MASTERARBEIT

Titel der Masterarbeit

„Distress sounds emitted by thorny catfishes (Doradidae) underwater and in air“

verfasst von

Lisa Marie Knötig BSc

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Betreuerin / Betreuer:	Ao. Univ.-Prof. Dr. Friedrich Ladich

Contents

ABSTRACT

Background: Thorny catfishes produce stridulation sounds with pectoral fins and drumming sounds with the swimbladder in distress situations when hand-held in water and in air. Researchers have argued that those sounds are aimed at different receivers (predators) in different media. The aim of this study was to analyse sounds, compare characteristics of sounds emitted in both media in order to investigate the functional significance of distress sounds.

Methodology/Principal Findings: Five representatives of the family Doradidae (*Agamyxis pectinifrons*, *Amblydoras affinis*, *Hemidoras morrisi*, *Megalodoras uranoscopus* and *Oxydoras niger*) were investigated. Fish were hand-held and sounds emitted in air and underwater were recorded. The following sound characteristics were analyzed - number of sounds, sound duration, dominant and fundamental frequency, sound pressure level and peak-to-peak amplitudes - and compared between media. Furthermore, they were correlated to fish size (standard length, body weight). All species produced stridulation sounds in both media but only three species produced drumming sounds in air. Most characteristics of stridulation sounds (number of sounds, sound duration, frequency) differed between media but no such differences were found in drumming sounds. Number of sounds emitted decreased over time while duration of sounds increased. Dominant frequency of stridulation sounds decreased and sound pressure level increased with body size.

Conclusions/Significance: Characteristics of stridulation sounds but not of drumming sounds were affected by media. This is most likely due to differences in the density of media and sound producing mechanisms. The hypothesis that catfish produce more stridulation sounds in air and more drumming sounds in water due to different predation pressure (birds versus fish) could not be confirmed. Therefore, it is assumed that stridulation sounds serve as distress sounds in both media, whereas drumming sounds might mainly be used as intraspecific communication signals in water.

Keywords: water vs. air, sound characteristics, Doradidae, stridulation sounds, drumming sounds, distress sounds.

INTRODUCTION

Currently more than 3000 species of catfish distributed among 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 a review see Fine and Ladich 2003 and Ladich and Fine 2006). Broadband stridulation sounds are produced by pressing of ridges of the dorsal process of the pectoral spine against the floor of the spinal fossa of the pectoral girdle during fin movement (Sörensen 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 sound type produced by catfishes are low frequency drumming sounds, produced when the swimbladder is vibrated (Sörensen 1895, Tavolga 1971, Abu-Gideiri and Nasr 1973, Kastberger 1977, Ladich 2001).

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 (Tavolga 1962, Pfeiffer and Eisenberg 1965, Gainer, 1967, Kastberger 1977, Fine et al. 1997, Ladich 1997, Kaatz and Lobel 1997, 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 or warn kin or conspecifics or to warn predators by alerting them to the spines which can lead to major injuries and even death of predators (Sörensen 1895, Mahajan 1963, Pfeiffer and Eisenberg 1965, Myrberg 1981, Schachner and Schaller 1981, Ladich 1997, Kaatz 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 that connects fast-contracting drumming muscles with the swimbladder (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). 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 disturbance situation in air or water (Tavolga 1960, Pfeiffer and Eisenberg 1965, Schachner and Schaller 1981, Kaatz 1999, Heyd and Pfeiffer 2000) and only a few species (the mochokid Wahrinidi *Synodontis schall,* two doradids *(Agamyxis pectinifrons* and the Raphael catfish *Platydoras armatulus;* formerly *P. costatus)* and two pimelodids *(Pimelodus blochii and Pimelodus pictus*)) are known to produce both types of sounds in water or air (Abu-Gideiri and Nasr 1973, Ladich 1997). Kastberger (1977) found only drumming sounds in disturbance context in the granulated catfish *Pterodoras granulosus* (formerly *Doras maculates*)*, Megalodoras uranoscopus* and *Oxydoras niger* in water. Ladich (1997) found in his study that waveforms 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. (2004) conducted a study on disturbance sounds (drumming sounds) of the Atlantic croaker *Micropogonius undulatus* where they compared characteristics of sounds produced in air and water. Their study showed that there were no spectral but rather temporal differences in the sounds in the two media.

Besides the medium body size can influence sound characteristics in fishes (Ladich et al. 1992, Myrberg et al. 1993). In catfish relationships between body size and sound duration, dominant frequency as well as sound intensity has been described (Abu-Gideiri and Nasr 1973, Kaatz 1995, Ladich 1997, Pruzsinszky and Ladich 1998, Fine et al. 2004, Lechner et al 2010). Little is known if media have an influence on these relationships.

The aim of the study was therefore three-fold, (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) and (2) to analyse differences in sound characteristics between species, between media and in relation to fish size. Thorny catfishes were chosen because they are known to produce both types of sounds in both media (Ladich 1997, Kaatz 1999, Fine and Ladich 2003). The following five species of the doradid family were investigated namely the whitebarred catfish *Agamyxis pectinifrons, Amblydoras affinis, Hemidoras morrisi, M. uranoscopus* and the ripsaw catfish *O. niger.* The third goal was to find out if differences in sound characteristics between media might shed some light on the question if distress sounds are aimed at different receivers (predators) in different media.

METHODS

Animals

Three to twelve individuals of *A. affinis, A. pectinifrons, H. morrisi, M. uranoscopus* and *O. niger* were investigated (Tab. 1). All fish were purchased from tropical fish suppliers (Transfish, Munich, Germany, and Ruinemans, 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 bottom of aquaria was covered with sand. The tanks of *A. pectinifrons* and *A.affinis* were 90 x 30 x 30 cm in size (width x height x depth), that of *H. morrisi* 70 x 40 x 50 cm, and of *M. uranoscopus* 100 x 50 x 50 cm and of *O. niger* 100 x 35 x 50 cm in size. A 12 h: 12 h light-dark cycle was maintained and the temperature was kept at 25°C ± 1°C. Fish were fed frozen chironomid larvae, flake food or food pellets four to five 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.

After sound recordings fish were weighed and measured (Tab. 1). Standard length (SL) was measured as standard length 2 following Holcik et al. (1989). Length of left pectoral spine was measured from onset to the tip. The study protocol was approved by the Austrian Federal Ministry of Science and Research, permit number GZ 66.006/0023-II/10b/2008.

Tab. 1: Species, number of individuals and size ranges of experimental subjects used in this study. N - number of individuals, SL - standard length, TL - total length, W - weight,

Species	**N**	**W** (g)	**SL** (mm)	**TL** (mm)
Agamyxis pectinifrons	7	7.1 – 9.1	59 – 66	67 – 76
Amblydoras affinis	5	4.6 – 11.7	65 – 75	65 – 82
Hemidoras morrisi	12	6.3 – 16.9	84 – 138	97 – 162
Megalodoras uranoscopus	10	34.6 – 68.9	118 – 160	144 – 195
Oxydoras niger	3	165.1 – 178.4	217 – 237	253 – 270

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), a video camera (Sony VX1) and a HiFi-S-VHS-video cassette recorder (JVC HR-S4700EG). Video recordings were carried out to distinguish between sounds produced during adduction and abduction of the pectoral fin. Sound pressure levels (SPL) were recorded using a sound level meter (Brüel and Kjaer 2250), which recorded different SPL measures and stored the data on a SD-card. The distance from fish to sound level meter was 25 cm (Fig. 1).

Sound recording took place in a sound proof room constructed as a faraday cage at 25 ± 1°C. Individuals were marked by clipping 1 - 2 lateral thorns. 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 produce any sounds recordings were repeated after a minimum of one day. Minimum number of sounds recorded per fish was 10 (stridulation) sounds.

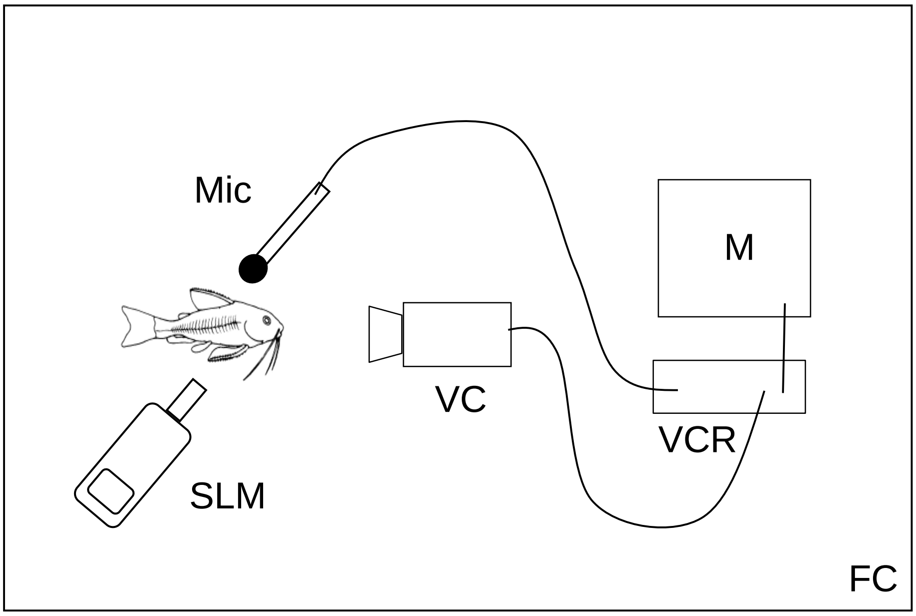

Fig 1: Experimental setup for sound and video recording of doradids in air. M - monitor, Mic - condenser microphone, SLM - sound level meter, VC - video camera, VCR - video cassette recorder. Fish drawing after Ladich (2001).

Sound and video recordings in water

Underwater sound recordings took place in a plastic tub (height 16 cm, diameter 39 cm). Walls of this tub were lined on the inside by acoustically absorbent material (air-filled packing foil) and the bottom was covered with fine sand. 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 then connected to the video cassette recorder (JVC 4700 EG). 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 (Fig. 2). Sound recording took place in a sound proof room constructed as a faraday cage at 25 ± 1°C.

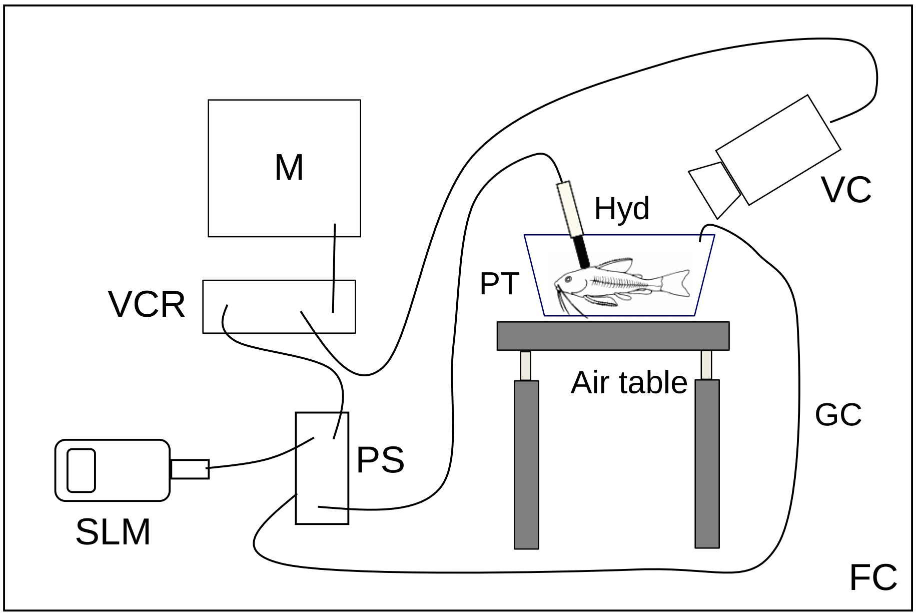

Fig. 2: Experimental setup for sound and video recording underwater. FC - faraday cage, GC - grounding cable, Hyd - hydrophone, M - monitor, PS - power supply, PT - plastic tub, SLM - sound level meter, VC - video camera, VCR - video cassette recorder. Fish drawing after Ladich (2001).

