds using their pectoral fins and drumming (DR) sounds via a swimbladder mechanism in distress situations when hand held in water and in air. It has been argued that SR and DR sounds are aimed at different receivers (predators) in different media. The aim of this study was to analyse and compare sounds emitted in both air and water in order to test different hypotheses on the functional significance of distress sounds. Five representatives of the family Doradidae were investigated. Fish were hand held and sounds emitted in air and underwater were recorded (number of sounds, sound duration, dominant and fundamental frequency, sound pressure level and peak-to-peak amplitudes). All species produced SR sounds in both media, but DR sounds could not be recorded in air for two species. Differences in sound characteristics between media were small and mainly limited to spectral differences in SR. The number of sounds emitted decreased over time, whereas the duration of SR sounds increased. The dominant frequency of SR and the fundamental frequency of DR decreased and sound pressure level of SR increased with body size across species. The hypothesis that catfish produce more SR sounds in air and more DR sounds in water as a result of different predation pressure (birds versus fish) could not be confirmed. It is assumed that SR sounds serve as distress sounds in both media, whereas DR sounds might primarily be used as intraspecific communication signals in water in species possessing both mechanisms.

KEY WORDS: Water versus air, Sound characteristics, Doradidae, Stridulation sounds, Drumming sounds, Distress sounds, Predation

INTRODUCTION

Currently, more than 3000 species of catfish distributed in 36 families are known (Ferraris, 2007), and representatives of at least 22 families are able to produce sounds (Parmentier et al., 2010). Catfishes produce two types of sounds due to two different sound-producing mechanisms (for reviews, see Fine and Ladich, 2003; Ladich and Fine, 2006). Broadband stridulation (SR) sounds are produced by pressing ridges of the dorsal process of the pectoral spine against the floor of the spinal fossa of the pectoral girdle during fin movement (Sørensen, 1895; Bridge and Haddon, 1889; Pfeiffer and Eisenberg, 1965; Schachner and Schaller, 1981; Fine et al., 1997; Fine and Ladich, 2003; Kaatz et al., 2010; Parmentier et al., 2010). These sounds can be produced when the fin is moved

towards the body ('adduction') and away from the body ('abduction'); in some species (e.g. pimelodids) sounds are only produced during abduction (Pfeiffer and Eisenberg, 1965; Ladich, 1997; Kaatz, 1999; Heyd and Pfeiffer, 2000; Lechner et al., 2010; Parmentier et al., 2010). The second type of sound produced by catfishes is low-frequency drumming sounds, produced when the swimbladder is vibrated (Sørensen, 1895; Tavalga, 1971; Abu-Gideiri and Nasr, 1973; Kastberger, 1977; Ladich, 1997; Ladich, 1999).

Catfishes produce sounds in several behavioural contexts. Representatives of several families vocalize during courtship and agonistic behaviours (Abu-Gideiri and Nasr, 1973; Schachner und Schaller, 1981; Pruzsinszky and Ladich, 1998; Kaatz, 1999; for reviews, see Amorim, 2006; Ladich and Myrberg, 2006). Numerous species emit sounds in distress situations when they were caught, prodded or hand held (Tavalga, 1962; Pfeiffer and Eisenberg, 1965; Gainer, 1967; Kastberger, 1977; Fine et al., 1997; Ladich, 1997; Kaatz and Lobel, 1999; Kaatz, 1999; Heyd and Pfeiffer, 2000; Kaatz et al., 2010; Kaatz and Stewart, 2012). However, the biological significance of the distress sounds remains unclear. Potential functions could be to repel predators, by alerting them to the spines that could lead to major injuries, to attract more predators in order to distract the first predator from the prey (predator-attraction hypothesis) or to warn kin or conspecifics (Sørensen, 1895; Mahajan, 1963; Pfeiffer and Eisenberg, 1965; Masters, 1979; Myrberg, 1981; Schachner and Schaller, 1981; Ladich, 1997; Kaatz, 1999; Wise et al., 1999; Heyd and Pfeiffer, 2000; Kaatz et al., 2010).

Doradids are known to produce two different sound types: stridulation sounds with their pectoral fins by abducting and adducting them, and drumming sounds which are produced by the elastic spring, a thin disc-shaped bony plate, which vibrates the swimbladder via fast contractions of drumming muscles (contractor muscles) (Kastberger, 1977; Ladich, 2001; for a review, see Fine and Ladich, 2003). Doradids are known to be active sound producers in disturbance situations such as when being hand held (Pfeiffer and Eisenberg, 1965; Kastberger, 1977; Ladich, 1997; Kaatz, 1999; Heyd and Pfeiffer, 2000; Kaatz and Stewart, 2012). Sound production in other contexts is still unknown.

Interestingly, catfish produce disturbance sounds in air and in water. Most of the experiments conducted previously focused only on water (Kastberger, 1977; Schachner and Schaller, 1981; Abu-Gideiri and Nasr, 1973; Kaatz et al., 2010; Kaatz and Stewart, 2012) or air (Pfeiffer and Eisenberg, 1965; Heyd and Pfeiffer, 2000). Representatives of numerous families (pimelodids, mochokids, doradids) produced mainly stridulation sounds in a disturbance situation in air or water (Tavalga, 1960; Pfeiffer and Eisenberg, 1965; Schachner and Schaller, 1981; Kaatz, 1999; Heyd and Pfeiffer, 2000) and only a few species (the mochokid *Wahrindi Synodontis schall*, two doradids (*Agamyxis pectinifrons* and the Raphael catfish *Platydoras armatus*; formerly *P. costatus*) and two pimelodids (*Pimelodus blochii* and *Pimelodus pictus*) are known to

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produce both types of sounds in water or air (Abu-Gideiri and Nasr, 1973; Ladich, 1997). Kastberger (Kastberger, 1977) found only drumming sounds in a disturbance context in the granulated catfish *Pterodoras granulosus* (formerly *Doras maculatus*), *Megalodoras uranoscopus* and *Oxydoras niger* in water. Ladich (Ladich, 1997) observed that characteristics of stridulation and drumming sounds of doradids and pimelodids recorded in air and underwater were basically similar, but ratios of peak-to-peak amplitudes and ratios of total sound duration of stridulation and drumming sounds in the two media differed significantly. Fine et al. (Fine et al., 2004) conducted a study on disturbance sounds (drumming sounds) of the Atlantic croaker *Micropogonius undulates*, where they compared characteristics of sounds produced in air and water. Their study showed that pulse duration became longer in water, whereas the dominant frequency was unaffected.

In addition to the medium, body size can also influence sound characteristics in fishes (Ladich et al., 1992; Myrberg et al., 1993). In catfish, the relationship between sound duration, dominant frequency and sound intensity to body size has been described (Abu-Gideiri and Nasr, 1973; Kaatz, 1995; Ladich, 1997; Pruzsinszky and Ladich, 1998; Fine et al., 2004; Lechner et al., 2010), but is not known whether the sound medium has an influence on these relationships.

Ladich (Ladich, 1997) proposed that catfish produce more high-frequency stridulatory sounds than drumming sounds in air in order to startle aerial predators (e.g. birds) and vice versa more drumming sounds underwater to repel piscivorous predators. Kaatz (Kaatz, 1995; Kaatz, 1999; Kaatz, 2002) hypothesized that different sound types are produced in different behavioural contexts. Stridulatory sounds are emitted in agonistic contexts such as towards predators whereas drumming sounds are produced for intraspecific communication. Finally, Heyd and Pfeiffer (Heyd and Pfeiffer, 2000) observed that stridulatory mechanisms are absent in catfishes possessing a chemically elicited fright reaction.

The aims of our study were therefore threefold: (1) to record sounds produced under standardized hand-held conditions in air and under water and analyse their sound characteristics (number of sounds, sound duration, frequency, sound pressure level and amplitude ratios between different sound types); (2) to analyse differences in sound characteristics between species, between media and in relation to fish size; and (3) to determine whether different distress sounds are aimed at different receivers (predators) in different media. Thorny catfishes were chosen because they are known to produce both types of sounds in both media. Five species of the doradid family were investigated: the whitebarred catfish *Agamyxis pectinifrons*, *Amblydoras affinis*, *Hemidoras morrisoni*, *M. uranoscopus* and the ripsaw catfish *O. niger*.

