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Titel der Diplomarbeit

„Sex-specific differences in agonistic behaviour, sound production and auditory sensitivity in the callichthyid armoured catfish *Megalechis thoracata*“

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In loving memory
to my dear parents
Ali & Zdenka Hadjiaghai

"It is said some lives are linked across time
connected by an ancient calling
that echoes through the ages."

Prince of Persia: The Sands of Time

Contents

Abstract

Background: Data on sex-specific differences in sound production, acoustic behaviour and hearing abilities in fishes are rare. Representatives of numerous catfish families are known to produce sounds in agonistic contexts. The aim of the present study was to investigate agonistic behaviour, sound production and hearing abilities in males and females of a callichthyid catfish.

Methodology/Principal Findings: One adult male, seven subadult males and nine subadult females of the armoured catfish *Megalechis thoracata* were investigated. Agonistic behaviour displayed during male-male and female-female dyadic contests and sounds emitted were videotaped and recorded, sound characteristics analysed and hearing was measured using the auditory evoked potential (AEP) recording technique. Male pectoral spines were on average 1.7-fold longer than those of females. Visual and acoustic threat displays differed between sexes. Males produced low-frequency harmonic barks at longer distances and thumps at close distances, whereas females emitted broad-band pulsed crackles at close distance to the conspecific. Female aggressive sounds were significantly shorter than those of males (167 ms versus 219 to 240 ms) and showed a significantly higher dominant frequency (562 Hz versus 132 to 403 Hz). Sound duration and sound level were positively correlated with body and pectoral spine length, but dominant frequency was only (negatively) correlated to spine length. Both sexes showed similar U-shaped hearing curves with lowest thresholds between 0.2 and 1 kHz and a drop in sensitivity above 1 kHz. The main energies of sounds were located at the most sensitive frequencies.

Conclusions/Significance: Current data demonstrate that both male and female *M. thoracata* produce aggressive sounds, but the behavioural contexts and sound characteristics differ between sexes. Sexes do not differ in hearing, but it remains to be clarified, if this is a general pattern among fish. This is the first study, which describes sex-specific differences in agonistic behaviour within a fish species.

Keywords: Callichthyidae, sex-specific differences, agonistic behaviour, acoustic signals, sound characteristics, auditory evoked potentials (AEP), hearing

1. Introduction

There exists a wealth of knowledge on sound generating mechanisms, sound production during agonistic and reproductive behaviour, and hearing in fishes (for reviews see Amorim 2006, Ladich and Fine 2006, Ladich and Myrberg 2006, Myrberg and Lugli 2006, Ladich and Fay 2013). Despite this wealth of knowledge, data on sex-specific differences in sonic organs, sound production and in particular in hearing are very limited.

Studies in several families such as Gadidae, Ophidiidae, Batrachoididae, Osphronemidae and Sciaenidae have described sexual dimorphism of sound-generating structures (Templeman and Hodder 1958, Takemura et al. 1978, Hill et al. 1987, Connaughton et al. 2002, Rowe and Hutchings 2004). Pectoral as well as swimbladder mechanisms are typically larger in males than females. Kratochvil (1985) found that pectoral sonic muscles were larger in male than female gouramies (genus *Trichopsis,* family Osphronemidae). Pruzsinszky and Ladich (1998) revealed that pectoral fin spines of male peppered corydoras *Corydoras paleatus* were relatively longer than those of females. In representatives of several families such as Batrachoididae (e.g oyster toadfish *Opsanus tau* and midshipman *Porichthys notatus;* Fine et al. 1990, Brantley et al. 1993a), Sciaenidae (e.g. Japanese croaker *Argyrosomus japonicus*, Ueng et al. 2007) and Gadidae (e.g. haddock *Melanogrammus aeglefinus*, Templeman and Hodder 1958), sonic muscles were larger in males than of females. A recent study by Kéver et al. (2012) revealed that besides larger drumming muscles in male cusk-eel *Ophidion rochei* females lacked a rocker bone on the swimbladder, typically found in males.

Investigations on agonistic behaviour often revealed that both sexes are generating sounds and that sex-specific differences in agonistic sounds are rather small (Myrberg et al. 1965, Ladich 1990, 2007, Lagardère et al. 2005). This differs considerably from the reproductive context, where only males seem to emit advertisement or courtship calls, except in the *T. vittata* (Ladich 2007). Acoustic displays are always occurring in combination with visual displays during agonistic interactions, which generally start, when opponents are detected visually. Brawn (1961) mentioned that in both sexes of the Atlantic cod *Gadus morhua* (formerly *G. callarias*), conspecifics were intimidated by a threat display, which was accompanied by grunting sounds. Myrberg et al. (1965) noted that males and females of the jewelfish *Hemichromis bimaculatus* produced pulsed br-r-r sounds before attacking an intruder. In the flier cichlid *Archocentrus centrarchus* (formerly *Cichlasoma centrarchus*), female attacks on males are often accompanied by low-frequency growls (Schwarz 1980). Pruzsinszky and Ladich (1998) reported that during dyadic encounters males of *C. paleatus*