Sound analysis

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, USA).

A. pectinifrons, A. affinis, H. morrisi, M. uranoscopus, and *O. niger* produced sounds during adduction (AD) and abduction (AB) of pectoral fins (Fig. 4). Additionally, drumming sounds were emitted.

The first minute of the sound recording file was analysed, starting at the moment when the fish was held in the final position at the same height as the microphone or hydrophone. As fish almost immediately started producing sounds when taken by hand, the first minute was always analysed. In each individual, ten AD- and AB-sounds were examined for both air and water. For drumming sounds (DR) a minimum of 5 sounds per fish were analysed.

The following sound characteristics were determined for stridulation and drumming sounds recorded in air and underwater:

Number of sounds: Total number of sounds produced by the fish within first minute was counted. The one minute sound file was then divided up into four 15 s time periods each. Then number of AB- and AD-stridulation and drumming sounds produced in each quarter was determined to investigate if the number of sounds emitted changed over time. If a sound occurred at the border of two 15 s time periods, the sound was counted in the first of these two periods (e.g. a sound starting at second 14.5 and ending at second 15.5 was counted within the first time period) (Fig. 3).

Sound duration (SD): Measured was the total length of one AD-, AB- stridulation sounds or one single drumming sound. Duration of ten AD-, AB- stridulation sounds and of drumming sounds was measured for each fish (Fig. 4). Additionally the duration of five AD- and AB-sounds per each 15 s time period was measured in order to see if duration changed over time (Fig. 3).

Dominant frequency (DF): 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. 5). Ten AD- and ten AB-sounds were measured.

Fundamental frequency (FF): Fundamental frequencies of ten 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. 8).

Peak-to-peak-Amplitude: Relative peak-to-peak-amplitude of sounds were determined for ten AD-, ten AB- stridulation sounds and ten drumming-sounds by measuring relative voltages of the highest pulse within an AB and AD stridulation sound or drumming sounds and calculating the ratio between two amplitudes (Fig. 4). Thus amplitude ratios between AD- and AB-sounds (AD/AB ratio) and between stridulation and drumming sounds (SD/DR ratio) have been determined.

Sound pressure level: Absolute SPLs of stridulation and drumming sounds were determined using the software Evaluator (Brüel &Kjaer Types 7820 and 7821). For measuring SPLs RMS Fast time weighting and A as well as Z frequency weighting were used (LAFmax and LZFmax). SPLs could not be determined for AD- and AB-stridulation sounds separately due to the temporal limitations of the sound level meter. 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 always higher than those of drumming sounds. A direct comparison between SPL in air and water was not possible due to differences in recording conditions.

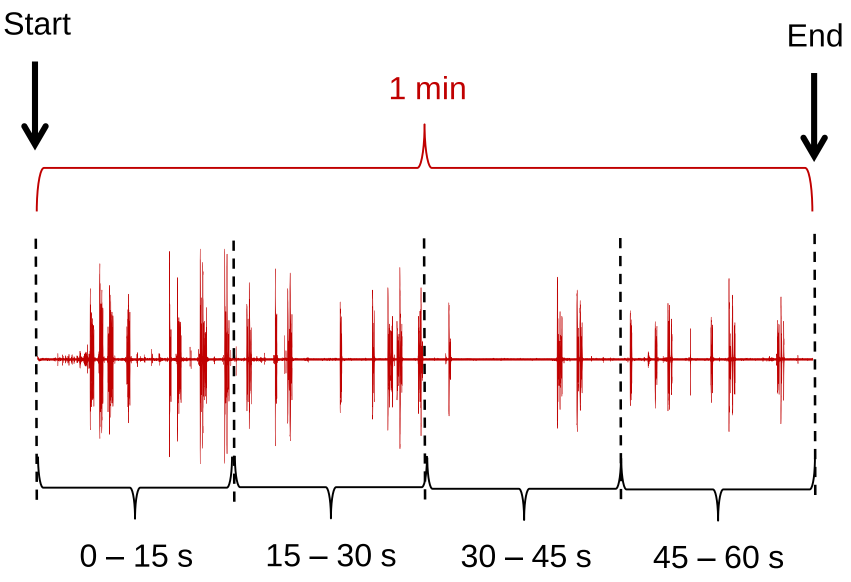

Fig. 3. Oscillogram of a one minute sound recording illustrating the time periods measured.

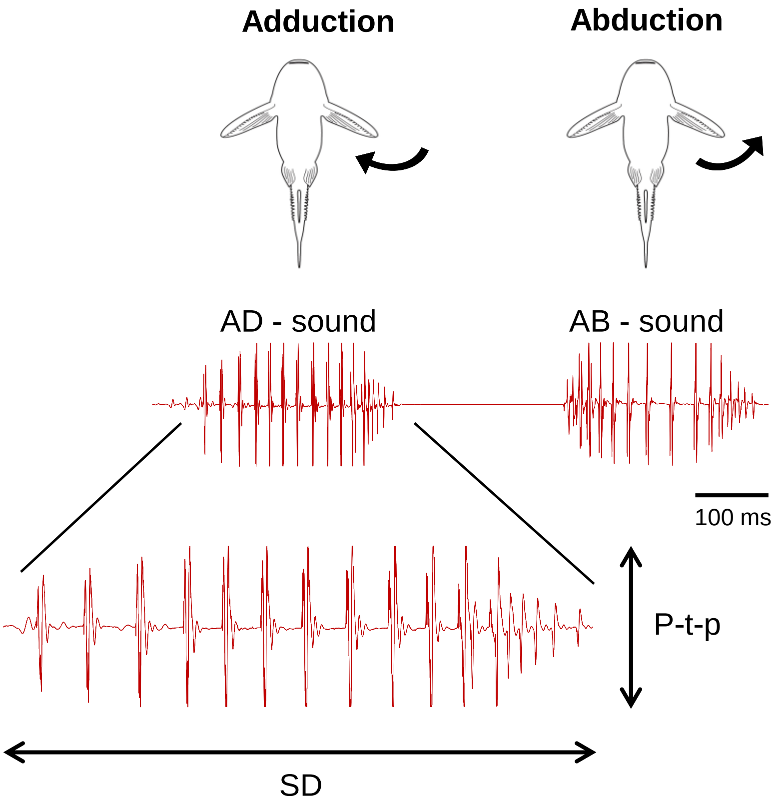

Fig. 4. Drawings of the ventral side of the catfish and oscillogram of AD- and AB-stridulation sound. The upper drawings illustrate the fin movement during production of AD- and AB-sound, the lower oscillograms shows sound characteristics determined. P-t-p - peak-to-peak amplitude, SD – sound duration. Modified after Papes and Ladich (2011).

Statistical analysis

All data were tested for normal distribution using the Kolmogorov-Smirnov-Test and when data were normally distributed, parametric tests were applied, otherwise non-parametric tests were applied. Means of sound characteristics of ten stridulation and five to ten drumming sounds were calculated for each fish and used for further analysis. Relationships between sound characteristics and morphological variables (e.g. frequency vs. standard length) were determined by Pearson's correlation coefficients. Data determined for the number of sounds and sound duration per 15 s time period was not normally distributed, therefore a Spearman rank correlation coefficient was calculated. Differences in characteristics of sounds emitted in the air and water were tested using paired T-tests. Additionally ratios of peak-to-peak amplitudes for AD- and AB-sounds (AD/AB) and for AD-sounds and drumming sounds (AD/DR or SR/DR) 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, USA). The significance level was set at $p < 0.05$.

RESULTS

Sound types

Stridulation and drumming sounds (Fig. 5, 7) were recorded in all five doradid species investigated.

Stridulation sounds

Stridulation sounds were emitted by all five doradid species during abduction (AB-sounds) and adduction (AD-sounds) of pectoral fins as soon specimens were handled. All specimen 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. 5 and 6) and were produced both in air and water. Mean sound duration of stridulation sounds ranged between 50 and 130 ms (Tab. 2).

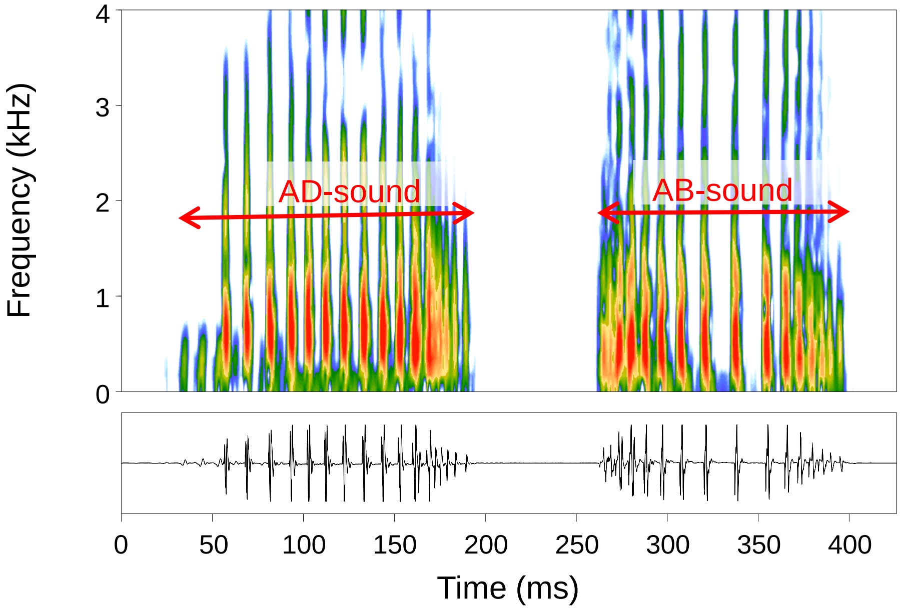

Fig. 5. Sonagram (top) and oscillogram (below) of two stridulation sounds of *M. uranoscopus* produced in water. Sampling rate 44 kHz, Filter bandwidth 250 Hz, hanning filter, overlap 75%.

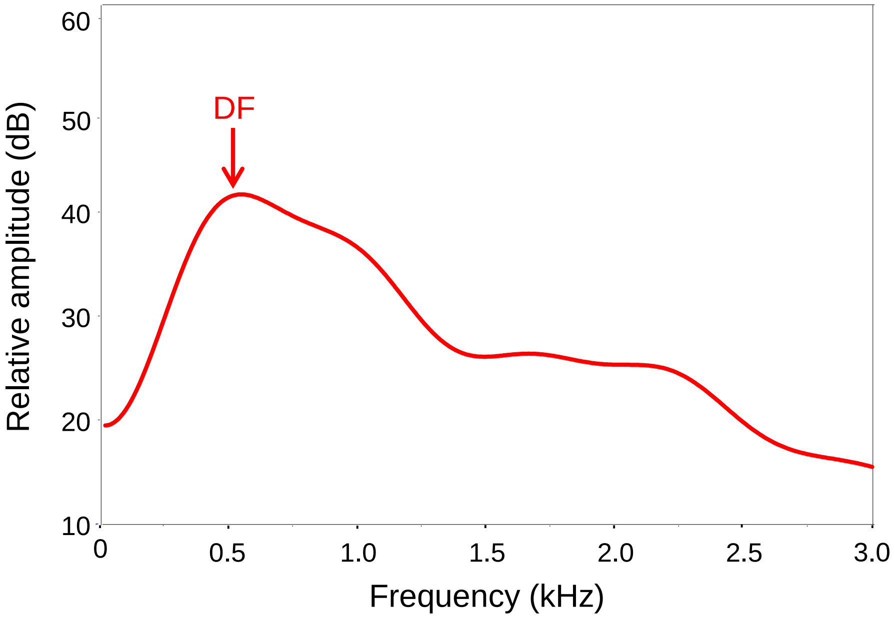

Fig. 6. Cepstrum-smoothed sound power spectrum of one AD stridulation sound of *M. uranoscopus* recorded in water. The dominant frequency (DF) is indicated by an arrow. Sampling rate 44 kHz, Filter bandwidth 10 Hz, hanning filter, overlap 50%, number of coefficients 80.