RESULTS

Sound types

Stridulation (stridulatory) sounds were emitted during abduction (AB) and adduction (AD) of pectoral fins (Fig. 1) as soon as specimens were handled. Stridulation and drumming sounds were recorded in all five species investigated (Figs 2–5). All specimens first produced AD sounds, which were then followed by AB sounds. Stridulation sounds were high-frequency sounds which consisted of series of broadband pulses (Fig. 2, Fig. 5) and were produced both in air and water. Mean duration of stridulation sounds ranged between 50 and 130 ms (Table 1).

Two types of drumming sounds were differentiated: single drumming sounds (Figs 3, 5) and a series of short drumming sound pulses (Fig. 4). Single drumming sounds were harmonic tones with

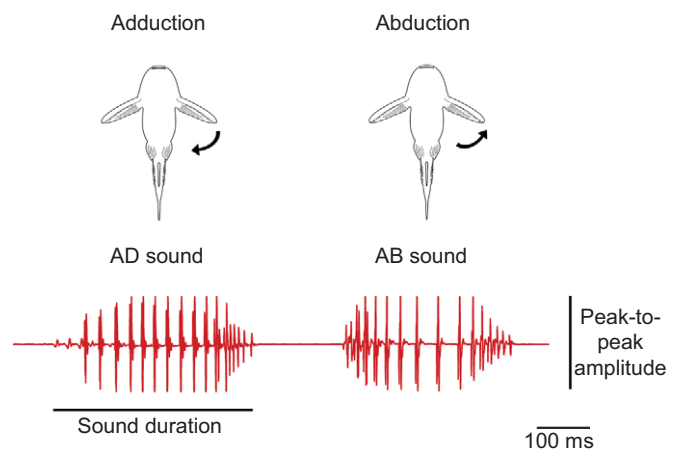


Fig. 1. Drawings of the ventral side of a thorny catfish and oscillograms of stridulatory sounds produced during adduction (AD) and abduction (AB) of pectoral fins. The upper drawings illustrate the fin movement and the lower oscillogram and sound characteristics measured. Modified after Papes and Ladich (Papes and Ladich, 2011).

main frequencies found in the first, second or third harmonic (Fig. 3). The main energies of drumming sounds were much lower than of stridulation sounds (Fig. 5; Table 1). Whereas all species produced single drumming sounds in water, only three out of five

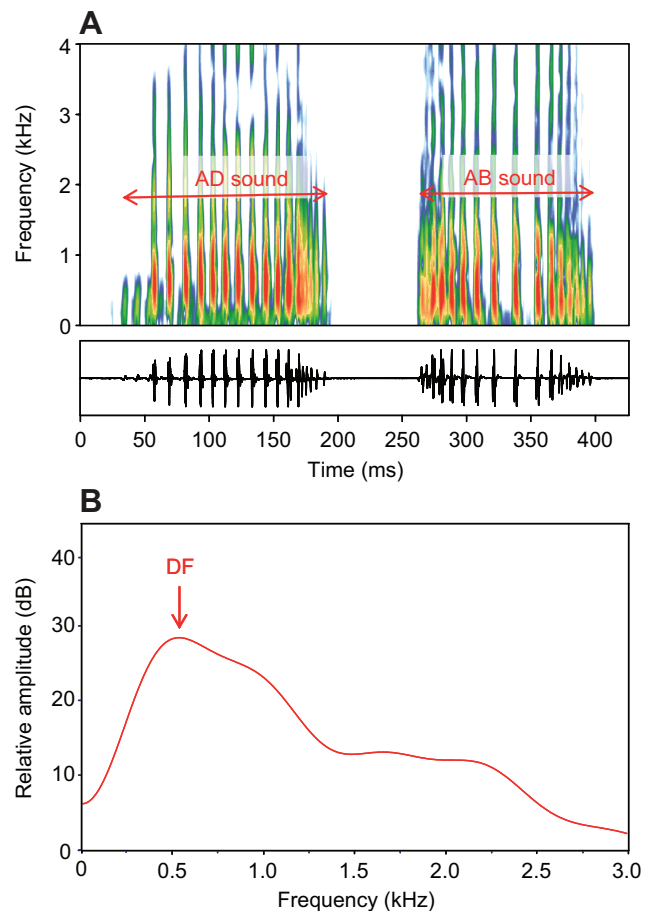


Fig. 2. Recordings of sounds produced by the thorny catfish *Megalodoras uranoscopus* in water. (A) Sonagram (top) and oscillogram (below) of two stridulation sounds. (B) Cepstrum-smoothed spectrum of one AD sound. The dominant frequency (DF) is indicated by an arrow. Sampling rate, 44 kHz; filter bandwidth, 250 Hz (A) and 10 Hz (B); Hanning filter.

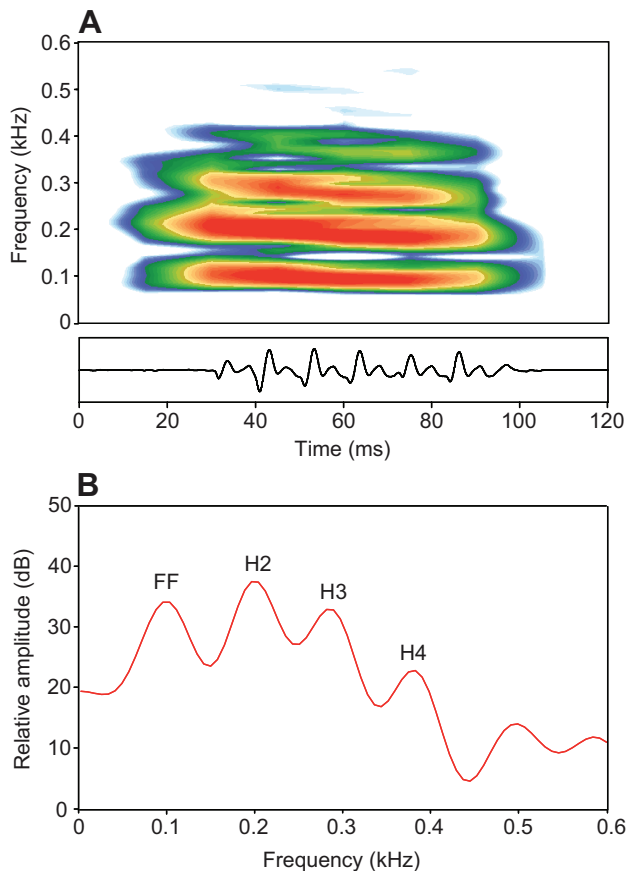


Fig. 3. Recordings of sounds produced by the thorny catfish *Oxydoras niger* in water. (A) Sonogram (top) and oscillogram (below) and (B) cepstrum-smoothed power spectrum of a single drumming sound. The sonogram shows four harmonics, with the highest energy found in the second harmonic. FF, fundamental frequency; H2, H3, H4, 2nd, 3rd and 4th harmonics. Sampling rate, 8 kHz; filter bandwidth, 10 Hz; Hanning filter.

species (*H. morrisi*, *M. uranoscopus*, *O. niger*) emitted single drumming sounds in air. The mean sound duration was ~60–80 ms in air and ~70–270 ms in water (Table 1).

A series of short drumming pulses were recorded in two individuals of *M. uranoscopus* in air and in seven individuals in

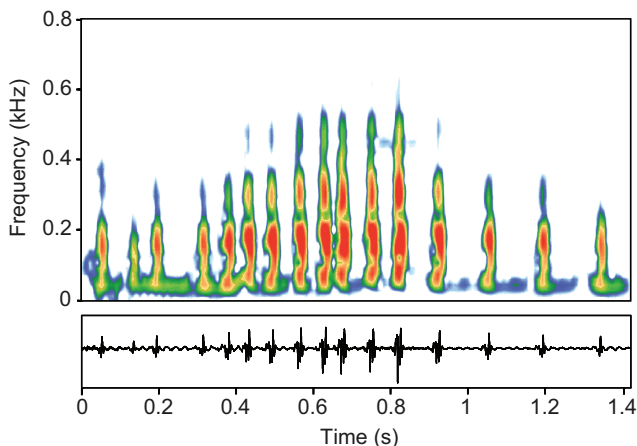


Fig. 4. Drumming sound pulses of *Megalodoras uranoscopus* emitted in water. Sonogram (top) and oscillogram (below) of a series of 16 drumming sound pulses. Sampling rate, 44 kHz; filter bandwidth, 25 Hz; Hanning filter.