did not behave aggressively towards each other, which differs considerably from the closely related callichthyid catfish *M. thoracata*, in which aggressive behaviour was observed in both sexes (Mayr 1987). Male and female *T. vittata* produced croaking sounds alternately, while beating pectoral fins rapidly, spreading unpaired fins and circling forcefully in a head-to-tail position (Ladich 2007). Acoustic behaviour of the male green damselfish *Abudefduf abdominalis* was always associated with a lunge towards or chase of another fish and commonly with erection of unpaired fins (Maruska et al. 2007). Ladich (1989) noted that in the European river bullhead *Cottus gobio*, both sexes produced two sound types, while defending their territories and that females vocalized less than males. Male pinhead pearlfish *Carapus boraborensis* emitted shorter pulses than females (Lagardère et al. 2005). Both male and female *T. vittata* produced long, high-intensity croaking sounds during agonistic encounters, which did not differ in sound characteristics (Ladich 2007). Simões et al. (2008) found out that the male agonistic sounds of the zebra mbuna *Maylandia zebra* (formerly *Pseudotropheus zebra*) lasted longer and consisted of more pulses than those of females. A previous study in the callichthyid armoured catfish *Megalechis thoracata* (formerly *Hoplosternum thoracatum*) showed that corresponding to the behavioural contexts, males and females uttered different types of pectoral sounds (Mayr 1987). This differs considerably from investigations on *C. paleatus*, in which males produced trains of sounds during dyadic contests, whereas no stridulation sounds could be recorded from females during social interactions (Pruzsinszky and Ladich 1998).

All otophysans including catfishes possess a Weberian apparatus, which connects the swimbladder to the inner ears and distinctly improves their hearing ability (for reviews see Ladich and Bass 2003, Ladich and Popper 2004, Ladich 2013). Gee and Graham (1978) mentioned that the swimbladder in *M. thoracata* is very small and Burgess (1989) noted that callichthyids possess a short, paired and encapsulated swimbladder. A comparison between catfish species, which possess tiny encapsulated or large free swimbladders, revealed that the latter hear better in particular above 1 kHz (Ladich 1999, Lechner and Ladich 2008). Sex-specific differences in hearing sensitivities have not been described in fish so far. No difference in sensitivity was found in the callichthyid *C. paleatus*, the Atlantic molly *Poecilia mexicana* and the *A. abdominalis* (Ladich 1999, Maruska et al. 2007, Schulz-Mirbach 2010). Only, Maruska et al. (2012) found out that both sexes of the social cichlid fish *Astatotilapia burtoni* showed differences in hearing abilities, depending on the dominance of males and on the reproductive state in females.

Bradbury and Vehrencamp (1998, 2011) stated that acoustic communication is defined as transmission of information by a sender to a receiver with mutual potential benefits. Accordingly, a match of spectral contents of sounds and best hearing sensitivity of the intended receiver, and vice versa, should be preferred by natural selection (Ladich 1999, Maruska et al. 2007). Auditory sensitivity was found to match the characteristics of sounds produced in the frequency domain in some species (Cohen and Winn 1967, Myrberg and Spires 1980, Stabentheiner 1988, Ladich and Yan 1998, Maruska et al. 2007, Lechner et al. 2010), but mismatch could be observed in others (Fine 1981, Ladich 1999, 2000).

The aims of the present study were to investigate sex-specific differences in (1) sound generating mechanisms, (2) in agonistic behaviour, (3) in sound characteristics, (4) in the auditory abilities, and finally (5) to find out if the dominant frequencies of sounds correlates with the best hearing sensitivity in the callichthyid catfish *M. thoracata*.

2. Material and Methods

2.1. Animals

17 specimens of *M. thoracata* were used for the studies, seven subadult males (78 - 86.2 mm standard length, 12.2 - 19.1 g body mass), nine subadult females (71.3 - 87 mm, 9.8 - 17.1 g) and one adult male (106 mm, 32.9 g). It is assumed that fish were subadult according to Mayr (1987), who claimed that first reproductive behaviour in this species is shown at the age of two or two and a half years. Moreover, no reproductive behaviour could be observed during the present study. This species is a bottom-dwelling fish from slow-flowing rivers, pools, drainage ditches, and swampy areas in South America (Burgess 1989) and known for building and guarding floating foam nests (Mol 1993). Furthermore, *M. thoracata* performs air-breathing by gulping air at the water surface, since their accessory respiratory organ is the intestine (Gee and Graham 1978, Burgess 1989).

Fish were obtained from a local pet shop and a fish farmer, respectively. According to the fish farmer, fish hatched in October 2010 and behavioural experiments were carried out from August to November 2011. The sex of the fish could be determined by inspection of the genital papillae, the distance between coracoids and the size of pectoral fins. Males possess genital papillae, a narrower gap between coracoids and longer, thicker and orange-coloured pectoral spines (Burgess 1989). Due to the individually spotted body pattern, the subjects could be easily distinguished from each other.

Fish were kept in three tanks, which were similarly equipped with half flower pots and tubes as shelters, plants, roots and a sand bottom. Community tanks of subadult fish measured 110 x 30 x 55 cm (width x height x depth) and the tank of the adult male was 90 x 30 x 30 cm in size. Four males and four females and three males and five females, respectively were kept together. A 12:12 hour light:dark cycle was provided and the water temperature was kept at 25 ± 1°C. The aquaria were filtered by external filters in order to reduce noise. Fish were fed frozen chironomid larvae and occasionally artificial food (flakes and tablets) five to six times a week. All experimental procedures used in the current study were performed with the approval of the Austrian Federal Ministry of Science and Research, permit number GZ 66.006/0023-II/10b/2008.