Drumming sounds

Two types of drumming sounds were differentiated: single drumming sounds (Fig. 7, 8) and series of short drumming sound pulses (Fig. 9). Single drumming sounds were harmonic tones with main energy found in the first, second or third harmonic (Fig. 7, 8). Main energies of drumming sounds were much lower than of stridulation sounds (Fig. 10).

Whereas all species produced single drumming sounds in water only three out of five species (*H. morrisi*, *M. uranocopus*, *O. niger*) emitted single drumming sounds in air. In these three species not all individuals emitted single drumming sounds. Drumming sounds were often produced simultaneously with stridulation sounds. Therefore, only in seven individuals in *H. morrisi*, two individuals in *M. uranocopus* but in all three individuals of *O. niger* drumming sounds could be analysed in air. In water, however, in all five species single drumming sounds were determined in all individuals, except for *A. affinis*, where only two individuals produced drumming sounds, and *M. uranoscopus,* where three individuals emitted single drumming sounds. The mean sound duration ranged between 60 – 80 ms in air and 70 – 270 ms in water (Tab. 2). Drumming sounds are therefore in a similar sound duration range as stridulation sounds in air and a little bit longer in water.

Series of short drumming pulses were found in two individuals in air and in seven individuals in water of *M. uranoscopus,* and also in one individual of *O. niger* in air. No series of short drumming pulses were found in *A. pectinifrons*, *A. affinis* and *H. morrisi* in both media and in *O. niger* in water. Drumming pulses were always produced in series. Pulses were more intense in the middle of a series such as in *M. uranoscopus* in which series of drumming pulses sounded like a motorcycle (Fig. 9). Series of drumming pulses were much longer than single drumming sounds (0.5 - 1.45 s in *M. uranoscopus* and 2.8 s in *O. niger*).

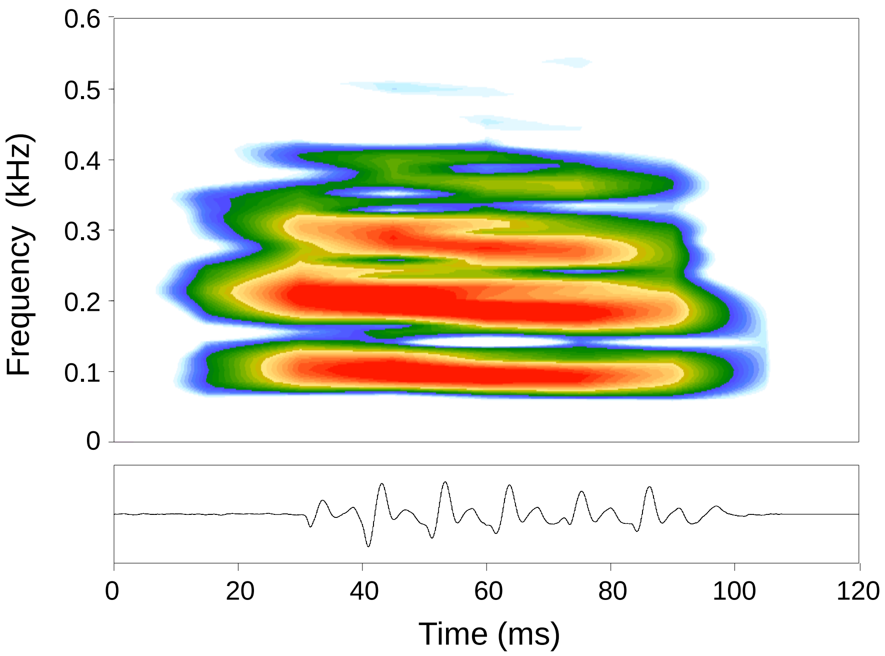

Fig. 7. Sonogram (top) and oscillogram (below) of a single drumming sound of *O. niger* in water. The sonogram shows 4 harmonics with the highest energy found in the second harmonic. Sampling rate 8 kHz, Filter bandwidth 10 Hz, hanning filter, overlap 50%.

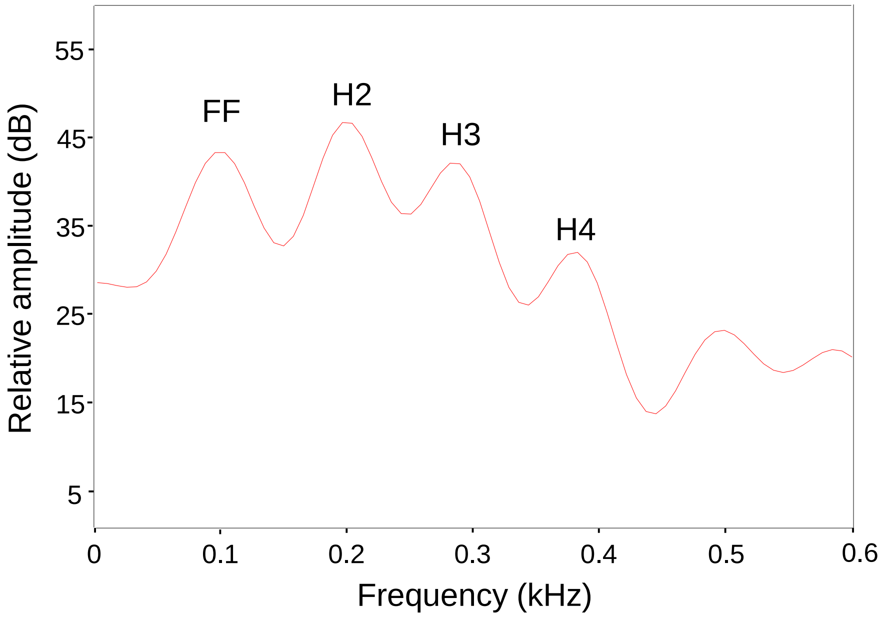

Fig. 8. Cepstrum-smoothed sound power spectrum of the single drumming sound of *O. niger* shown in figure **7**. FF – fundamental frequency; H2, H3, H4 - 2nd, 3rd and 4th harmonic. Sampling rate 8 kHz, Filter bandwidth 10 Hz, hanning filter, overlap 50%, number of coefficients 80.

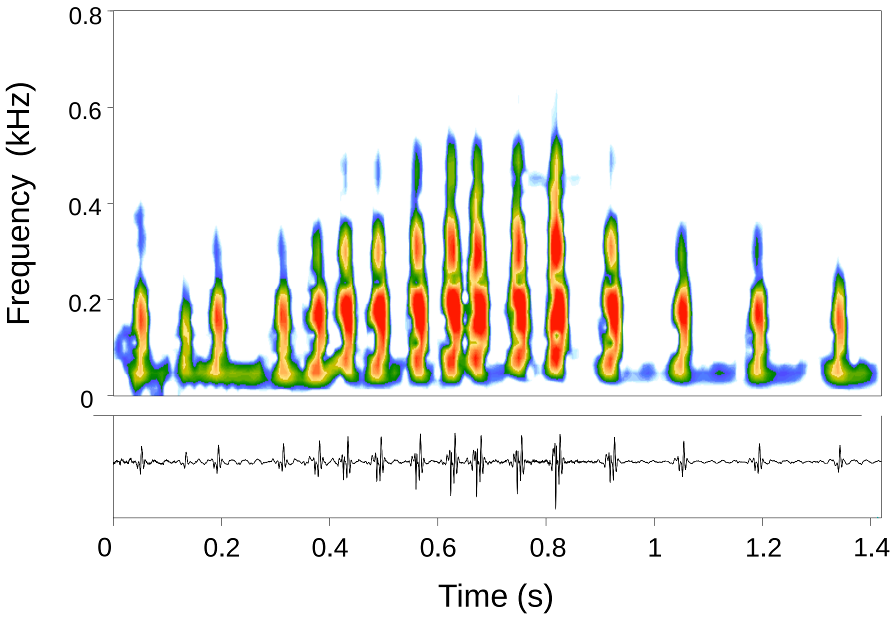

Fig. 9. Sonogram (top) and oscillogram (below) of a series of 16 drumming sound pulses of *M. uranoscopus* emitted in water. Sampling rate 44 kHz, Filter bandwidth 25 Hz, hanning filter, overlap 50%.

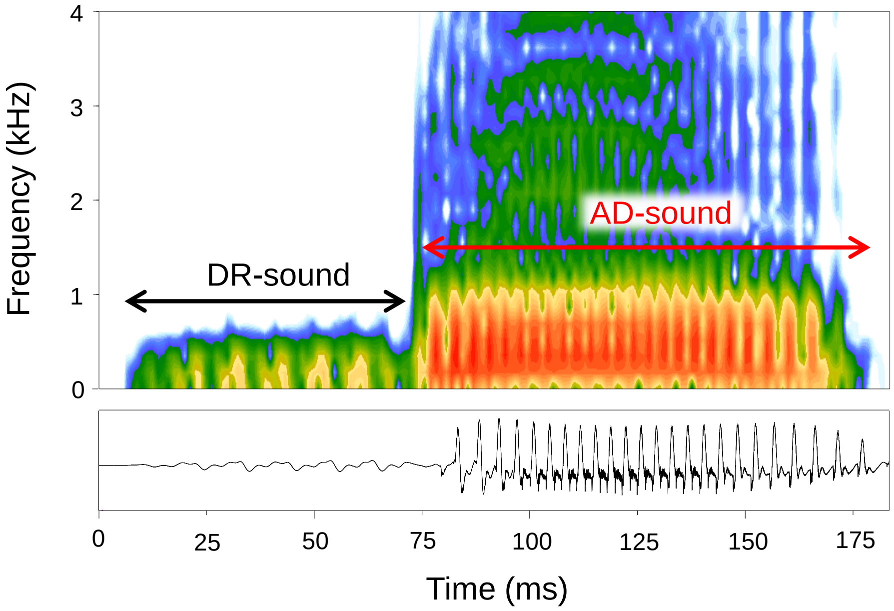

Fig. 10. Sonagram (top) and oscillogram (below) of a drumming sound (DR-sound) and of an adduction stridulation sound (AD-sound) of *M. uranoscopus* in water. Sampling rate 44 kHz, Filter bandwidth 200 Hz, hanning filter, overlap 75%.

Number of sounds

Whereas all individuals produced stridulation sounds in both media only three out of five species (*H. morrisi*, *M. uranoscopus* and *O. niger*) emitted drumming sounds in air. Only *M. uranoscopus* and one individual of *O. niger* produced series of drumming sounds. Therefore, only single drumming sounds were for further analysed.

Number of stridulation sounds produced in air and underwater ranged from 19 to 52 within the first minute for stridulation sounds and 0 to 52 for drumming sounds and did not differ between media within a species except for *H. morrisi, w*hich emitted significantly more stridulation sounds in air than underwater (T-test, $t = 3.354$, $df = 11$, $p < 0.01$) (Tab. 2). No drumming sounds could be recorded in air in *A. pectinifrons* and *A. affinis*. *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. morris* produced significantly more drumming sounds in air (T-test, $t = 2.492$, $df = 11$, $p < 0.05$), while *O. niger* emitted significantly more drumming sounds in water (T-test, $t = -4.849$, $df = 2$, $p < 0.05$).