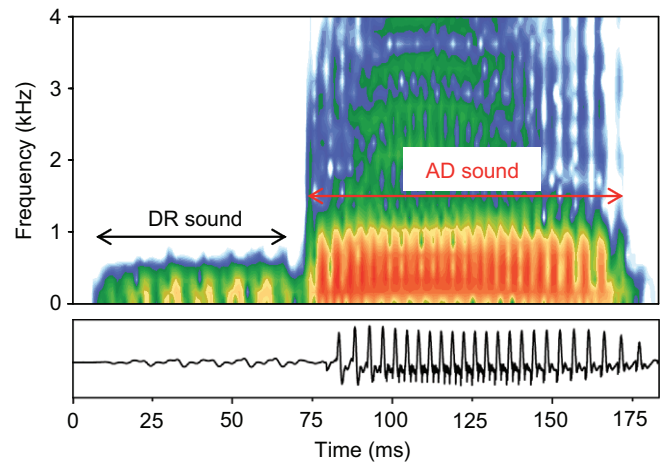


Fig. 5. Single drumming sound and adduction stridulation sound of *Megalodoras uranoscopus* emitted in water. Sonogram (top) and oscillogram (below) of a drumming sound (DR sound) and adduction stridulation sound (AD sound) of *M. uranoscopus* in water. Sampling rate, 44 kHz; filter bandwidth, 200 Hz; Hanning filter.

water and in one individual of *O. niger* in air. No drumming pulses were found in the other species. Drumming pulses were always produced in series. Pulses were more intense in the middle of a series such as in *M. uranoscopus* (Fig. 4). The series of drumming pulses was much longer than single drumming sounds (0.5–1.45 s in *M. uranoscopus* and 2.8 s in *O. niger*).

Number of sounds

Number of sounds produced in air and underwater ranged from 19 to 52 within the first minute for stridulation sounds and from 0 to 52 for drumming sounds, and did not differ between media within species except for *H. morrisi*, which emitted significantly more stridulation sounds in air than underwater (t -test, $t=3.354$, d.f.=11, $P<0.01$) (Table 1). *H. morrisi* produced the highest number of stridulation and drumming sounds in water and in air. The number of drumming sounds produced in air and water differed significantly in two out of three species in which sounds were recorded in both media. *H. morrisi* produced significantly more drumming sounds in air (t -test, $t=2.492$, d.f.=11, $P<0.05$), while *O. niger* emitted significantly more drumming sounds in water (t -test, $t=-4.849$, d.f.=2, $P<0.05$). The ratio of the number of stridulation to drumming sounds did not differ significantly between media in any species that made both types of sound in both media.

The number of stridulation sounds produced decreased over time in all species in both media, except in *O. niger*. Repeated-measures (RM) ANOVA revealed a significant change in the number of sounds produced in subsequent 15 s periods (Fig. 6). Similarly, the number of single drumming sounds decreased over time for all species that produced drumming sounds (both media: *H. morrisi*; only water: *M. uranoscopus* and *A. pectinifrons*). RM-ANOVA revealed no significant change for *M. uranoscopus* in air or for *O. niger* in both media.

Sound duration

The mean duration of stridulation sounds ranged from 67 to 126 ms in AD sounds and from 58 to 122 ms in AB sounds in both air and water (Table 1). Duration of AD and AB sounds differed in three out of five species between media. AD sounds were longer in water than in air in *A. pectinifrons* and *M. uranoscopus*, but shorter in *H. morrisi* (Fig. 7). In contrast, AB sounds were longer in *M.*

Table 1. Characteristics of sounds produced in air and water by the doradid species investigated

	Medium	<i>Agamyxis pectinifrons</i>	<i>Amblydoras affinis</i>	<i>Hemidoras morrisi</i>	<i>Megalodoras uranoscopus</i>	<i>Oxydoras niger</i>
No. of SR sounds	Air	48.7±3.9	24.8±6.0	51.5±2.5**	32.0±4.9	33.7±8.2
	Water	49.1±1.4	19.0±3.9	38.0±3.7	26.0±3.6	37.7±7.1
No. of DR sounds	Air	0	0	51.5±4.0*	16.3±5.4	7.7±4.1*
	Water	30.0±4.5	16.0±9.0	39.4±4.3	21.8±2.3	34.7±5.8
Sound duration (ms)						
	AD sounds	Air	116.9±4.1**	91.4±2.4	74.1±0.8**	116.2±1.1*
	Water	131.4±1.1	95.6±1.2	67.4±0.7	126.2±1.9	83.4±1.6
AB sounds	Air	115.4±5.1	82.2±1.4	60.4±0.4	88.6±2.5*	80.8±2.7
	Water	121.7±3.8	78.9±1.0	57.7±0.5	98.4±1.2	93.0±2.9
DR sounds	Air	–	–	64.8±29.2	79.2±6.1	70.3±0.8
	Water	276.3±15.9	88.0±18.9	74.7±6.6	70.6±4.1	138.7±12.4
Dominant frequency (kHz)						
	AD sounds	Air	2.4±0.2*	1.7±0.1*	2.3±0.2***	1.9±0.2*
	Water	1.5±0.1	1.8±0.1	1.6±0.1	0.9±0.1	0.5±0.01
AB sounds	Air	1.6±0.1**	2.8±0.2	2.2±0.1***	1.0±0.1***	1.2±0.04
	Water	1.5±0.2	1.8±0.2	1.6±0.1	1.0±0.1	0.7±0.01
Fundamental frequency (Hz)						
	DR sounds	Air	–	–	107±2	99±2
	Water	107±3	169±7	75±7	92±2	94±2

AD, adduction; AB, abduction; DR, single drumming; SR, stridulation.

Statistically significant differences in sound characteristics between air and water: * $P<0.05$, ** $P<0.01$, *** $P<0.001$. Values are means ± s.e.m.

uranoscopus in water than in air. The mean sound duration of drumming sounds ranged between 65 and 79 ms in air and 71–276 ms in water (Table 1). The duration of drumming sounds, however, did not differ between air and water. The duration of AD and AB sounds increased over time in all species in both media. RM-ANOVA revealed a significant difference in duration of AB and AD sounds over 15 s time periods, except for AB sounds in *A. pectinifrons* in air, for AD sounds in *H. morrisi* in water and for AD and AB sounds in *O. niger* in both media (Fig. 8). No such effects were observed for drumming sounds.

Dominant and fundamental frequency

The mean dominant frequency of stridulation sound ranged between 0.8 and 2.8 kHz in air and between 0.5 and 1.8 kHz in water. The mean dominant frequency of AD and AB sounds was significantly higher in air than in water in all species except in *O. niger* for AD and AB sounds and in *A. affinis* for AB sounds (Fig. 9; Table 1). Fundamental frequencies of single drumming sounds were found

between 91 and 107 Hz in air and 75–169 Hz in water (Table 1). Mean fundamental frequencies of drumming sounds emitted in air and in water did not differ significantly (Table 1).

Larger animals produced sounds with lower frequencies than smaller animals. Dominant frequencies of AD and AB sounds decreased significantly with standard length in water and air across species (Coefficient of determination: $R^2=0.41–0.55$, $N=37$, $P<0.01$) (Fig. 10). Fundamental frequency of drumming sounds decreased with size in water (SL: $R^2=0.52$, $N=27$, $P<0.05$) but not in air (SL: $R^2=0.10$, $N=12$, n.s.) (Fig. 11).