2.2. Morphological measurements

After behaviour and sound recordings body mass, total length, standard length and length of the pectoral spine of each contestant were measured. The pectoral spine length (PSL) was measured from the juncture of the spine with the outer body surface to its tip using digital callipers. The relative pectoral spine length (rPSL) was calculated following the formula rPSL = PSL/TL, where TL is the total length.

2.3. Recording of behaviour and sounds

All agonistic encounters were performed from August 2011 to November 2011. Fish were kept for three months in holding tanks before the start of behavioural experiments. The video and sound recordings were carried out in a walk-in soundproof room, which was constructed as a Faraday cage. The experiments were carried out in a test tank (70 x 40 x 35 cm), whose walls were lined on the inside, except for the front glass, with acoustically absorbent material (air-filled packing wrap) to reduce resonances and reflections. The water temperature was maintained at 25 ± 1°C. The test tank was placed on a table that rested on a vibration-isolated plate.

The behaviour and acoustic signals were recorded using a hydrophone (Brüel & Kjaer 8101, sensitivity -184 dB re 1 V μPa^{-1}), which was connected to a power supply (Brüel & Kjaer 2804) and placed close to the back wall in the centre of the aquarium. Both the hydrophone and video camera (Sony CCD-VX1E) were connected to a HiFi S-VHS video cassette recorder (JVC HR-S4700 EG/E). HiFi audio and S-video signals were stored simultaneously on S-VHS HiFi videotapes (FUJIFILM Super VHS PRO SE-240). Sound pressure levels (RMS Fast, L weighting) were measured in parallel with the sound recordings

using a sound level meter (Brüel & Kjaer Mediator 2238) connected to the power supply (Fig. 1). The observer was always hidden behind a curtain during recording tests. External filters of the test tank were switched off and the hydrophone was placed inside twenty minutes before start of experiments.

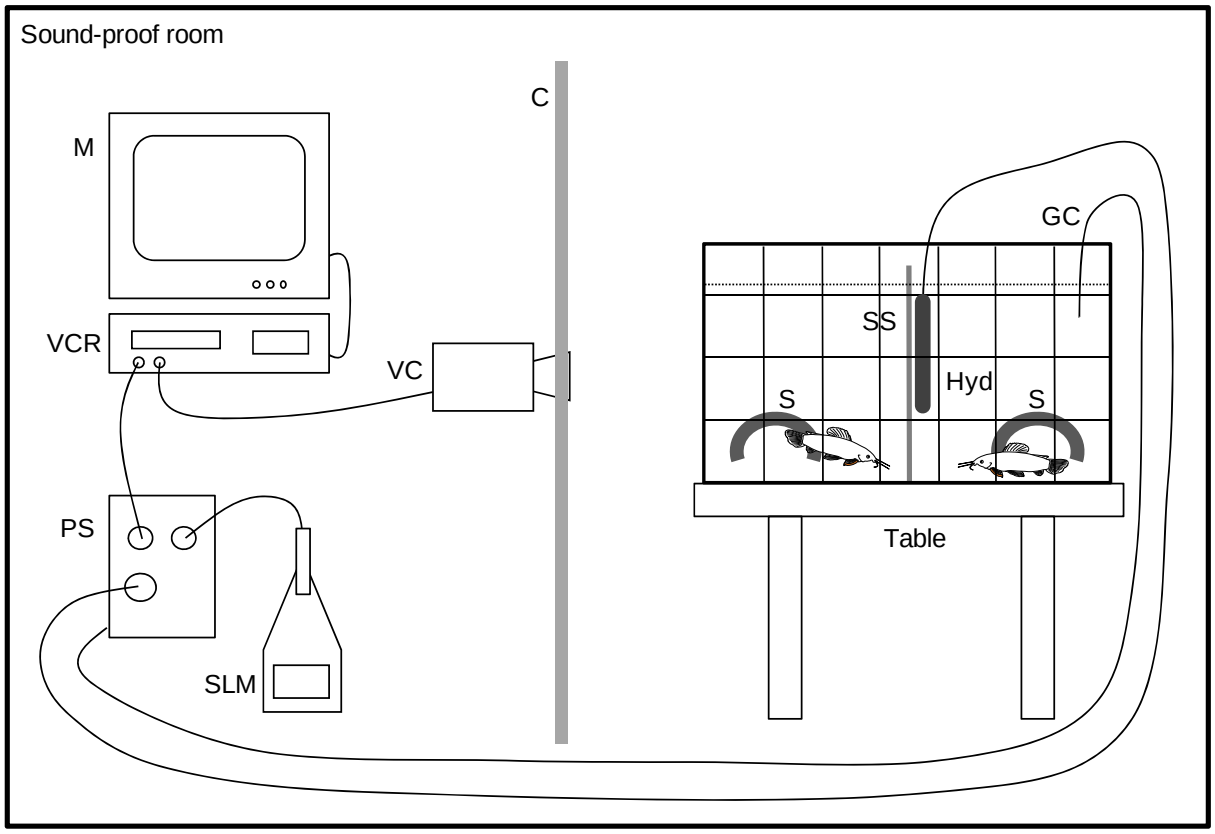

Fig. 1. Experimental setup for the recording of agonistic behaviour and sound production in *M. thoracata*. Abbreviations: C - curtain, GC - grounding cable, Hyd - hydrophone, M - monitor, PS - power supply, S - shelter, SLM - sound level meter, SS - separating sheet, VC - video camera, VCR - video cassette recorder.