The ratio of the number of stridulation and drumming sounds (SR/DR) did not differ significantly between media in three species (*H. morrisi*, *M. uranoscopus* and *O. niger*). The ratios for *A. affinis* and *A. pectinifrons* could not be compared for a media effect due to the lack of drumming sounds in air (paired T-test: *H. affinis*: $t = 0.600$, $N = 11$, n.s., *M. uranoscopus*: $t = 2.156$, $N = 5$, n.s., *O. niger*: $t = 6.353$, $N = 1$, n.s.).

Number of stridulation sounds produced decreased with time in all species in both media except in *O. niger* (*A. pectinifrons*: Spearman-correlation-coefficient, air: $r_s = -0.89$, $N = 28$, $p < 0.001$, water: $r_s = -0.95$, $N = 28$, $p < 0.001$, *A. affinis*: air: $r_s = -0.79$, $N = 20$, $p < 0.001$, water: $r_s = -0.71$, $N = 20$, $p < 0.001$, *H. morrisi:* air: $r_s = -0.85$, $N = 48$, $p < 0.001$, water: $r_s = -0.74$, $N = 48$, $p < 0.001$, *M. uranoscopus*: air: $r_s = -0.66$, $N = 40$, $p < 0.001$, water: $r_s = -0.75$, $N = 40$, $p < 0.001$, *O. niger*: air: $r_s = -0.39$, $N = 12$, n.s., water: $r_s = -0.43$, $N = 12$, n.s.) (Fig. 11). The same trend could be found for single drumming sounds over time for the two species which vocalized in air (*H. morrisi* and *M. uranoscopus*) and for all species in water, in which the number of sounds produced also decreased over time (*A. pectinifrons*: air: no data, water: $r_s = -0.66$, $N = 28$, $p < 0.001$, *A. affinis*: air: no data, water: $r_s = -0.83$, $N = 8$, $p < 0.001$, *H. morrisi:* air: $r_s = -0.72$, $N = 48$, $p < 0.001$, water: $r_s = -0.56$, $N = 48$, $p < 0.001$, *M. uranoscopus*: air: $r_s = -0.40$, $N = 32$, $p < 0.01$, water: $r_s = -0.56$, $N = 40$, $p < 0.001$, *O. niger*: air: $r_s = -0.36$, $N = 12$, n.s., water: $r_s = -0.65$, $N = 12$, $p < 0.01$).

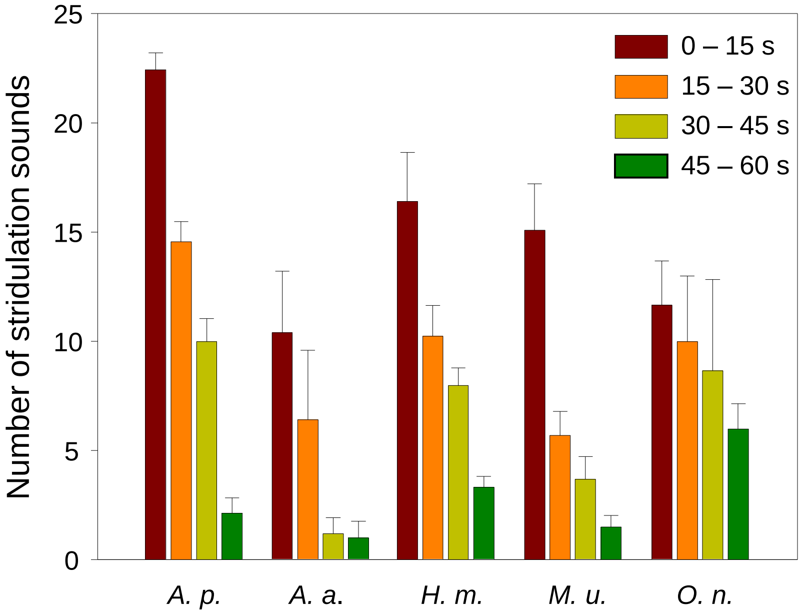

Fig. 11. Mean (± S.E.M.) number of stridulation sounds of doradid species produced in water within consecutive 15 s time periods. The different colours represent the different time period intervals. *A. p. – Agamyxis pectinifrons*, *A. a. – Amblydoras affinis*, *H. m. – Hemidoras morrisi*, *M. u. – Megalodoras uranoscopus*, *O. n. – Oxydoras niger*.

Table 2: Mean (± S.E.M.) characteristics of sounds produced in air (A) and water (W) for doradid species investigated. AD - adduction sound, AB – abduction sound, DF – dominant frequency (kHz), DR – single drumming sounds, FF – fundamental frequency (kHz), N – number of sounds, SC – sound characteristics, SD – sound duration (ms), SR – stridulation sounds. *) Asterisks indicate statistically significant differences in sound characteristics between air and water: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. For abbreviations of species names see Fig. 11.

SC	*A. p.*	*A. a.*	*H. m.*	*M. u.*	*O. n.*
N SR – A	48.71 ± 3.91	24.80 ± 5.95	51.50 ± 2.45 **	32.00 ± 4.91	33.67 ± 8.17
N SR – W	49.14 ± 1.35	19.00 ± 3.92	38.00 ± 3.71	26.00 ± 3.59	37.67 ± 7.13
N DR – A	0	0	51.50 ± 3.96 *	16.33 ± 5.34	7.67 ± 4.10 *
N DR – W	30.00 ± 4.45	16.00 ± 9.00	39.42 ± 4.33	21.82 ± 2.26	34.67 ± 5.78
SD AD – A	116.87 ± 4.09 **	91.37 ± 2.42	74.05 ± 0.77 **	116.20 ± 1.14 *	83.90 ± 2.06
SD AD – W	131.42 ± 1.09	95.55 ± 1.19	67.41 ± 0.70	126.18 ± 1.88	83.38 ± 1.58
SD AB – A	115.39 ± 5.09	82.16 ± 1.41	60.37 ± 0.39	88.56 ± 2.49 *	80.80 ± 2.66
SD AB – W	121.72 ± 3.75	78.91 ± 1.02	57.66 ± 0.54	98.34 ± 1.15	92.98 ± 2.85
SD DR – A	-	-	64.84 ± 29.18	79.18 ± 6.06	70.27 ± 0.76
SD DR – W	276.30 ± 15.87	88.04 ± 18.93	74.65 ± 6.60	70.60 ± 4.10	138.67 ±12.38
DF AD – A	2.37 ± 0.21 *	1.73 ± 0.14 *	2.26 ± 0.14 ***	1.89 ± 0.21 *	0.83 ± 0.03
DF AD – W	1.53 ± 0.09	1.77 ± 0.11	1.64 ± 0.07	0.93 ± 0.08	0.51 ± 0.01
DF AB – A	1.56 ± 0.11 **	2.82 ± 0.17	2.22 ± 0.14 ***	1.04 ± 0.11 ***	1.21 ± 0.04
DF AD – W	1.51 ± 0.17	1.76 ± 0.15	1.56 ± 0.11	0.95 ± 0.05	0.74 ± 0.01
FF DR – A	-	-	0.107 ± 0.002	0.099 ± 0.002	0.091 ± 0.003
FF DR – W	0.107 ± 0.003	0.169 ± 0.007	0.075 ± 0.007	0.092 ± 0.002	0.094 ± 0.002

Sound duration

The mean duration of stridulation sounds was 70 - 125 ms in AD-sounds and 50 -120 ms in AB-sounds both for air and water (Tab. 2). Duration of AD- and AB-stridulation 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. 12). In contrast, AB-sounds were only longer in *M. uranoscopus* in water than in air. Mean sound duration of drumming sounds ranged between 60 – 80 ms in air and 70 – 270 ms in water (Tab. 2). Durations of drumming sounds, on the other hand, did not differ between air and water.

Sound duration of AD- and AB-sounds increased over time in all species in both media, except for *H. morrisi* for AD-sounds in water and for *O. niger* for AD- and AB-sounds both in air (Fig. 13 and Tab. 3). Such an effect was not found in drumming sounds.

Table 3: Correlation between sound duration (SD) and 15s time period of AD- and AB-sounds in air (A) and water (W) for doradid species investigated. N - number of individuals p - level of significance, r_s - Spearman correlation coefficient.

Sound type	**Statistical Parameters**	***A. pectinifrons***	***A. affinis***	***H. morrisi***	***M. uranoscopus***	***O. niger***
AD-sound Air	r_s	0.40	0.42	0.54	0.58	0.34
	p	< 0.05	< 0.01	< 0.01	< 0.01	n. s.
AD-sound Water	r_s	0.72	0.42	0.10	0.51	0.56
	p	< 0.01	< 0.05	n. s.	< 0.01	< 0.05
AB-sound Air	r_s	0.35	0.56	0.45	0.50	0.50
	p	< 0.05	< 0.01	< 0.01	< 0.01	n. s.
AB-sound Air	r_s	0.58	0.51	0.32	0.35	0.76
	p	< 0.01	< 0.05	< 0.05	< 0.05	< 0.01

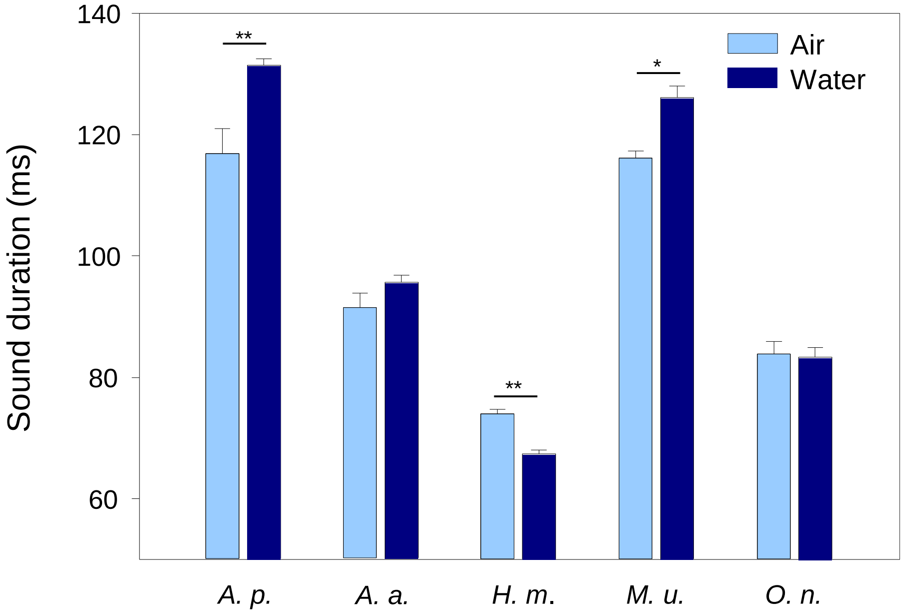

Fig. 12. Mean (± S.E.M.) sound duration of AD-sounds emitted in both media for doradid species. Significance of differences: * $p < 0.05$, ** $p < 0.01$. For abbreviations of species names see Fig. 11.