Sound pressure level

Sound pressure levels (SPLs) differed between stridulation and drumming sounds. Mean SPLs of stridulation sounds in air ranged from 47 to 55 dB re. 20 μ Pa (LAF_{max}, 25 cm distance in air) and from 60 to 62 dB re. 20 μ Pa (LZF_{max}) and in water ranged from 126 to 132 dB re. 1 μ Pa (LAF_{max}, 5–10 cm distance) and from 127 to 140 dB re. 1 μ Pa (LZF_{max}). For drumming sounds, SPLs varied

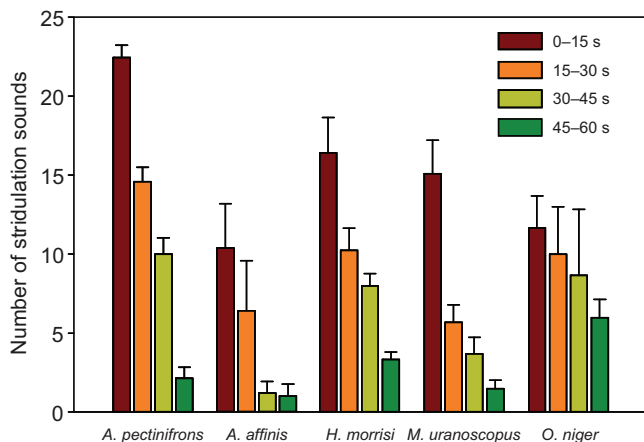


Fig. 6. Number of stridulation sounds of doradid species produced in water within over consecutive 15 s time periods. Different colours represent different time periods. Values are means + s.e.m.

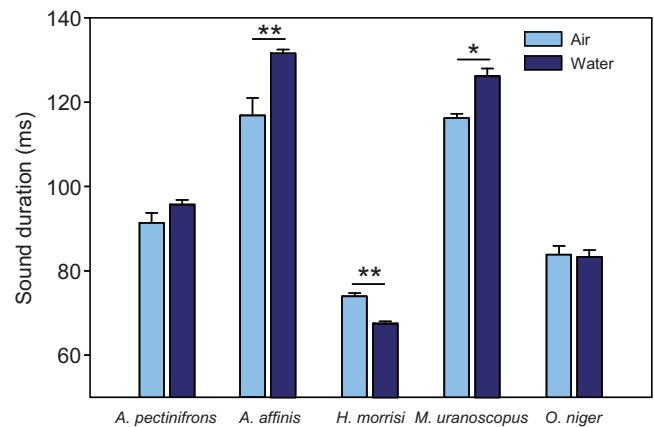


Fig. 7. Duration of adduction stridulation sounds emitted in air and water for five doradid species. * $P<0.05$, ** $P<0.01$. Values are means + s.e.m.

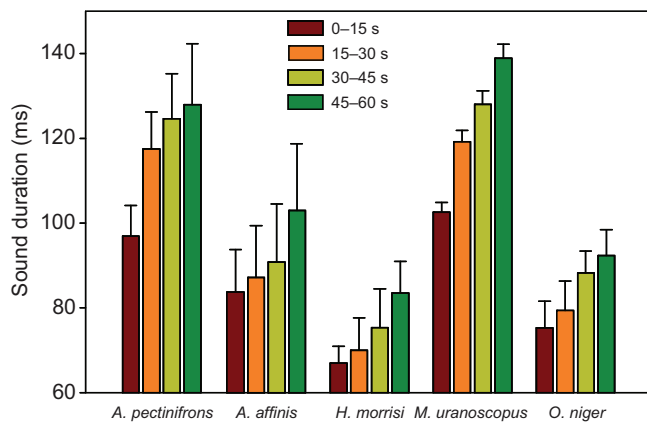


Fig. 8. Duration of adduction stridulation sounds produced in air in four consecutive 15 s time periods for five doradid species. Values are means + s.e.m.

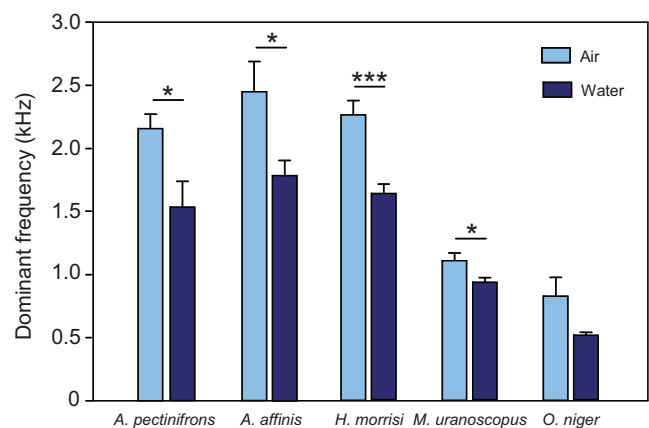


Fig. 9. Dominant frequency of adduction stridulation sounds emitted in air and water for five doradid species. * $P < 0.05$, *** $P < 0.001$. Values are means + s.e.m.

between 32 and 35 dB re. 20 μ Pa (LAF_{max}) and between 58 and 59 dB re. 20 μ Pa (LZF_{max}) in air and between 88 and 112 dB re. 1 μ Pa (LAF_{max}) and between 107 and 132 dB re. 1 μ Pa (LZF_{max}) in water (Table 2). The SPL of the single drumming sounds of *O. niger* could not be determined separately in air because single drumming sounds always occurred together with high-amplitude stridulation sounds.

Larger fish emitted louder sounds than smaller fish. The SPL (LAF_{max} and LZF_{max}) of stridulation sounds increased with standard length in all fish in both media (LAF_{max} in air: $R^2=0.18-0.67$, $N=37$, $P < 0.05$) (Fig. 12). Similarly, SPLs of drumming sounds increased with body size (standard length) in water (LAF_{max} in water: $R^2=0.45$; LZF_{max} : $R^2=0.61$; both: $N=27$, $P < 0.01$). Because of a lack of data, a correlation for drumming sounds produced in air could not be calculated.

Peak-to-peak amplitude ratios of stridulation sounds

Peak-to-peak amplitudes of AD sounds were higher than of AB sounds in *A. affinis*, *H. morrisi* and *M. uranoscopus* in both media, indicating that AD sounds were louder than AB sounds (Fig. 13). No such difference was observed in *A. pectinifrons* and *O. niger*. Ratios of peak-to-peak amplitudes of AD and AB sounds did not differ between media in any species.

Pectoral spine length

Absolute pectoral spine length in the five species investigated were between 13.9 and 52 mm and varied significantly between species (ANOVA: $F=22.596$, d.f.=4,32, $P < 0.001$). Relative pectoral spine

length (PL/SL) ranged from 0.19 to 0.23 (*A. pectinifrons*: 0.21; *A. affinis*: 0.19; *H. morrisi*: 0.22; *M. uranoscopus*: 0.23; *O. niger*: 0.20) and did not differ between species (ANOVA: $F=0.786$, d.f.=4,32, n.s.). Neither absolute nor relative pectoral spine length correlated with sound duration.

DISCUSSION

Sound types

Our experiments have shown that all thorny catfish species investigated, namely *A. pectinifrons*, *A. affinis*, *H. morrisi*, *M. uranoscopus* and *O. niger*, produced stridulation and drumming sounds in air and in water when hand-held except for two species (*A. pectinifrons* and *A. affinis*), which did not make drumming sounds in air. The production of high-frequency broad-band stridulation sounds and low-frequency drumming sounds have also been described in other catfish studies where sounds were either recorded in air or in water, or even in both media (Ladich, 1997). Parmentier et al. (Parmentier et al., 2010) mentioned that representatives of 18 out of 22 sonic catfish families produce pectoral stridulation sounds. It is not mentioned, however, in which media sounds were recorded and whether the remaining four families only produce drumming sounds or no sounds at all. Kaatz and Stewart (Kaatz and Stewart, 2012) report that 25 species of doradoids (families Doradidae and Auchenipteridae) produce swimbladder disturbance sounds in water.