In order to reduce prior dominance experience, fish were isolated for five days in isolation tanks (50 x 30 x 27 cm) and then for two more days in the test tank before experiments. Fish in each dyadic pairing came from different holding tanks. Test tank was divided by an opaque plastic sheet. Both halves were equipped with a half flower pot as shelter, plants and a sand bottom. On day eight, the separating sheet between two males or two females was removed and video and sound recordings started. Each dyadic encounter

lasted for thirty minutes, with fish being separated after this period. Then, fish were observed for additional ten minutes to find out, if sounds were produced without visual contact. Due to the small number of individuals and the fact that acoustic displays occurred only rarely, animals were used repeatedly in order to achieve a higher number of agonistic contests and thus sound recordings. But the same fish were never paired twice. After morphological measurements both individuals were returned to the community tanks.

2.4. Analysis of behaviour and sounds

Each sound was digitized using a sampling rate of 11 kHz (16 bit resolution) and analysed using Cool Edit 2000 (Syntrillium Software Corporation, Phoenix, USA) and ST^x Soundtools 3.7.8. (Institute of Sound Research at the Austrian Academy of Sciences). Only sounds with a good signal-to-noise ratio were analysed. The following acoustic variables were measured from sounds recorded during dyadic agonistic encounters:

Sound duration (SD): the total length between the onset and the end of a single call or a series of sounds (Fig. 2).

Dominant frequency (DF): the frequency with the highest amplitude within a power spectrum. In order to better representation of the energy distribution, the dominant frequency of sounds was determined from cepstrum-smoothed power spectra. Harmonic sounds are characterized in a power spectrum by the presence of several regularly spaced peaks, in which the frequencies of the harmonic peaks are multiples of that of the lowest peak (fundamental frequency). The harmonic content of a sound was controlled by overlaying a harmonic grid.

Sound pressure level (SPL): measured in dB re 1µPa (RMS Fast, L weighting). In consideration to compensate the varying distances of vocalizing fish to the hydrophone, a correction factor was calculated. Therefore, the test tank was divided into 21 sectors (each measuring 10 x 10 cm) by using a grid applied on the front glass of the aquarium (Fig. 1). The sector in which a fish emitted sounds was noted. Because sounds of *M. thoracata* were of low energy, pink noise was chosen for calculating a correction factor. Short tone bursts were played back at a constant SPL from a small loudspeaker (Fuji 7G06, 8 Ohm, 0.8 W), in each of the 21 sectors and the SPLs were noted. The relative difference of the SPL measured in the sector nearest to the hydrophone (3 cm away) and the other sectors were calculated and added to the SPL values of fish sounds measured before. Thus, a distance-independent absolute SPL value could be determined for each sound emission.

The aim of the behavioural analyses was only to describe all behavioural patterns (elements), which occurred during male-male and female-female agonistic contests. All

behavioural patterns shown during a total of 24 agonistic encounters were classified, according to the description presented in table 1. The number of acoustic signals and visual displays such as attack, circling and head nodding was counted for each experiment and individual.

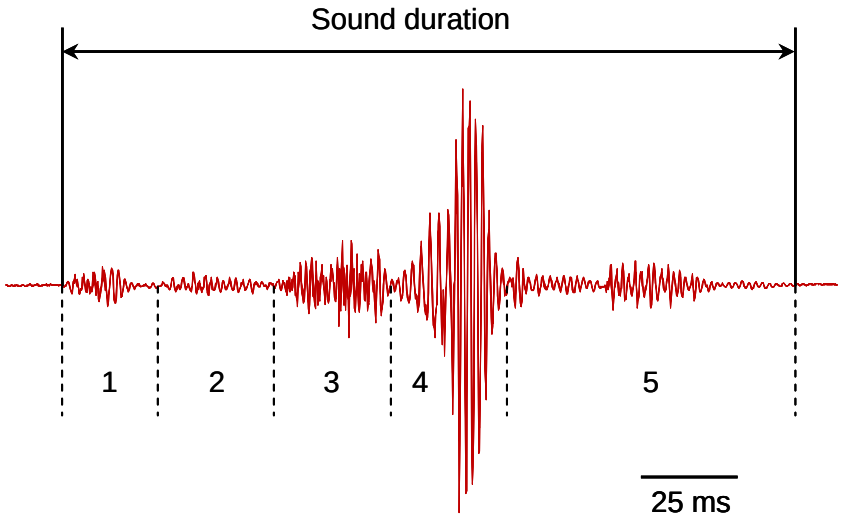

Fig. 2. Oscillogram of a sound series produced by a female *M. thoracata* in an agonistic context showing the sound duration analysed. Dotted lines delimit the single elements (1 - 5, 4 = main element) measured, which varied in waveform envelope.