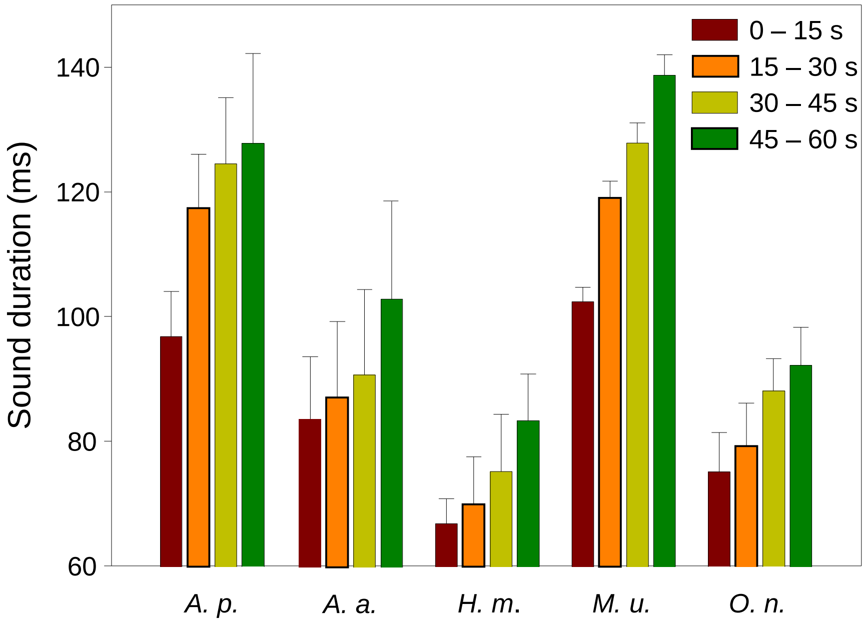

Fig. 13. Mean (± S.E.M.) duration of AD-sounds produced in water in consecutive 15 s time periods. For abbreviations of species names see Fig. 11.

Dominant and fundamental frequency

Mean dominant frequency of stridulation sound ranged between 0.8 - 2.8 kHz in air and between 0.5 - 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. 14 and Tab. 2). Fundamental frequencies of single drumming sounds were found between 90 - 110 Hz in air and 70 - 170 Hz in water (Tab. 2). Mean fundamental frequencies of drumming sounds emitted in air and in water did not differ significantly (Tab. 2).

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 (AD-sounds air: Pearson correlation coefficient, $r = - 0.73$, $N = 37$, $p < 0.01$, AD-sounds water: $r = - 0.72$, $N = 37$, $p < 0.01$, AB-sounds air: $r = - 0.64$, $N = 37$, $p < 0.01$, AB-sounds water: $r = - 0.74$, $N = 37$, $p < 0.01$) (Fig. 15). Similarly dominant frequencies of AD- and AB-sounds were negatively correlated to body weight in water and air (AD-sounds air: $r = - 0.69$, $N = 37$, $p < 0.01$, AD-sounds water: $r = - 0.70$, $N = 37$, $p < 0.01$, AB-sounds air: $r = - 0.63$, $N = 37$, $p < 0.01$, AB-sounds water: $r = - 0.72$, $N = 37$, $p < 0.01$). Fundamental frequency decreased with size in water (SL: $r = - 0.39$, $N = 27$, $p < 0.05$; weight: $r = - 0.38$, $N = 27$, $p < 0.05$) but not in air (SL: $r = - 0.32$, $N = 12$, $p =$ n. s.; weight: $r = - 0.45$, $N = 12$, $p =$ n. s.).

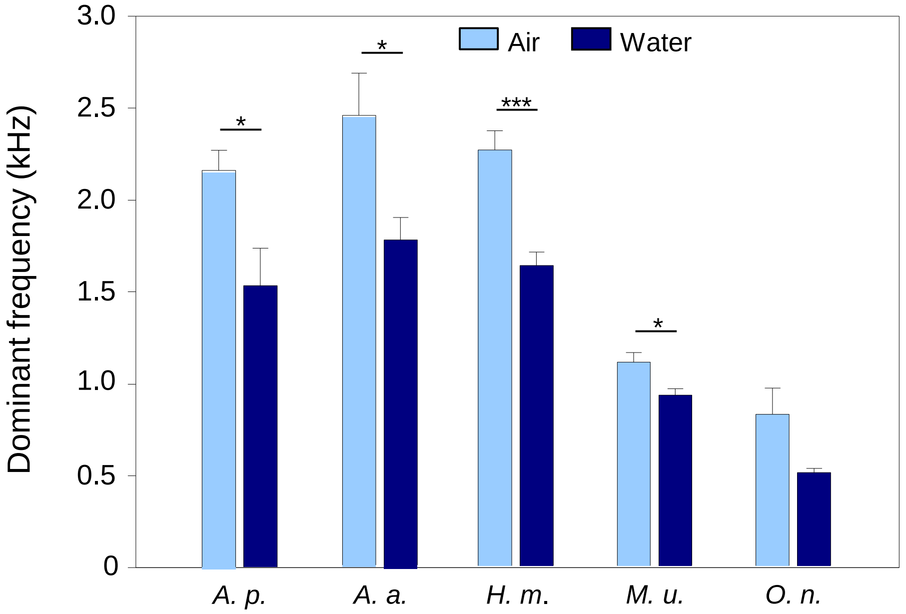

Fig. 14. Mean (± S.E.M.) dominant frequency of AD-sounds emitted in both media. Significance of differences: * $p < 0.05$, *** $p < 0.001$. For abbreviations of species names see Fig. 11.

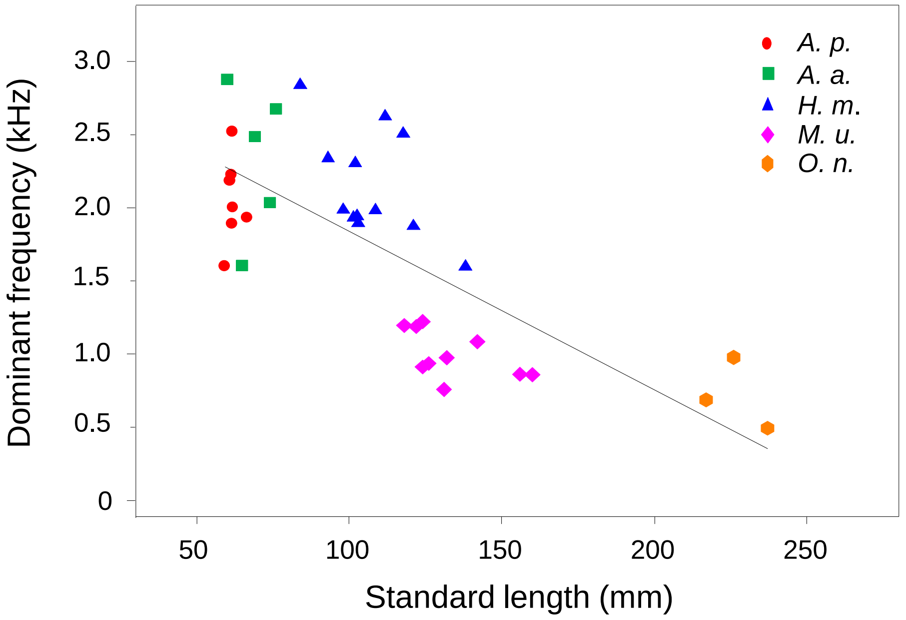

Fig. 15. Correlations between dominant frequency of AD-sounds and standard length in water. Regression equation: frequency = 3.03 kHz – 10.8 x standard length, r = - 0.72, $p < 0.01$. For abbreviations of species names see Fig. 11.

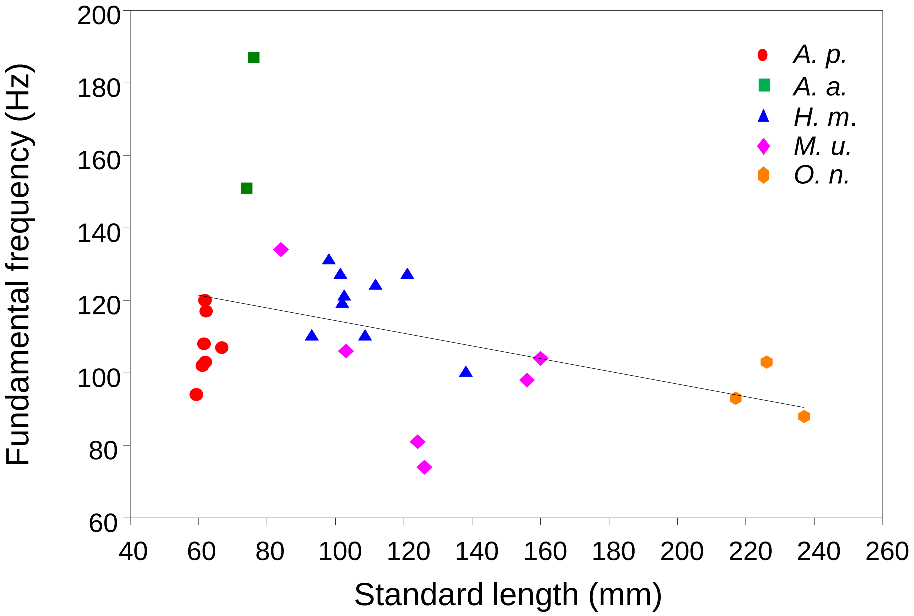

Fig. 16: Correlations between fundamental frequency of drumming sounds and standard length in water. Regression equation: frequency = 132 Hz – 0.18 x standard length, $r = -0.39$, $p < 0.05$. For abbreviations of species names see Fig. 11.

Sound pressure level

SPLs differed between stridulation and drumming sounds, as well between media. Mean SPLs of stridulation sounds in air ranged from 47 - 55 dB re 20 µPa (LAFmax) and from 60 - 62 dB re 20 µPa (LZFmax) and ranged in water from 126 - 131 dB re 1 µPa (LAFmax) and from 127 - 139 dB re 1 µPa (LZFmax). For drumming sounds SPLs varied between 31 - 35 dB re 20 µPa (LAFmax) and between 54 - 59 dB re 20 µPa (LZFmax) in air and in water between 88 - 111 dB re 1 µPa (LAFmax) and between 107 - 131 dB re 1 µPa (LZFmax) (Tab. 4). SPL of *O. niger*'s single drumming sounds could not be determined in air because single drumming sounds always occurred together with high-amplitude stridulation sounds.

Larger fish emitted louder sounds than smaller fish. SPL (LAFmax and LZFmax) of stridulation sounds increased with standard length in all fish in both media (LAFmax in air: Pearson-correlation-coefficient, $r = 0.65$, $N = 37$, $p < 0.01$; LZFmax in air: $r = 0.42$, $N = 37$, $p < 0.05$; LAFmax in water: $r = 0.37$, $N = 37$, $p < 0.05$, LZFmax in water: $r = 0.82$, $N = 37$, $p < 0.01$) (Fig. 17). Similarly, SPLs of drumming sounds increased with body size (standard length) in water (LAFmax in water: $r = 0.67$, $N = 27$, $p < 0.01$; LZFmax: $r = 0.78$, $N = 27$, $p <$

0.01). Due to a lack of data a correlation for drumming sounds produced in air could not be calculated.

Tab. 4: Means (± S.E.M) sound pressure levels (SPL) of sounds produced in air (A) and water (W) for the doradid species investigated. DR – drumming sounds, LAFmax – RMS Fast time weighting, A frequency weighted sound level, LZFmax – Fast, Z frequency weighted sound level, SR – stridulation sounds. For abbreviations of species names see Fig. 11.