Drumming sounds were produced less consistently and at much lower levels than stridulatory sounds in both media in our study. The

Table 2. Sound pressure levels of sounds produced in air and water by the doradid species investigated

	Medium	<i>Agamyxis pectinifrons</i>	<i>Amblydoras affinis</i>	<i>Hemiodoras morrisi</i>	<i>Megalodoras uranoscopus</i>	<i>Oxydoras niger</i>
LAF_{max} SR sounds	Air	47.2 \pm 0.7	49.0 \pm 0.7	53.2 \pm 0.7	55.5 \pm 0.6	53.7 \pm 0.9
	Water	126.6 \pm 0.5	129.1 \pm 1.2	129.7 \pm 0.6	129.1 \pm 1.5	132.0 \pm 0.5
DR sounds	Air	–	–	35.2 \pm 1.3	31.7 \pm 0.9	–
	Water	94.1 \pm 2.0	88.4 \pm 1.3	109.4 \pm 2.0	97.0 \pm 3.4	111.6 \pm 2.6
LZF_{max} SR sounds	Air	60.3 \pm 0.4	60.2 \pm 0.6	60.1 \pm 0.4	62.1 \pm 0.8	61.7 \pm 0.7
	Water	127.1 \pm 0.5	129.4 \pm 1.1	130.5 \pm 0.6	134.7 \pm 1.4	139.9 \pm 0.5
DR sounds	Air	–	–	59.4 \pm 1.4	59.8 \pm 0.5	–
	Water	117.4 \pm 2.7	107.4 \pm 1.2	119.2 \pm 0.7	111.3 \pm 2.3	131.9 \pm 3.5

DR, single drumming; LAF_{max} , RMS fast-time weighting A-frequency-weighted sound level; LZF_{max} , fast, Z-frequency-weighted sound level; SR, stridulation. Values are means \pm s.e.m.

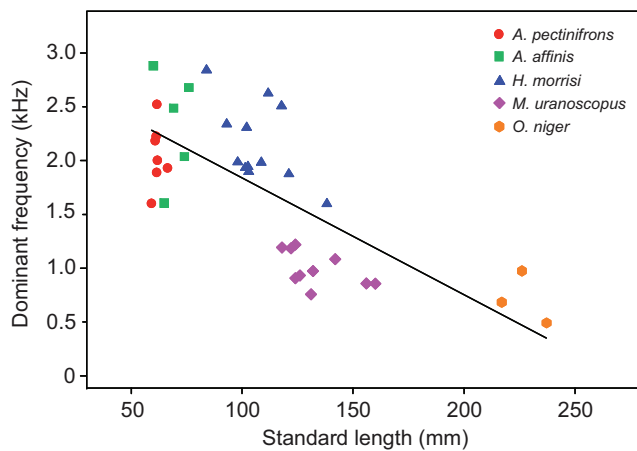


Fig. 10. Correlation between dominant frequency of adduction stridulation sounds recorded in air and standard length. Regression equation: Frequency=3.03 kHz–10.8×standard length; $R^2=-0.53$; $P<0.01$.

lack of drumming sound recordings in two doradid species in air is probably due to the low levels of these sounds which might in addition have been overlapped by the much louder stridulatory sounds and thus might not have been detected. This assumption is supported by the observation that drumming sounds have been recorded in air in *A. pectinifrons* in a previous study (Ladich, 1997).

Typically, thorny catfish in the current study started stridulation with an adduction movement of pectoral spines followed by abduction. The current observation is confirmed by Kaatz (Kaatz, 1999) but differs from previous studies, which described that the production of stridulation sounds always started with abduction sounds (Pfeiffer and Eisenberg, 1965; Ladich, 1997). One explanation could be that fish in the previous studies did not lock their spines in a right angle before producing sounds.

Two different types of drumming sounds are described in the present study: single drumming sounds and series of short drumming pulses. Ladich (Ladich, 1997) mentioned similar types of drumming sounds in *P. armatulus* when hand held. Kaatz and Stewart (Kaatz and Stewart, 2012) also found two types of drumming sound in their study on doradoids. Sounds were either continuous waveforms lacking interpulse periods or they were pulsed with fixed temporal intervals. Kaatz and Stewart (Kaatz and

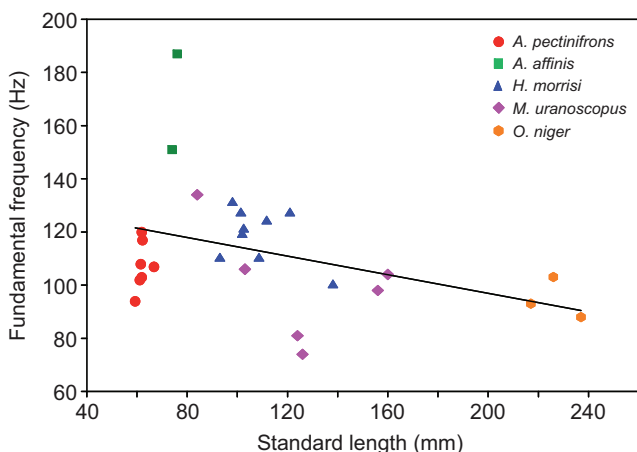


Fig. 11. Correlations between fundamental frequency of drumming sounds recorded in water and standard length. Regression equation: Frequency=132 Hz–0.17×standard length; $R^2=-0.15$; $P<0.05$.

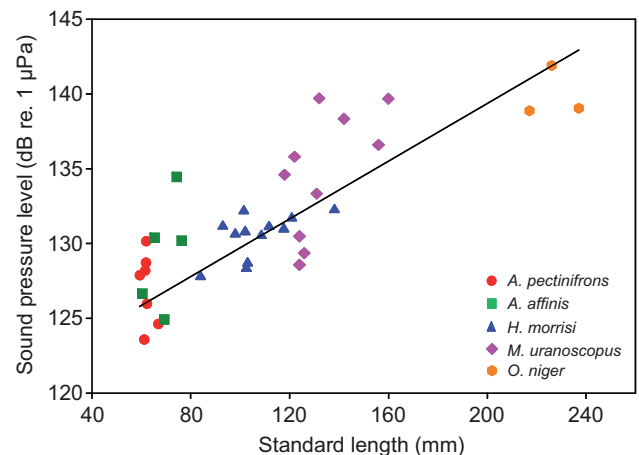


Fig. 12. Correlation between sound pressure level (LZF_{max}) of stridulation sounds recorded in water and standard length. Regression equation: SPL=120.1 dB re. 1 μPa+0.10×standard length; $R^2=0.67$; $P<0.01$.

Stewart, 2012) found pulsed drumming sounds in four out of 25 doradoid species, including *M. uranoscopus*. Similar to the current study they mentioned that *M. uranoscopus* produced mainly pulsed drumming sounds.

Based on these data it is concluded that all representatives of the family Doradidae emit stridulation and drumming sounds in distress situations in both media. In addition, it is assumed that all members of this family produce sounds during abduction and adduction movement of pectoral fins, in contrast to members of other catfish families such as pimelodids (Ladich, 1997). However, it remains to be investigated whether all doradids are able to generate two types of drumming sounds.