Tab. 1. Description of the behavioural repertoire shown during dyadic male-male and female-female interactions of *M. thoracata*, following the definitions of Mayr (1987), except for fin beating, jerk and sneaking. m - males, f - females.

Behavioural pattern	Brief Description
Non-aggressive behaviour	
Air gulping (m, f)	Air intake at the water surface.
Comfort (m, f)	Remaining in stationary position on the bottom, alone or with another fish.
Swimming (m, f)	Directed and non directed locomotion of individuals.
Digging (m, f)	Picking up sand with mouth and spitting it out immediately.
Aggressive behaviour	
Approach (m, f)	Fish swam in the direction of another individual.
Attack (m, f)	Fin displaying or approaching another fish, stopping suddenly before forcefully hitting the other with its tail.
Chase (m, f)	One fish rapidly pursued another individual.
Circling (f)	Two females swam in an anti-parallel (head-to-tail) orientation with their erected dorsal and caudal fin.
Fin beating (m, f)	Two male or female opponents performed undulating movements with their erected fins during fin displays or circling.
Fin display (m)	Two males moved towards each other, in a parallel, anti-parallel position or various angles spreading all their fins. Additionally, at high intensities, the caudal part of the body was erected in a distinct angle.
Fleeing (m, f)	Continued escape reaction in response to a chase. Fish swam rapidly away from the aggressor.
Head nodding (f)	Females showed serial vertical up and down movements of their heads in different positions to each other.
Jerk (m)	Males moved their heads rapidly away and towards the opponent while bending their body C-like.
Sneaking (f)	One female following the opponent by a snake-like movement on the bottom.
Strike (f)	One female swam rapidly toward the opponent while vocalizing.

2.5. Auditory sensitivity measurements

Auditory sensitivity was determined using the non-invasive auditory evoked potential (AEP) recording technique, originally reported and evaluated by Kenyon et al. (1998) and modified by Wysocki and Ladich (2005 a, b).

Test animals were mildly immobilized by injecting intramuscularly Flaxedil (gallamine triethiodide; Sigma-Aldrich Handels GmbH, Vienna, Austria). The dosage applied was 11.42 - 15.13 μg g^{-1} for males and 10.79 - 14.52 μg g^{-1} for females, thus enabling the immobilized fish to produce slight opercular movements. All auditory measurements were carried out in an oval plastic tub (diameter 45 x 33 cm, water depth 12 cm, 1 cm layer of sand), lined on the inside with acoustically absorbent air-filled packing wrap to reduce resonances and reflections. The tub was positioned on an air table (TMC Micro-g 63-540, Technical Manufacturing Corporation, Peabody, MA, USA), which rested on a vibration-isolated concrete plate (Fig. 3). The entire experimental setup was enclosed in a walk-in soundproof chamber (interior dimensions: 3.2 x 3.2 x 2.4 m), which was constructed as a Faraday cage.

The subjects were positioned in the centre of the tub, so that the nape of the head was at the water surface. Respiration pipettes were inserted into the animal's mouth, according to their size. Respiration was achieved through a simple, temperature-controlled (25 ± 1 °C), gravity-fed water circulation system. A small piece of tissue paper was placed on the fish head to keep it moist and ensure proper contact of electrodes during experiments. The AEPs were recorded using silver wire electrodes (diameter 0.38 mm), which were pressed firmly against the fish's skin. The recording electrode was placed at the brainstem region and the reference electrode cranially between the nares. Shielded electrode leads were attached to the differential input of an a.c. preamplifier (Grass P-55, Grass Instruments, West Warwick, RI, USA; gain 100x, high-pass at 30 Hz, low-pass at 1 kHz). A ground electrode was placed underwater near the subject.

Sound stimuli presentation and AEP waveform recording were achieved using a Tucker-Davis Technologies (Gainesville, FL, USA) modular rack-mount system (TDT System 3) controlled by a PC containing a TDT digital signal processing board and running TDT BioSig RP software. A dual-cone speaker (Wharfedale Pro Twin 8, frequency response: 65 Hz - 20 kHz ± 3 dB), mounted 0.5 m above the fish in the air, was used to present tone stimuli during testing. Acoustic stimuli consisted of tone bursts presented at a repetition rate of 21 s^{-1}. Hearing thresholds were determined at the following frequencies: 0.1, 0.2, 0.3, 0.5, 1, 2, 3 and 4 kHz, always presented in random order. A hydrophone (Brüel & Kjaer 8101;

frequency range 1 Hz - 80 kHz ± 2 dB; voltage sensitivity -184 dB re 1 V μPa^{-1}) was positioned on the right side of the fish (approximately 2 cm away) to determine absolute stimulus SPLs underwater in close proximity to the subjects. For the enhancement of the hydrophone signal (1000 x), a second custom-built preamplifier was used.