SPL	***A. p.***	***A. a.***	***H. m.***	***M. u.***	***O. n.***
LAFmax SR - A	47.23 ± 0.71	49.03 ± 0.74	53.24 ± 0.65	55.47 ± 0.60	53.71 ± 0.91
LAFmax SR - W	126.60 ± 0.54	129.07 ± 1.24	129.71 ± 0.57	129.08 ± 1.50	131.97 ± 0.49
LAFmax DR - A	-	-	35.15 ± 1.26	31.68 ± 0.93	-
LAFmax DR - W	94.07 ± 1.95	88.35 ± 1.30	109.38 ± 1.96	97.03 ± 3.42	111.57 ± 2.57
LZFmax SR - A	60.30 ± 0.41	60.16 ± 0.62	60.07 ± 0.38	62.05 ± 0.76	61.71 ± 0.66
LZFmax SR - W	127.05 ± 0.52	129.39 ± 1.14	130.45 ± 0.55	134.65 ± 1.34	139.94 ± 0.54
LZFmax DR - A	-	-	59.41 ± 1.40	59.78 ± 0.47	-
LZFmax DR - W	117.36 ± 2.65	107.41 ± 1.22	119.17 ± 0.68	111.34 ± 2.34	131.94 ± 3.53

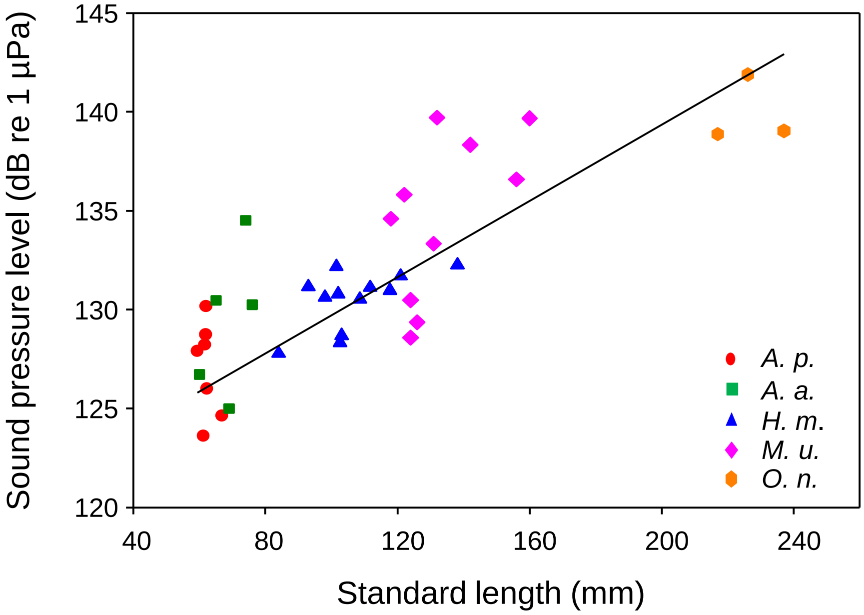

Fig. 17. Correlation between sound pressure level (LZFmax) of stridulation sounds and standard length in water**.** Regression equation: SPL = 120.1 dB re 1 µPa + 0.10 x standard length, r = 0.82, p < 0.01. For abbreviations of species names see Fig. 11.

Peak-to-peak-amplitude ratios

Peak-to-peak amplitudes of AD-sounds were higher than of AB-sounds (Fig. 17). Ratios of peak-to-peak amplitudes of AD- and AB-sounds did not differ between media (*A. pectinifrons*: T-test, t = 0.238, df = 6, n.s.;, *A. affinis*: t = - 1.390, df = 4, n.s.; *H. morrisi*: t = - 1.677, df = 11, n.s.; *M. uranoscopus*: t = 1.823, df = 9, n.s.; *O. niger*: t = - 1.325, df = 2, n.s.) (Fig. 18).

Peak-to-peak-amplitude ratios for stridulation and drumming sounds (SR/DR) were between 5.8 and 15.9 in air and between 6.4 and 47.8 in water indicating that stridulation sounds were always much louder than drumming sounds. Differences between media were only found in *H. morrisi* which had a significantly higher ratio in water than in air (T-test, t = - 2.595, df = 6, p = 0.04) (Fig. 19). No drumming sounds were recorded in air in *A. pectinifrons* and *A. affinis*, therefore no ratios were calculated for air. Interestingly, the p-t-p-amplitude-ratio in *A. affinis* in water was on average 14 times larger than the p-t-p-amplitude-ratios of the other species.

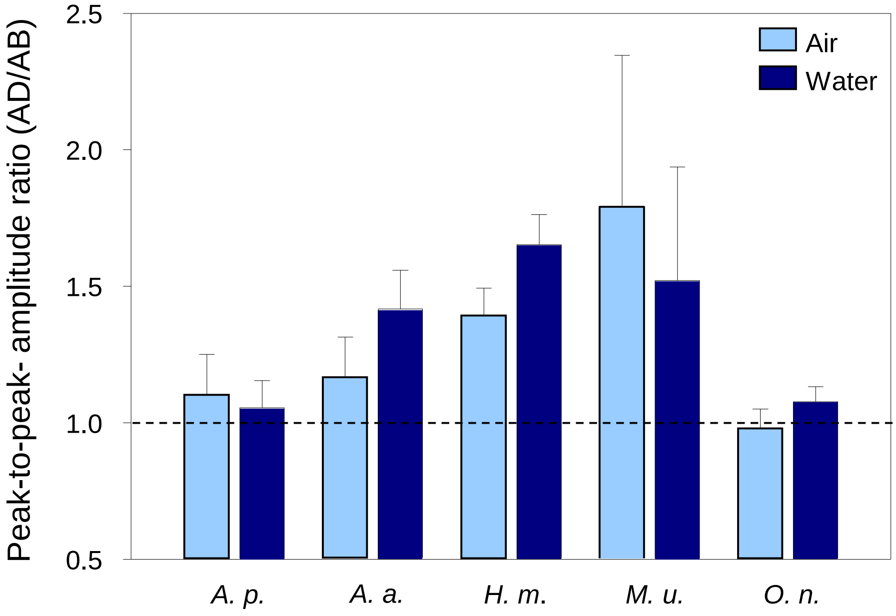

Fig. 18. Mean (+ S.E.M.) peak-to-peak-amplitude ratio (AD/AB) in both media in doradid species investigated. Note that ratios did not differe between media in any species. For abbreviations of species names see Fig. 11.

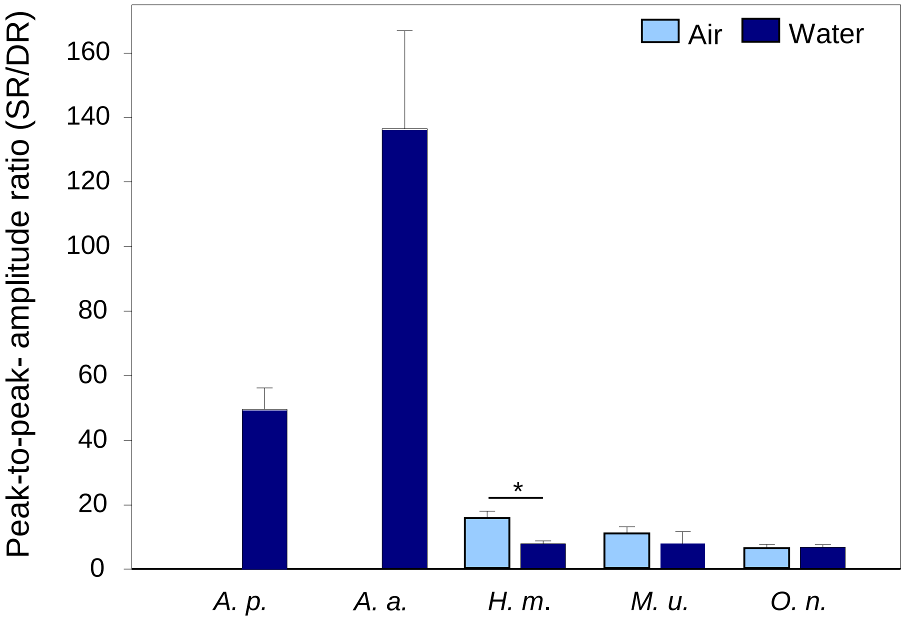

Fig. 19. Mean (+ S.E.M.) peak-to-peak-amplitude ratio (SR/DR) in different media. Significance of differences: * $p < 0.05$. DR – drumming sound, SR – stridulation sound. For abbreviations of species names see Fig. 11.

Pectoral spine length

Absolute pectoral spine length in the five investigated species were between 13.9 and 52 mm and varied significantly between species (ANOVA: F = 22.596, df = 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, df = 4, 32, n.s.). Absolute and relative pectoral spine length were not correlated with sound duration (Pearson correlation coefficient: absolute: pectoral spine length vs. AD sound duration: r = 0.087, N = 37, n.s., pectoral spine length vs. AB sound duration: r = - 0.186, N = 37, n.s; relative: pectoral spine length vs. AD sound duration: r = 0.010, N = 37, n.s., pectoral spine length vs. AB sound duration: r = - 0.114, N = 37, n.s).

DISCUSSION

Sound types

The 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 utter drumming sounds in air.

The production of high-frequency, broad-band stridulation sounds and low-frequency, drumming sounds were also described in other catfish studies where sounds were either recorded in air or in water, or even in both media (Schachner and Schaller 1981, Ladich 1997, Kaatz 1999, Heyd and Pfeiffer 2000, Fine and Ladich 2003, Parmentier et al. 2010). Parmentier et al. (2010) mentioned that of representatives of 22 sonic catfish families 18 produce pectoral stridulation sounds. It is not mentioned, however, in which media and if those other four families are only producing drumming sounds. Kaatz and Stewart (2012) mentioned that 25 species of doradoids (Doradidae and Auchenipteridae) produce swimbladder disturbance sounds in water.

Drumming sounds were produced less consistently than stridulatory sounds in both media. Only three out of five species investigated in this study produced drumming sounds in air and in those species not even all individuals produced drumming sounds, whereas almost all individuals of all five species emitted drumming sounds in water. Interestingly, Ladich (1997) recorded drumming sounds in air in *A. pectinifrons* whereas this has not been the case in the present study. One explanation may be that these low level sounds were not detectable at larger distance used in present as compared to the prior study (25 cm vs. 5-8 cm). However, due to a lack of comparative data it remains unclear if differences between media exist and if these are due to biological or methodical reasons.

Typically, thorny catfish in the current study started stridulation with an adduction movement of pectoral spines followed by abduction. Typically, pairs of stridulation sounds (AD- and AB-sound) were produced. The current observation is confirmed by 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 the terminology got confused or that fish in the previous studies did not lock their spines in a right angle before producing sounds.

Two different types of drumming sounds were described in the present study: single drumming sounds and series of short drumming pulses. Ladich (1997) mentioned similar types of drumming sounds in *P. armatulus* when hand-held. Kaatz and Stewart (2012) also found two drumming sound types in their study on doradoids. Sounds were either continuous waveforms lacking interpulse periods or they were pulsed with fixed temporal intervals. Kaatz and Stewart (2012) found pulsed drumming sounds in four out of 25 doradoid species including *M. uranoscopus*. Similar to my 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 unclear if all species are able to generate two types of drumming sounds.

Number of sounds

The number of stridulation sounds recorded within 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. Number of drumming sounds was similar in both media in *M. uranoscopus*, significantly higher in air in *H. morrisi*, lower in *O. niger* whereas no drumming sounds were recorded in air in two species (*A. pectinifrons* and *A. affinis*). The lack of drumming sound production in air could be due to methodical reasons as mentioned previously or due to functional differences as discussed in the following. Pfeiffer and Eisenberg (1965) 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 my study. This difference in vocalizing activity between Pfeiffer and Eisenberg's (1965) and my study might be due to the different species used and/or different levels of arousal as Schachner and Schaller (1981) suggested in their study: the higher the arousal of the fish the higher the number of sounds. Kastberger (1977) mentioned that *M. uranoscopus* and *O. niger* emitted 6 - 9 drumming sounds per minute in water which is much less than in my study. Kaatz (1999) found that 27 out of 42 catfish species produced significantly more stridulation sounds than drumming sounds when hand-held in all 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*. Kaatz (1999) found that those species had weak pectoral girdles, thin pectoral fin spines, reduced spine ornamentation and reduced or absent lateral bony structures. This could be a hint that it is more effective in these species to produce drumming sounds than stridulation sounds. In my study *H. morrisi* produced stridulation and drumming sounds simultaneously when hand-held. Producing two sound types at the same time might be a more effective way of distress signalling in this species than producing just one sound type.