Number of sounds

The number of stridulation sounds recorded within the first minute did not differ between media except for one species (*H. morrisi*), indicating that fish were similarly stressed when hand held independent of the medium. No such common trend could be observed in drumming sounds. The number of drumming sounds was similar in both media in *M. uranoscopus*, significantly higher in air in *H. morrisi* and lower in *O. niger* (and lacking in *A. pectinifrons* and *A. affinis*). Pfeiffer and Eisenberg (Pfeiffer and Eisenberg, 1965)

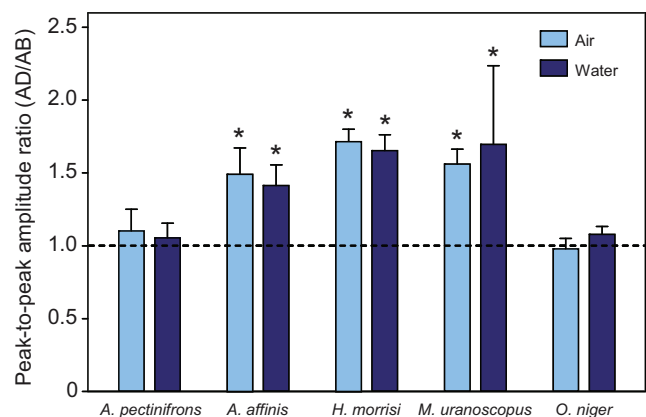


Fig. 13. Peak-to-peak amplitude ratios of adduction and abduction stridulation sounds in air and water in doradid species investigated. Asterisks indicate that adduction (AD) sounds were louder than abduction (AB) sounds.

reported that the doradid species *Platydoras hancockii* (formerly *Amblydoras hancockii*), *Agamyxis albomaculatus* and *P. armatulus* produced 46 to 71 stridulation sounds within 15–20 s in air. Thus, they emit many more sounds than catfish in the present study. Kastberger (Kastberger, 1977), however, mentioned that *M. uranoscopus* and *O. niger* emitted 6–9 drumming sounds per minute in water, which is much less than in the current study. These differences in vocalizing activity might be due to the different species used and/or different levels of arousal. Kaatz (Kaatz, 1999) found that 27 out of 42 catfish species produced significantly more stridulation sounds than drumming sounds when hand held in three environments (air, underwater in the field and in aquaria). She found four catfish species in which the mean number of drumming sounds was significantly higher than the number of stridulation sounds, such as in one species of the genus *Hemidoras*. The latter species had weaker pectoral girdles and thinner pectoral fin spines, indicating that drumming might be a more effective way of anti-predator signalling.

The fact that the number of stridulation sounds produced decreased over time was described and quantified for the first time. The decrease in vocalizing activity is probably due to muscle fatigue and perhaps due to a decline in the level of arousal (Schachner and Schaller, 1981). Another explanation could be that catfish switch from distress sound production to pectoral spine locking as a more effective weapon against predators (Fine and Ladich, 2003; Bosher et al., 2006).

Sound duration

The mean duration of stridulation sounds in the present study ranged from 70 to 125 ms in AD sounds and 50 to 120 ms in AB sounds in both media. The duration of stridulation sounds has been described for several species of doradids in air. Pfeiffer and Eisenberg (Pfeiffer and Eisenberg, 1965) found that the duration of AD sounds recorded in air was shorter than of AB sounds in *P. hancockii* (80 versus 110 ms), in *A. albomaculatus* (110 versus 140 ms) and in *P. armatulus* (90 versus 120 ms). Similarly, Ladich (Ladich, 1997) found that AD sounds were shorter in *A. pectinifrons* (95 versus 110 ms) but not in *P. armatulus* (70 ms) and Heyd and Pfeiffer (Heyd and Pfeiffer, 2000) described a sound duration of 102 ms for stridulation sounds in *A. pectinifrons*. These previous data from sounds recorded in air agree with the results for sound duration in the present study. Sound durations for stridulation sounds recorded in water have not yet been described in doradids and thus results could not be compared. The duration of stridulation sounds measured in water for representatives of other catfish families, such as the pimelodid *Rhamdia sebae* (10–150 ms) and the mochokid *Synodontis schoutedeni* (20–90 ms) cover a broader range of sound durations than doradids in the present study (Schachner and Schaller, 1981; Lechner et al., 2010).

The comparison between media reveals no common trend (AD sounds were significantly longer in water in *A. pectinifrons* and *M. uranoscopus*, significantly shorter in *H. morrisoni*; AB sounds were longer in water in *M. uranoscopus*, no trend in the other four species). Therefore, the medium itself might not influence pectoral fin movements and sound duration in doradids. The duration of AD and AB sounds increased over time in all five doradid species investigated. This change in sound duration and subsequently pulse periods is probably due to muscle fatigue. This indicates that in distress sounds temporal patterns are less important for communication than they are in reproductive behaviour (Myrberg et al., 1978; Fine et al., 2004).

Ladich (Ladich, 1997) found that the duration of AD sounds varied across families and increased with relative spine length. Interestingly,

spines were relatively longer in *Platydoras armatulus* than *A. pectinifrons* (Ladich, 1997), but they did not vary in the five doradid species in the present study. Absolute spine lengths were not correlated with sound duration within doradids, which may be explained by the large variety in durations of abduction and adduction movements due to different levels of arousal and muscle fatigue.

The duration of single drumming sounds ranged from 60 to 80 ms in air and from 70 to 270 ms in water and did not differ in any species between media. The duration of drumming sounds produced by other doradid species in air and water ranged between 10 ms and 1.5 s (Kastberger, 1977; Ladich, 1997; Kaatz and Lobel, 2001). Interestingly, the duration of single drumming sounds decreased with body size in water but not in air. In contrast to stridulation sounds, duration of drumming sounds did not decrease with time. Fine et al. (Fine et al., 2004) found a longer pulse duration in drumming sounds emitted in water in the sciaenid *Micropogon undulatus*, but no change in sound duration.

Main frequencies of sounds

The dominant frequency of stridulation sounds was significantly higher in air than in water in four out of five species in the present study. It is assumed that this is also the case in the fifth species, *O. niger*, although this could not be shown because of the small number of specimens available in this study. Previous studies recorded sounds either in water or in air, and thus no direct comparison between the two media is possible. Lower dominant frequency of sounds in water compared with air is perhaps due to the different densities of media and recording conditions. Fish were recorded in a small tub under water but not in air. However, the lack of a difference between media in fundamental frequency of drumming sounds may be explained by the fact that the fundamental frequency reflects the muscle contraction rate of drumming muscles controlled by firing patterns of sonic motor nuclei in the brainstem (Ladich and Bass, 2011) and not by resonance phenomena within the body or the environment. Thus, different physical parameters of the two media do not affect the neuron firing patterns. Fine et al. (Fine et al., 2004) also found no significant difference in fundamental frequency in the sciaenid *M. undulatus* between media. Hence, the bladder is vibrated in a similar pattern at a similar frequency.

The dominant frequency of catfish stridulation sounds described previously in doradids, mochokids, pimelodids and callichthyids ranged from 0.5 to 4 kHz in air and water (Pfeiffer and Eisenberg, 1965; Schachner and Schaller, 1981; Ladich, 1997; Pruzsinszky and Ladich, 1998; Kaatz, 1999; Heyd and Pfeiffer, 2000; Fine and Ladich, 2003; Lechner et al., 2010; Papes and Ladich, 2011). Therefore, current results (0.5–3 kHz) correspond with the frequency ranges previously described.

Dominant frequency of stridulation sounds decreased with increasing body size across species (standard length and body mass). The same trend was already described in representatives of numerous fish families such as in callichthyids, mochokids, gurnards, mormyrids, croaking gouramis, damselfish and toadfish (Ladich et al., 1992; Myrberg et al., 1993; Crawford, 1997; Pruzsinszky and Ladich, 1998; Henglmüller and Ladich, 1999; Wysocki and Ladich, 2001; Amorim and Hawkins, 2005; Vasconcelos and Ladich, 2008; Lechner et al., 2010; Parmentier et al., 2010). Ladich (Ladich, 1997) found such a correlation in one out of two doradid species, namely in *P. armatulus* but not in *A. pectinifrons*, which might have been due to the small size range in the previous study.

The fundamental frequency of drumming sounds in catfish families investigated ranged from 50 to 200 Hz in air (Kastberger,

1977; Ladich, 1997; Heyd and Pfeiffer, 2000; Fine and Ladich, 2003; Fine et al., 2004) and 100 to 500 Hz in water (Schachner and Schaller, 1981; Fine et al., 2004). Doradids of the current study fall within this range of frequencies described previously (*P. armatulus*: 96 Hz; *A. pectinifrons*: 114 Hz; *O. niger*: 80–100 Hz; *M. uranoscopus*: 120 Hz).