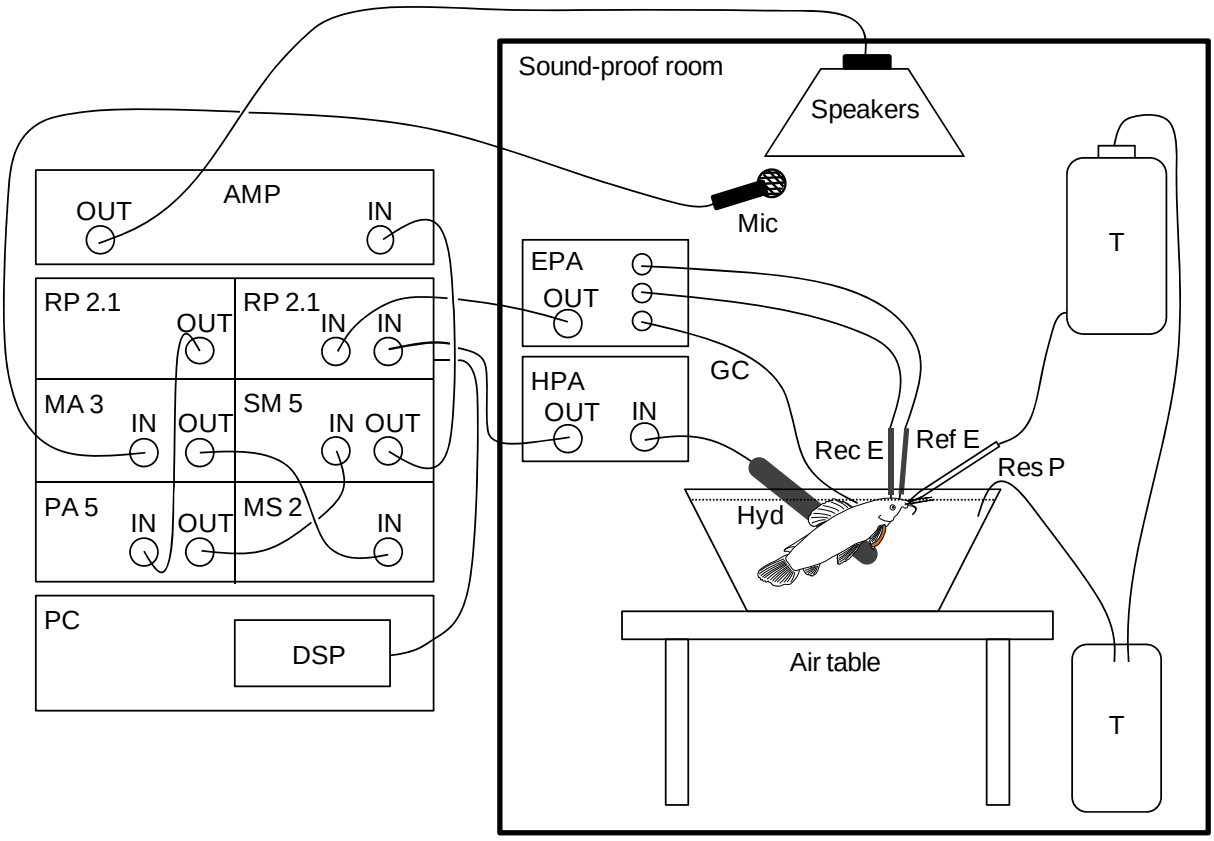

Fig. 3. Experimental setup for AEP measurement. Abbreviations: AMP - Amplifier, DSP - digital sound processing card, EPA - electrode preamplifier, GC - grounding cable, Hyd - hydrophone, HPA - hydrophone preamplifier, Mic - microphone, MA 3 - microphone amplifier, MS 2 - microphone speaker, PA 5 - programmable attenuator, PC - personal computer, Rec E - recording electrode, Ref E - reference electrode, Res P - respiratory pipette, RP 2.1 - realtime processor, SM 5 - signal mixer, T - water tanks.

For each test condition, the stimuli were presented at opposite polarities (180° phase shifted) and the corresponding AEPs were averaged together by the BioSig RP software in order to eliminate stimulus artefacts. At SPLs close to the threshold, this procedure was performed at least twice and the AEP traces were overlaid to examine, if they were repeatable.

The SPL values of tone burst stimuli were reduced in 4 dB steps. By overlaying replicate traces, the lowest SPL, where an identifiable and repeatable AEP trace could be obtained, was regarded as threshold.

2.6. Statistical analysis

All data were tested for normal distribution using the Kolmogorov-Smirnov-test and when data were normally distributed, parametric statistical tests were applied. Means of sound characteristics (duration, dominant frequency and SPL) were calculated for each male (N = 7) and for each female (N = 8) and used for further analyses. Relationships between morphological variables (standard length, pectoral spine length, relative pectoral spine length) and sound characteristics were determined by Pearson's correlation coefficients and linear regressions. Correlations were calculated by including all males, which produced a certain sound type, and all females. Thus, a correlation was calculated for all males, which produced barks, and all females and a correlation for all males, which produced thumps, and all females.

Additionally, a one-way analysis of variance (ANOVA) was performed, followed by a Bonferroni post-hoc test, in order to determine sex-specific differences in sound characteristics of each aggressive sound type. Differences in relative pectoral spine length between sexes were tested using paired T-test. A total of 244 sounds were used for analyses.