The fact that the number of stridulation sounds produced decreased over time was described for the first time in my study. 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 would be that catfish switch from distress sound production to pectoral spine locking as a more effective reaction to predators (Bosher et al., 2006).

Sound duration

The mean duration of stridulation sounds in the present study ranged from 70 - 125 ms in AD-sounds and 50 -120 ms in AB-sounds in both media. Durations of stridulation sounds have been described for several species of doradids in air. Pfeiffer and Eisenberg (1965) found that the duration of AD-sounds were shorter than of AB-sounds in *P. hancockii* (80 vs. 110 ms), in *A. albomaculatus* (110 vs. 140 ms) and in *P. armatulus* (90 vs 120 ms). Similarly, Ladich (1997) found that AD-sounds were shorter in *A. pectinifrons* (95 vs. 110 ms) but not in *P. armatulus* (70 ms) and Heyd and Pfeiffer (2000) described a sound duration of 102 ms for stridulation sounds in *A. pectinifrons*. These previous data gained 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 literature for doradids and thus results could not been compared. Durations of stridulation sounds gained in water of 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 range than doradids in my study (Schachner and Schaller 1981, Lechner et al. 2010).

The comparison between media reveals no common trend (AD sounds significantly longer in water in *A. pectinifrons* and *M. uranoscopus*, significantly shorter in *H. morrisi*, AB-sounds longer in water in *M. uranoscopus*, no trend in other four species). Therefore, the medium itself might not influence the sound duration in doradids.

Sound duration of AD-sounds and AB-sounds increased over time in all five doradid species investigated. This change in sound duration and subsequently pulse periods is most likely due to muscle fatigue. It indicates that in distress sound temporal patterns are less important for communication than in reproductive behaviour (Myrberg 1978; Fine et al. 2004). Ladich (1997) claimed that duration of stridulation sounds is movement dependent and Heyd and Pfeiffer (2000) also mentioned a high variability in sound duration in catfishes.

Ladich (1997) found that duration of AD-sounds varied across families and increased with relative spine length. Relative spine size differed among doradids according to Ladich (1997) but did not in the five doradid species in the present study. Interestingly, absolute spine length was not correlated to sound duration indicating a large variety in durations of abduction and adduction movements among species due to different levels of arousal and muscle fatigue.

The duration of single drumming sounds ranged from 60 - 80 ms in air and 70 - 270 ms in water and did not differ in any species between media. Durations 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, 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 increase with time. Fine et al. (2004) found no difference in sound duration in drumming sounds emitted in water and in air in the sciaenid *M. undulatus*. The authors, on the other hand, described that sound duration increases within time and explained that it takes longer to complete a muscle twitch with on-going time and they also point to a “getting tired” of the muscles.

Main energies of sounds

Dominant frequency of stridulation sounds was significantly higher in air than in water in four out of five species in the present study. I assume that this is also the case in the fifth species *O. niger* although this could not be shown due to the small number of specimen 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. Dominant frequency could differ in the two media due to different characteristics of water and air. Lower dominant frequency of sounds in water compared to air is perhaps due to the different recording conditions. Fish were recorded in a small tub under water but not in air. The lack of a difference between media in fundamental frequency of drumming sounds may be explained by the fact that 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 will not affect the neuron firing patterns. Fine et al. (2004) also found no significant difference in fundamental frequency in the sciaenid *M. undulatus* between media. They described that the muscle origin, insertion and action will not change in air. Hence will the bladder be vibrated in a similar pattern and frequency.

Dominant frequency of catfish stridulation sounds described previously ranged in doradids, mochokids, pimelodids and callichthyids from 0.5 - 4 kHz in air and water (Pfeiffer and Eisenberg 1965, Schachner and Schaller 1981, Ladich 1997, Pruzsinszky and Ladich 1998, Kaatz 1999, Kaatz 2002, Heyd and Pfeiffer 2000, Fine and Ladich 2003, Lechner et al. 2010, Papes and Ladich 2011). Therefore my results (0.5 – 3 kHz) go along with the frequency ranges previously described by other authors.

Dominant frequency of stridulation sounds decreased with increasing body size (standard length and body weight). The same trend was already described in representatives of numerous fish families such as in callichthyids, mochokids, gurnards, mormyrids, croaking guramis, 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 (1997) found such a correlation in one out of the two doradid species, namely *P. armatulus* but not in A. *pectinifrons* which might have been due to small size differences in this study.

Fundamental frequency of drumming sounds in catfishes ranged from 50 – 200 Hz in air (Kastberger 1977, Ladich 1997, Heyd and Pfeiffer 2000, Fine and Ladich 2003, Fine et al.

2004) and 100 – 500 Hz in water (Schachner and Schaller 1981, Fine et al. 2004). Ladich (1997) described fundamental frequencies of drumming sounds in air in *P. armatulus*-at around 96 Hz and in *A. pectinifrons* at 114 Hz. Kastberger (1977) found fundamental frequencies of drumming sounds in *O. niger* and *M. uranoscopus* between 80 to 100 Hz and Kaatz and Stewart (2012) found fundamental frequencies in water in *M. uranoscopus* at 122 Hz and in *O. niger* at 99 Hz, the research agrees with the results in this study.

Fundamental frequency of drumming sounds decrease with increasing body size in water showing that larger fish exhibit lower muscle contraction rates than smaller fish. This phenomenon was not observed in air, partly because the number of individuals drumming in air was small. 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. Fundamental frequency also decreases with fish size in the weakfish (Connaughton et al. 2000, 2002) and the whitemouth croaker (*Micropogonias furnieri*) (Tellechea et al. 2010). Fine et al. (2004) suggested therefore that croakers could estimate relative size of the caller equally in aerial and underwater recordings. 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 (Hill 1950, Wainwright and Barton 1995). Those lower frequency sounds produced by larger fish might act as “honest signals”, as those 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) also found no significant differences in amplitude ratios within doradids.

Amplitudes of stridulation sounds were in all cases much higher than of drumming sounds in my experiments. Ladich (1997) made the same observation in *P. armatulus* and *A. pectinifrons.* Schachner and Schaller (1981) described the same trend in the pimelodid *R. sebae* with a SPL of 150 dB re 1 µPa for stridulation sounds and 130 dB re 1 µPa for drumming sounds both in water. Kaatz (1999) confirmed this and stated that stridulation sounds are generally louder than drumming sounds in a large number of catfish but no measurements are provided. Schachner and Schaller (1981) claimed that sound intensity depends on the arousal of fish.

The p-t-p-amplitude ratio of stridulation and drumming sounds (SR/DR) did not differ between media in *M. uranoscopus* and *O. niger* but in *H. morrisi* which had a significant higher ratio in air than in water. Ladich (1997) found that p-t-p-amplitude ratios of stridulation and drumming sounds were also significantly higher in air than underwater in both doradid species (*A. pectinifrons* and *P. armatulus*). Interestingly, both species in which drumming sounds could not be recorded in air (*A. pectinifrons* and *A. affinis*) had a very high SR/DR p-t-p-amplitude ratio in water. This means that drumming sounds were of lower amplitude than stridulation sounds, especially in smaller species. A reason could be that producing drumming sounds is not so effective in smaller species as in larger species with larger swimbladders which might be able to produce louder low frequency drumming sounds. Therefore it might be more effective to produce just stridulation sounds and no drumming sounds in air.

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 gurami *Trichopsis vittata* (Wysocki and Ladich 2001), the sciaenid C*ynoscion regalis* (Connaughton et al. 2000) and in the mochokid catfish *S. schoutedeni* (Lechner et al. 2010). Fine et al. (1997) and Lechner et al. (2010) assume that the amplitude of sounds depend 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 intra-individual variation of SPLs.

Functional considerations

The fact that doradids possess two very different sonic mechanisms points to different biological tasks (Heyd and Pfeiffer 2000, Fine and Ladich 2003). It was assumed that a possible function of distress sounds is to warn and protect from predators because the production of stridulation sounds is linked to spine locking and might indicate difficulties in swallowing the sound producer (Sörensen 1895, Mahajan 1963, Pfeiffer and Eisenberg 1965, Schachner and Schaller 1981, Ladich 1997, Kaatz 1999, Heyd and Pfeiffer, 2000). 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 sounds (stridulation sounds) against aerial predators. Support for this theory comes from the hearing sensitivities in non-oscine birds which possess best sensitivities between 1 - 4 kHz (Dooling 1982, Ladich 2010) in contrast to fish species which are able to detect low frequency sounds (Ladich and Popper 2004). In my study no species produced relatively more stridulation sounds in air than in water in the two media. If we assume that *A. pectinifrons* and *A. affinis* did not produce drumming sounds in air but only in water, this would confirm Ladich's hypothesis, as fish would rather produce drumming sounds in water than in air. My suggestion therefore would be that stridulation sounds are produced in all media in disturbance context while drumming sound production is more depend on the media. The fact that stridulation sounds are often produced in disturbance situations in air and water in catfishes has been found in several studies (Tavolga 1960, Pfeiffer and Eisenberg 1965, Abu-Gideiri and Nasr 1973, Schachner and Schaller 1981, Ladich 1997, Kaatz 1999, Heyd and Pfeiffer 2000). Kaatz (1999) explained that stridulation sounds are more effective disturbance sounds as they are louder than drumming sounds and could function as warning signals. Drumming sounds in catfishes, on the other hand, have been described numerous times as intraspecific signals and function as signals for communication with conspecifics (Tavolga 1960, Abu-Gideiri and Nasr 1973, Schachner and Schaller 1981, Kaatz 1999). Drumming sounds have a lower frequency than stridulation sounds and water might be a better medium to transport those over a longer distance. However, this is not the case in shallow water due to the frequency cut-off phenomenon which limits the propagation of low frequency sounds (Rogers and Cox 1988, Mann 2006). Producing sounds to communicate with conspecifics in air would not make sense in but sounds could be directed towards predators in both media. Evidence that stridulation sounds are produced in both media whereas drumming sounds are more regularly produced in water would support the role of stridulation sounds as a predator repelling mechanism.

Bosher et al. (2006) observed that only 20 % of channel catfish *Ictalurus punctatus* produced stridulation sounds when attacked by a largemouth bass *Micropterus solmoides.* This indicates that stridulation sounds do not necessarily function as a warning signal and repel piscivorous predators in water. Pectoral spine locking seems to be a far better defence mechanism against predators than trying to warn predators by producing stridulation sounds. Bosher et al. (2006) could also find a learning effect in *M. solmoides*: bass preferred channel catfish with clipped pectoral spines and ingested less intact catfish. Fixed pectoral and dorsal spines in struggling fish increases its effective size and is then more difficult to be swallowed by gape-limited aerial or aquatic predators (Fine and Ladich 2003). One function of stridulation sounds, therefore, would be classical Pavlovian conditioning: the 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 (1989) called this "dangerous prey hypothesis". Spines lead to severe injuries in the soft tissues of predators

(Bosher et al., 2006). Dead pelicans were found with channel catfishes (species was not mentioned) with erected pectoral spines stuck in the throats of the birds, assuming that this was the cause for the death of the pelicans (Glahn and King 2004).

I suggest therefore, that the production of stridulation sounds in comparison to drumming sounds is independent of the medium, that stridulation sounds are more likely produced in disturbance and predator context in doradids. Drumming sounds are more likely produced in water as intraspecific communication signals. Stridulation sounds could therefore function as warning signals, especially in air, going along with the warning hypothesis of Ladich (1997) and catfish should produce stridulation sounds when caught by aerial predators and pulled out of the water to increase the chances of survival. In water catfish should rather lock their spines to make it harder for the predators to swallow the prey than using them for sound production. The media therefore might function as kind of an “indicator” for catfish which sounds are most useful to produce in different contexts.