The fundamental frequency of drumming sounds decreases with increasing body size across species in water showing that larger fish and species exhibit lower muscle contraction rates than smaller fish. This phenomenon was not observed in air, probably because the number of individuals producing drumming sounds in air was small. Abu-Gideiri and Nasr (Abu-Gideiri and Nasr, 1973) found a similar tendency in the mochokid *Synodontis schall* in water. Larger fish emitted deep and strong grunts whereas smaller fish emitted sounds with a higher frequency. The fundamental frequency also decreases with fish size in the weakfish (Connaughton et al., 2000; Connaughton et al., 2002) and the whitemouth croaker (*Micropogonias furnieri*) (Tellechea et al., 2010). Fine et al. (Fine et al., 2004) suggested therefore that croakers could estimate relative size of the caller equally in aerial and underwater recordings. Connaughton et al. (Connaughton et al., 2002) suggest that larger muscles with longer fibers would take longer to complete a contraction, resulting in a lower frequency in drumming sounds in larger fish. Those lower-frequency sounds produced by larger fish might act as ‘honest signals’, because these are hard to imitate (Sargent et al., 1998).

Sound amplitudes

Peak-to-peak amplitude ratios did not differ significantly between AB and AD stridulation sounds uttered in air and water. This indicates that during adduction and abduction pectoral spines are rubbed with the same intensity in the groove of the pectoral girdle in both media (Ladich, 1997). Sound pressure levels of stridulation sounds were in all cases much higher than of drumming sounds in the current experiments. Ladich (Ladich, 1997) made the same observation in *P. armatulus* and *A. pectinifrons*. Schachner and Schaller (Schachner and Schaller, 1981) described the same trend in the pimelodid *R. sebae* with a SPL of 150 dB re. 1 μ Pa for stridulation sounds and 130 dB re. 1 μ Pa for drumming sounds, both in water. Kaatz (Kaatz, 1999) stated that stridulation sounds are generally louder than drumming sounds in a large number of catfishes but no measurements are provided. Schachner and Schaller (Schachner and Schaller, 1981) claimed that sound intensity depends on the arousal of fish.

The SPL of stridulation sounds increased with body length in doradids investigated. Such a correlation was found in several non-related species such as in the tigerfish *Therapon jarbua* (Schneider, 1961), the croaking gourami *Trichopsis vittata* (Wysocki and Ladich, 2001), the sciaenid *Cynoscion regalis* (Connaughton et al., 2000) and in the mochokid catfish *S. schoutedeni* (Lechner et al., 2010). Fine et al. (Fine et al., 1997) and Lechner et al. (Lechner et al., 2010) assume that the amplitude of sounds depends on anatomical constraints and on how long and hard fish press the dorsal process of the pectoral spine against the groove of the shoulder girdle, which could cause inter-individual variation of SPLs.

Functional considerations

The fact that doradids (and a few other catfish families) possess two very different sonic mechanisms points to different biological tasks (Heyd and Pfeiffer, 2000; Kaatz, 2002; Fine and Ladich, 2003; Boshier et al., 2006). It was assumed that a possible function of distress sounds is to warn and protect against predators because the production of stridulation sounds is linked to spine locking and

might indicate difficulties in swallowing the sound producer (Sørensen, 1895; Mahajan, 1963; Pfeiffer and Eisenberg, 1965; Schachner and Schaller, 1981; Ladich, 1997; Kaatz, 1999; Heyd and Pfeiffer, 2000). Ladich (Ladich, 1997) hypothesized that two different types of acoustic signals are aimed at different receivers: low-frequency sounds (drumming sounds) against aquatic and high-frequency stridulation sounds against aerial predators. Support for this notion comes from the hearing sensitivities in non-oscine birds which possess greatest sensitivities between 1 and 4 kHz (Dooling, 1982; Ladich, 2010) in contrast to many fish species which primarily detect low-frequency sounds (<1 kHz) (Ladich and Popper, 2004; Ladich and Fay, 2013). In the present study, doradids did not emit more stridulation sounds in air than in water. Therefore, we suggest that stridulation sounds are produced in both media in disturbance contexts whereas drumming sound production is more dependent on the medium. Several studies demonstrate that stridulation sounds are produced in disturbance contexts in air and water in catfishes (Tavolga, 1960; Pfeiffer and Eisenberg, 1965; Abu-Gideiri and Nasr, 1973; Schachner and Schaller, 1981; Ladich, 1997; Kaatz and Stewart, 1997; Kaatz, 1999; Heyd and Pfeiffer, 2000). Kaatz (Kaatz, 1999) stated that stridulation sounds are more effective disturbance sounds because they are louder than drumming sounds and could function as warning signals. Drumming sounds in catfishes, by contrast, have been described numerous times as intraspecific signals for communication (Tavolga, 1960; Abu-Gideiri and Nasr, 1973; Schachner and Schaller, 1981; Kaatz, 1999). Drumming sounds are of much lower frequency than stridulation sounds and might be more suitable for short distance communication owing to the frequency cut-off phenomenon, which limits the propagation of low-frequency sounds in shallow waters (Rogers and Cox, 1988; Crawford et al., 1997; Mann, 2006).

Boshier et al. (Boshier et al., 2006) observed that only 20% of channel catfish *Ictalurus punctatus* (members of this family do not possess drumming muscles) produced stridulation sounds when attacked by the largemouth bass *Micropterus salmoides*. This indicates that pectoral spine locking seems to be a far better defence mechanism against predators than stridulation alone (Fine and Ladich, 2003). Boshier et al. (Boshier et al., 2006) argue that predators learn to associate the pain of the pectoral spine with the stridulation sound and would therefore avoid this type of ‘dangerous’ prey when they hear stridulation sounds. Forbes (Forbes, 1989) called this effect the ‘dangerous prey hypothesis’. Spines lead to severe injuries in the soft tissues of predators (Boshier et al., 2006; Glahn and King, 2004). Boshier et al. (Boshier et al., 2006) furthermore argue that stridulatory sounds could potentially summon up other predators and increase the emitter’s chances of escape (predator-attraction hypothesis).

In conclusion, our data support the hypothesis that stridulatory sounds target predators in interspecific communication and that swimbladder sounds serve rather as intraspecific communication signals (Kaatz, 1995; Kaatz and Stewart, 1997; Kaatz and Stewart, 2012; Kaatz, 1999; Kaatz, 2002; Kaatz et al., 2010). This is in agreement with observations in various organisms, including insects, amphibians, birds and mammals, that loud and harsh broad-band sounds are emitted when animals are being attacked by predators (Bradbury and Vehrencamp, 2011). In addition, the observation by Heyd and Pfeiffer (Heyd and Pfeiffer, 2000) that stridulatory mechanisms are absent in catfishes that possess chemically elicited fright reactions indicates that broad-band sounds may serve primarily during predatory attacks.

The hypothesis that different sonic mechanisms in fish serve different functions, however, is not applicable to fish species, such

as callichthyid catfish or terapontids, which possess just one sonic mechanism. Males of the callichthyid genus *Corydoras* produce stridulation sound during courtship and disturbance (Pruzsinszky and Ladich, 1998; Kaatz and Lobel, 1999) whereas the trumpeter *Peleates octolineatus* emits swimbladder sounds during predatory attacks (Bessey and Heithaus, 2013). In order to prove that drumming and stridulation sounds serve different functions in doradids, comparative intraspecific and interspecific behavioural studies including different predators need to be carried out.

MATERIALS AND METHODS

Animals

Three to twelve individuals of *A. affinis*, *A. pectiniifrons*, *H. morrissi*, *M. uranoscopus* and *O. niger* were investigated (Table 3). All fish were purchased from tropical fish suppliers (Transfish, Munich, Germany and Ruinemans, The Netherlands). Fish were kept in community tanks which were filtered by external filters, planted and equipped with hiding places, e.g. half flower pots or tubes. The bottoms of aquaria were covered with sand. Tanks were between 70×40×50 cm (width × height × depth) and 100×50×50 cm in size. A 12 h: 12 h light:dark cycle was maintained and the temperature was kept at 25±1°C. Fish were fed frozen chironomid larvae, flake food or food pellets 4–5 days per week. The sex of the fish could not be determined because most of the fish were immature and sexing without sacrificing the animals was not possible. The length of the left pectoral spine was measured from the juncture of the spine with the outer body surface to its tip. The study protocol was approved by the Austrian Federal Ministry of Science and Research, permit number GZ 66.006/0023-II/10b/2008.