Mean hearing thresholds were determined for both sexes at each frequency. Thresholds obtained for males (N = 6) and females (N = 6) were compared by a two-way ANOVA using a general linear model, where one factor was sex and the other was frequency. The sex factor alone should reveal differences in sensitivity between sexes and combined with the frequency factor, if different tendencies exist at different frequencies of the audiograms.

All statistical tests were conducted by using PASW 18.0 (SPSS Inc., Chicago, USA). The significance level was set at $p \leq 0.05$. SigmaPlot 10.0 (Systat Software/Cranes Software Inc., Bangalore, India and San Jose, CA, USA) was employed for graphical illustrations.

3. Results

3.1. Pectoral fins

M. thoracata produced sounds by vibrating pectoral fins. The first pectoral fin rays were orange-coloured in males, but not in females. Pectoral spines were longer and thicker in males than in females. Pectoral spines (pectoral spine length/total length) of males were on overage

1.7-fold longer than in females (T-Test, t = 44.27, df = 15, $p \leq 0.01$) (Fig. 4). Microscopic dissection and inspection of an alcohol preserved adult male revealed that *M. thoracata* possessed no drumming muscles.

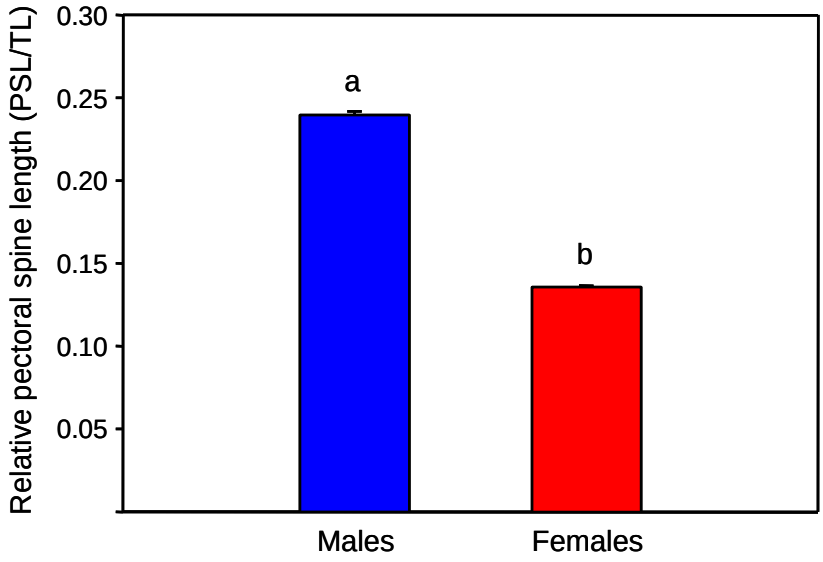

Fig. 4. Mean (+ SE) relative pectoral spine length of male and female *M. thoracata*. Different letters indicate statistically significant differences between sexes. PSL - absolute length of pectoral spine, TL - total fish length.

3.2. Agonistic behaviour

Aggressive interactions usually started after removal of the separating sheet and when opponents were detected visually. From time to time, the agonistic behavioural sequences were interrupted by air gulping, digging, resting close to each other or withdrawal into the shelter. For the description of behavioural patterns observed during thirteen male-male and eleven female-female encounters see table 1.

3.2.1. Male-male contests

Generally, one or both males started to approach each other and erected their fins (threatening fin display). Occasionally, this posture was followed by fin beating, which could last for several seconds. Head jerking followed and was accompanied by the production of two sound types, namely barks or thumps, which indicated high levels of aggression. Jerking could even occur without sound emission. Instead of vocalization, fin display was shown, and seldom individuals exhibited up to three jerks one after the other.

In twelve out of 13 encounters, barks and thumps were produced during aggressive interactions. Furthermore, in ten out of 13 contests, sound emission occurred in both contestants. Barks were emitted at various distances from a few centimetres up to a maximum of 40 centimetres away from the opponent. Before abduction of pectoral fins, a single adduction was observed. Barks were often produced during approaching and swimming (Fig. 5). Afterwards, the individual producing a sound mostly swam away and then again began to approach the conspecific. The latter could react with fin display or moving away from the other.

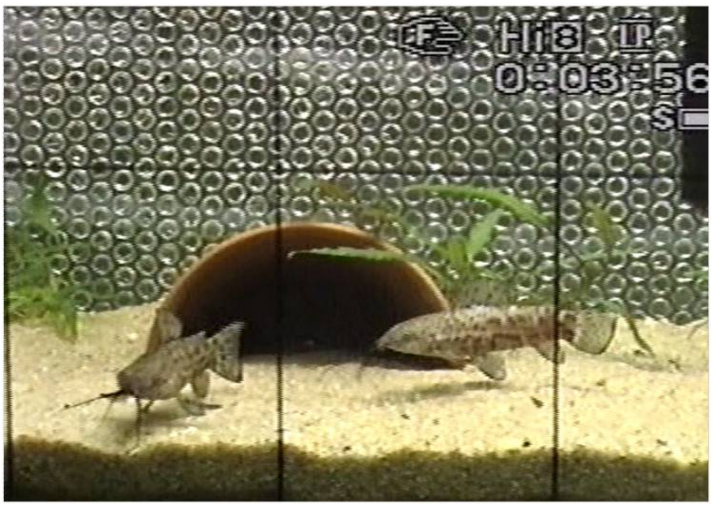

Fig. 5. Screen shot of a video recording showing two males in an agonistic contest. The illustration shows the right male approaching the opponent, shortly before uttering a bark.