Additionally, stridulation sounds and its sound characteristics (e.g. dominant frequency) are more affected by the different media than drumming sounds. My suggestion for an explanation would be the location of the stridulation apparatus (pectoral spines) on the outside of the fish which is therefore more exposed to the various characteristics of the two media, whereas the apparatus that produces drumming sounds (swimbladder mechanism) is situated within the fish’s body and sounds are therefore not as much affected by the different media. Time has an effect on both sounds concerning number of sounds and sound duration. This would be explained by muscle fatigue.

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ZUSAMMENFASSUNG

Dornwelse produzieren Stridulationslaute mit ihren Pectoralflossen und Trommellaute mit der Schwimmblase in Störungssituationen wenn sie in der Hand gehalten werden und das sowohl im Wasser als auch in der Luft. Wissenschaftler haben argumentiert, dass diese Laute an verschiedene Empfänger (Prädatoren) in verschiedenen Medien gerichtet sind. Das Ziel dieser Arbeit war es Laute zu analysieren, Eigenschaften von Lauten, die in beiden Medien erzeugt wurden, zu vergleichen um die funktionelle Bedeutung dieser Störungslaute zu untersuchen. Dazu wurden fünf Vertreter der Familie der Doradidae (*Agamyxis pectinifrons, Amblydoras affinis*, *Hemidoras morrisi*, *Megalodoras uranoscopus* and *Oxydoras niger*) verwendet. Die Fische wurden in der Hand gehalten und die Laute, die in Luft und Wasser abgegeben wurden, aufgenommen. Die folgenden Lauteigenschaften wurden analysiert – Lautanzahl, Lautdauer, dominante und fundamental Frequenz, Schalldruckpegel und die peak-to-peak Amplitude – und dann für die beiden Medien verglichen. Außerdem wurden sie mit der Fischgröße (Standardlänge, Körpergewicht) korreliert. Alle Arten produzierten Stridulationslaute in beiden Medien aber nur drei Arten produzierten Trommellaute in der Luft. Die meisten Lauteigenschaften von den Stridulationslauten (Lautanzahl, Lautdauer, Frequenz) unterschieden sich zwischen den Medien, solche Unterschiede konnten bei den Trommellauten jedoch nicht festgestellt werden. Die Anzahl der abgegebenen Laute sank mit der Zeit während die Lautdauer anstieg. Die dominante Frequenz der Stridulationslaute sank mit der Körpergröße, der Schalldruckpegel nahm jedoch mit zunehmender Körpergröße zu. Somit waren die Eigenschaften der Stridulationslaute vom Medium abhängig, die der Trommellaute blieben jedoch unbeeinflusst. Das lässt sich am wahrscheinlichsten aufgrund der unterschiedlichen Dichte der Medien erklären und der Mechanismen mit denen die Laute produziert werden. Die Hypothese, dass Welse mehr Stridulationslaute in Luft und mehr Trommellaute in Wasser produzieren aufgrund des unterschiedlichen Prädatorendruckes (Vogel versus Fisch) konnte nicht bestätigt werden. Daher wird angenommen, dass Stridulationslaute eher als Störungslaute in beiden Medien dienen, während Trommellaute wahrscheinlich eher als intraspezifische Kommunikationssignale im Wasser verwendet werden.

Keywords/ Schlagwörter: Luft vs. Wasser, Lauteigenschaften, Doradidae, Stridulationslaute, Trommellaute, Stresslaute.

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CURRICULUM VITAE

Persönliche Daten	Name: Lisa Marie Knötig BSc	
	Nationalität:	österreichisch
Schulbildung	1995 - 1999	Volksschule, Kolbnitz
	1999 - 2003	Bundesrealgymnasium, Spittal/Drau
	2003 - 2007	Bundesoberstufengymnasium, Spittal/Drau
Universitätsausbildung	2007 - 2010	Bachelor Zoologie, Universitäat Wien Titel Bachelorarbeit: „Das Flugverhalten von Stachellosen Bienen (Meliponini) in der Tropenstation La Gamba, Costa Rica“
	seit 9/2010	Master Verhaltens-, Kognitions- und Neurobiologie, Universität Wien
Beschäftigungsverhätnisse	2006 – 2008	jeweils 4 wöchige Mithilfe bei einem landwirtschaftlichen Betrieb (Herbert Hofer, 9821 Obervellach)
	2004, 2006 – 2009	jeweils 4 – 6 wöchiger Ferialjob als Servicekraft auf der Lammersdorfer Hütte / Millstatt
	2010	zweimonatiges Ferialpraktikum auf einer Farm (Areena East London) / Südafrika
	2011 – 2012	Servicekraft im Sommer beim Almgasthof Himmelbauer / Obervellach
Sonstiges	Ausbildung zur zertifizierten Waldpädagogin 3-wöchiges Tropenpraktikum auf der Tropenstation „La Gamba“ in Costa Rica (Februar 2010) mehrere Kurzaufenthalte im Ausland vor allem in den USA	

APPENDIX

Table. I. Mean sound characteristics in air.

	Air				
Characteristics	***A. pectinifrons***	***A. affinis***	***H. morrisi***	***M. uranoscopus***	***O. niger***
N	7	5	12	10	3
weight (g)	7.81	7.72	12.43	46.16	173.33
Standard length (mm)	62.05	68.80	106.75	133.50	226.67
Total length (mm)	72.44	74.40	125.33	163.20	261.00
AD sound duration (ms)	116.87	91.37	74.05	116.20	83.90
AB sound duration (ms)	115.39	82.16	60.37	88.56	80.80
AD dom. Frequency (kHz)	2.37	1.73	2.26	1.89	0.83
AB dom. Frequency (kHz)	1.56	2.82	2.22	1.04	1.21
SR LAFmax (dB re 20 µPa)	47.23	49.39	53.24	55.47	53.71
SRLZFmax (dB re 20 µPa)	60.30	60.16	60.07	62.05	61.71
NoS SR total	48.71	24.80	51.50	32.00	33.67
NoS SR 0 - 15 s	26.43	16.00	25.17	16.80	10.67
NoS SR 15 - 30 s	12.43	5.20	12.17	7.90	8.67
NoS SR 30 - 45 s	7.00	2.40	8.00	4.00	7.67
NoS SR 45 - 60 s	2.86	1.00	6.17	3.30	6.67
NoS DR total			51.50	16.33	7.67
NoS DR 0 - 15 s			22.00	8.33	1.33
NoS DR 15 - 30 s			12.75	3.78	0.00
NoS DR 30 - 45 s			10.75	2.44	2.67
NoS DR 45 - 60 s			6.83	1.78	3.67
Sound duration DPS				1384.50	2787.50
Sound duration SPS			64.84	79.18	70.27
Main frequency			0.107	0.099	0.091
LAFmax DR (dB re 20 µPa)			35.15	31.68	
LZFmax DR (dB re 20 µPa)			59.41	59.78	61.20
PtP-Amp DPS				0.20	0.02
PtP-Amp SDS			0.04	0.15	0.08
PtP-Amplitude SR (AD)	0.55	0.80	0.70	0.88	0.48
PtP-Amplitude SR (AB)	0.50	0.57	0.44	0.63	0.49

Table. II. Mean sound characteristics in water.

	Water				
Characteristics	***A. pectinifrons***	***A. affinis***	***H. morrisi***	***M. uranoscopus***	***O. niger***
N	7	5	12	10	3
weight (g)	7.81	7.72	12.43	46.16	173.33
Standard length (mm)	62.05	68.80	106.75	133.50	226.67
Total length (mm)	72.44	74.40	125.33	163.20	261.00
AD sound duration (ms)	131.42	95.55	67.41	126.18	83.38
AB sound duration (ms)	121.72	78.91	57.66	98.34	92.98
AD dom. Frequency (kHz)	1.53	1.77	1.64	0.93	0.51
AB dom. Frequency (kHz)	1.51	1.76	1.56	0.95	0.74
LAFmax SR (dB re 1 µPa)	126.60	131.97	129.07	129.71	129.08
LZFmax SR (dB re 1 µPa)	127.05	139.94	129.39	130.45	134.65
NoS SR total	49.14	37.67	19.00	38.00	26.00
NoS SR 0 - 15 s	22.43	11.67	10.40	16.42	15.10
NoS SR 15 - 30 s	14.57	10.00	6.40	10.25	5.70
NoS SR 30 - 45 s	10.00	8.67	1.20	8.00	3.70
NoS SR 45 - 60 s	2.14	6.00	1.00	3.33	1.50
NoS DR total	30.00	34.67	16.00	39.42	21.82
NoS DR 0 - 15 s	11.14	13.67	9.00	14.58	8.36
NoS DR 15 - 30 s	9.86	9.67	7.00	10.67	5.64
NoS DR 30 - 45 s	6.57	6.67	0.00	9.17	5.82
NoS DR 45 - 60 s	2.43	5.00	0.00	5.00	2.00
Sound duration DPS					365.85
Sound duration SPS	276.30	88.04	74.65	70.60	138.67
Main frequency	0.107	0.169	0.075	0.092	0.094
LAFmax DR (dB re 1 µPa)	94.07	111.57	88.35	109.38	97.03
LZFmax DR (dB re 1 µPa)	117.36	131.94	107.41	119.17	111.34
PtP-Amp DPS					0.08
PtP-Amp SDS	0.02	0.09	0.02	0.07	0.07
PtP-Amplitude SR (AD)	0.77	0.57	1.05	0.53	0.61
PtP-Amplitude SR (AB)	0.81	0.53	1.07	0.32	0.43

Table III. Sound duration per 15 s time periods per species in air and in water.

		15 s time periods			
	Sound duration	**0 - 15 s**	**15 - 30 s**	**30 - 45 s**	**45 - 60 s**
Air	*A. p.* AD SD	97.04	117.62	128.05	124.76
	A. p. AB SD	98.10	116.28	122.43	124.75
	A. a. AD SD	83.91	87.37	91.00	103.20
	A. a. AB SD	70.88	78.48	81.36	97.90
	H. m. AD SD	67.05	70.10	75.41	83.62
	H. m. AB SD	51.03	55.86	65.08	69.38
	M. u. AD SD	102.64	116.48	119.30	126.38
	M. u. AB SD	75.44	90.43	92.94	95.43
	O. n. AD SD	75.33	79.47	88.33	92.47
	O. n. AB SD	69.73	74.80	82.13	96.53
Water	*A. p.* AD SD	114.43	129.83	136.37	145.06
	A. p. AB SD	99.71	121.14	130.59	135.42
	A. a. AD SD	84.15	95.68	97.65	104.70
	A. a. AB SD	67.29	78.24	80.59	89.50
	H. m. AD SD	65.83	66.85	68.39	68.57
	H.m. AB SD	53.83	56.69	60.03	60.11
	M. u. AD SD	114.54	130.52	125.69	133.95
	M. u. AB SD	92.66	102.96	95.84	101.88
	O. n. AD SD	69.60	77.00	88.27	98.67
	O. n. AB SD	77.33	86.47	97.53	110.60

Table IV. Peak-to-peak-amplitude ratios.

Species	**ptp-amp ratio (AD/AB) air**	**ptp-amp ratio (AD/AB) water**	**ptp-amp ratio (SR/DR) air**	**ptp-amp ratio (SR/DR) water**
A. p.	1.10	1.05		49.48
A. a.	1.16	1.41		136.52
H. m.	1.39	1.65	15.66	7.85
M. u.	1.79	1.52	10.97	7.70
O. n.	0.98	1.08	6.40	6.64