Sound and video recordings in air

Fish were held horizontally by their dorsal spine and right pectoral spine. Distance to the microphone was 25 cm. The fish usually emitted sounds immediately when taken out of the water. The right pectoral fin was always fixed to avoid overlap of stridulation sounds which are usually produced simultaneously by both pectoral fins. The fish was recorded until it stopped producing sounds. Minimum recording time was 1 min.

Sounds were recorded using a condenser microphone (AKG C 1000 S, AKG Acoustics GmbH, Vienna, Austria), which was connected to the mic input of a HiFi-S-VHS video cassette recorder (VCR; JVC HR-S4700, EGVictor Company of Japan, Yokohama, Japan). Video recordings were made using a video camera (Sony VX1, Sony Corporation, Tokyo, Japan) connected to the same VCR in order to distinguish between sounds produced during adduction and abduction of the pectoral fin. Sound pressure levels (SPLs) were recorded using a sound level meter (Brüel & Kjaer 2250, including 4189 condenser microphone, Brüel & Kjaer GmbH, Vienna, Austria), which recorded different SPL measures simultaneously and stored data on an SD card. The distance from fish to sound level meter was 25 cm. Sound recording took place in a soundproof room constructed as a Faraday cage at 25±1°C. Individuals were marked by clipping 1–2 spines on their lateral bony plates. Each individual was recorded twice (once in air and once under water) with a minimum time period of 3 weeks between recordings. If an animal did not utter sounds, recordings were repeated after a minimum of 1 day. The minimum number of sounds recorded per fish was 10 (stridulation) sounds.

Table 3. Mass and size ranges of experimental subjects used in this study

Species	N	Mass (g)	SL (mm)
<i>Agamyxis pectiniifrons</i> Cope 1870	7	7.1–9.1	59–66
<i>Amblydoras affinis</i> Kner 1855	5	4.6–11.7	65–75
<i>Hemidoras morrissi</i> Eigenmann 1925	12	6.3–16.9	84–138
<i>Megalodoras uranoscopus</i> Eigenmann and Eigenmann 1888	10	34.6–68.9	118–160
<i>Oxydoras niger</i> Valenciennes 1821	3	165.1–178.4	217–237

N, number of individuals; SL, standard length.

Sound and video recordings in water

Underwater sound recordings took place in a plastic tub (height, 16 cm; diameter, 39 cm) several centimetres below the surface. In order to reduce resonance and reflection, the tub was lined on the inside with acoustically absorbent material (air-filled packing wrap). The tub was placed on a vibration-isolating air table (TMC Micro-g 63-540, Technical Manufacturing Corporation, Peabody, MA, USA). Again, sounds were recorded for at least 1 min.

Sounds were recorded using a hydrophone (Brüel & Kjaer 8101) connected to a power supply (Brüel & Kjaer 2804) which was connected to the mic input of the VCR. Fish were held 5–10 cm from the hydrophone in the middle of the plastic tub. The right fin was fixed again to avoid overlap of stridulation sounds generated simultaneously by both pectoral fins. For SPL measurements, the sound level meter (Brüel & Kjaer 2250) was recalibrated using a hydrophone calibrator (Brüel & Kjaer 4229), which was connected to the power supply. Sound recording took place in a soundproof room constructed as a Faraday cage at 25±1°C.

Sound analysis

The first minute of sound recording was analysed, starting at the moment when the fish was held in the final position at the same height as the microphone or hydrophone. Ten AD and AB sounds were examined for both air and water. For drumming sounds, a minimum of five sounds per fish were analysed. Sounds were analysed using STX 3.7.8, STX 4.0 (Institute of Sound Research at the Austrian Academy of Sciences) and Cool Edit 2000 (Syntrillium Software Corporations, Phoenix, AZ, USA). The following sound characteristics were determined for stridulation and drumming sounds recorded in air and underwater.

The total number of sounds produced by each fish within the first minute of the sound recording was counted. The 1 min sound recording was divided up into four 15 s time periods each. Then number of AB and AD sounds and drumming sounds produced in each 15 s period was determined to investigate whether the number of sounds emitted changed over time (Fig. 14). If a sound occurred in two adjacent 15 s time periods the sound was counted in the first of these two periods.

The total length of AD or AB sounds or of single drumming sound was measured. Duration of 10 AD and AB sounds, and drumming sounds was determined (Fig. 14). Additionally, the duration of five AD and AB sounds within each 15 s time period was measured in order to see whether duration changed over time.

Dominant frequencies of stridulation sounds were measured by using cepstrum-smoothed power spectra (filter bandwidth, 3 Hz; 75% overlap; number of coefficients, 100; Hanning filter; maximum frequency, 6 kHz) (Fig. 2B). 10 AD and 10 AB sounds were measured. Fundamental frequencies of 10 drumming sounds were measured by using cepstrum-smoothed power spectra (filter bandwidth, 2 Hz; 50% overlap; number of coefficients, 80; Hanning filter; maximum frequency, 1 kHz) (Fig. 3B).

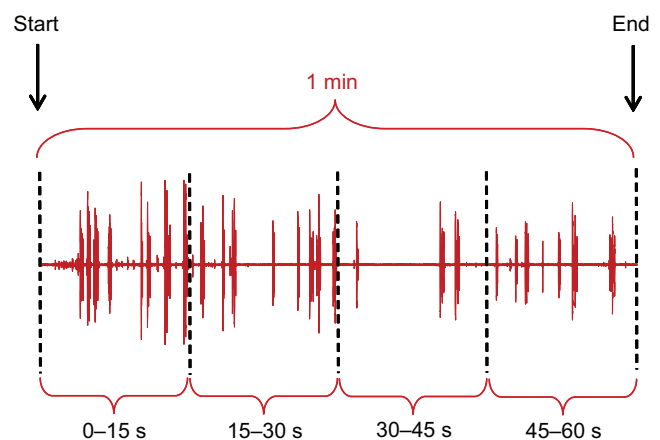


Fig. 14. Oscillogram of a 1 min sound recording illustrating the time periods measured.

Relative peak-to-peak-amplitude of 10 AD sounds and 10 AB sounds was determined by measuring relative voltages of the highest pulse within an AD sound and AB sound and calculating the ratio between these two amplitudes (AD/AB ratio) (Fig. 1).

Absolute SPLs of stridulation and drumming sounds were determined using the sound level meter and the software Evaluator (Brüel & Kjaer 7820 and 7821). For measuring SPLs, RMS fast time weighting (time constant, 125 ms) and two different frequency weightings were applied. A as well as Z frequency weightings were used (LAFmax and LZFMmax) because of differences in auditory sensitivities of fish and bird predators (e.g. herons). SPLs of AD and AB sounds could not be determined separately (due to the temporal limitations of the sound level meter), therefore, peak-to-peak ratios were calculated to determine difference in amplitude (see above). Absolute SPLs of drumming sounds could only be determined when they were not produced at the same time as stridulation sounds. SPLs of stridulation sounds were typically higher than those of drumming sounds. A direct comparison between SPLs in air and water was not possible due to differences in the impedance of the media, in the reference sound pressure (20 µPa in air and 1 µPa in water) and recording conditions.

Statistical analysis

All data were tested for normal distribution using the Kolmogorov–Smirnov Test. Since data were normally distributed, only parametric tests were applied. Means of sound characteristics of 10 stridulation and 5–10 drumming sounds were calculated for each fish and used for further analysis. Relationships between sound characteristics and morphological variables (e.g. frequency versus standard length) were determined by the coefficient of determination (R^2). Differences in characteristics of sounds emitted in air and water were tested using paired *t*-tests. Differences between the number of sounds and sound durations within a 15 s time period were calculated using RM-ANOVA. Additionally, ratios of peak-to-peak amplitudes for AD and AB sounds (AD/AB) were calculated in order to find a difference between the two media. All statistical tests were conducted by using PASW 18.0 (SPSS Inc., Chicago, IL, USA). The significance level was set at $P < 0.05$.

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Competing interests

The authors declare no competing financial interests.

Author contributions

L.K. and F.L. conceived and designed the experiments, analysed the data and wrote the paper; L.K. performed the experiments.

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