In contrast to barks, thumps only occurred in direct proximity (within one body length) to the opponent. Typically, opponents showed fin displaying in a parallel, anti-parallel position or at various angles to each other (Fig. 6), or swam close by while thumps were emitted. Thumps were produced in a typical oblique position towards the opponent. Opponents responded by producing a thump, by attacking or by fleeing.

During all experiments, a total of 40 attacks could be counted, often preceded by fin display and fin beating. Attacks were mainly performed by sound producers, occasionally accompanied by thumps. Besides these behavioural elements, chasing was observed. During chasing, barks were emitted by the pursuer.

Fig. 6. Screen shot of video recording during a male-male aggressive interaction. This sequence shows the typically threatening fin display with fins spread and the caudal part of the right male erected in a distinct angle. Shortly after this threatening display, the right fish produced a thump in an oblique anti-parallel position relative to the conspecific.

In five out of seven experiments, barks were even emitted after separating both fishes by the plastic sheet and thus, after they lost the visual contact. This type of vocalization mainly occurred in males, which produced many sounds during the dyadic contests. Only in one case, did the opponent emit barks as well. After separation by the plastic sheet, males generated barks while swimming or when approaching the separating sheet. Contestants were also touching the separating sheet with their barbels. Opponents reacted by changing position or swimming towards the separating sheet.

3.2.2. Female-female contests

Interactions started when a female approached the other, in a few cases by sneaking movements (Tab.1) close to the bottom. This sneaking behaviour toward the opponent was occasionally accompanied by the emission of crackles. Sounds were recorded in all female-female experiments. In four out of eleven contests, both females vocalized during agonistic interactions. They were produced close to the opponent (within one to two body lengths) (Fig. 7) and were generated by rapid pectoral fin movements. Shortly before uttering a crackle, the vocalizing fish may strike towards the opponent. Crackles were most frequently emitted when one female chased the other one. Swimming after each other or pursuit could pass into circling behaviour (Tab. 1), which lasted up to a maximum of 3 s. Sounds were uttered before, during or at the end of circling.

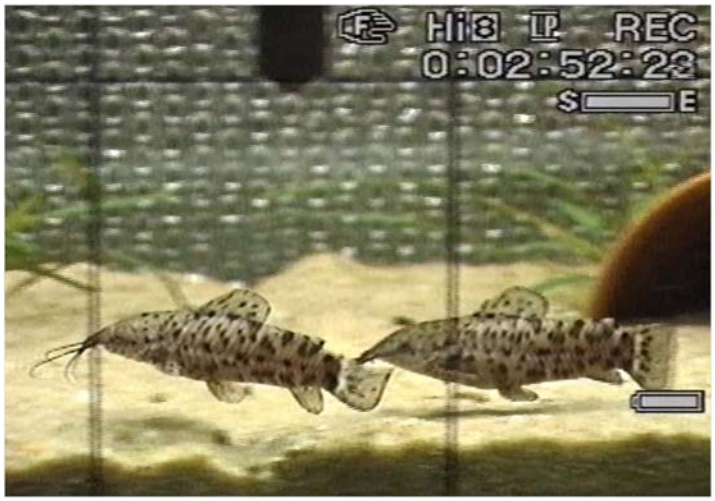

Fig. 7. Screen shot of video recording illustrating a female-female agonistic encounter. The right female emitted a series of crackles while swimming after the other female.

Head nodding was either performed by one fish or simultaneously by both opponents. Two to 18 head nods per individual were observed within a series. A total of 736 head nods was counted during eleven agonistic interactions and was exhibited at a higher rate by the vocalizing female. This threatening display could be elicited by the movement of one fish, when swimming by (even when above) the other, before and after circling and when resting to each other. Furthermore, interactions were characterized by a high rate of body contacts such as touching with barbels. Attacks only occurred four times, three were accompanied by crackles and one was exhibited shortly after head nodding.

In contrast to male-male encounters, in which both males vocalized, crackles were mainly produced by one female, seldom by both. Female-female contests were characterized by circling behaviour and the lack of jerks. Head nodding occurred in females, which could not be observed in any male-male interaction. While males beat their fins during fin displays, females did it during circling. Females only undulated their dorsal and caudal fins, whereas in males all fins were involved. Furthermore, females attacked less frequently than males and thus, were less aggressive.

3.3. Vocalizations

Three types of sounds were recorded during dyadic encounters and named onomatopoetically. Males produced barks and thumps and females crackles. Barks and thumps could be recorded in seven out of eight and crackles in eight out of nine animals. 376 barks, 66 thumps and 739

crackles were produced by fish during 24 interactions. No distress calls were produced when subjects were hand-held. Acoustic signals were non-audible to human listeners. Video analysis revealed that barks where produced during abduction of the pectoral fin. The movement of the pectoral fins (adduction and/or abduction) during the emission of thumps and crackles could not be determined.

3.3.1. Male agonistic sounds

Barks were low-frequency harmonic sounds showing frequency modulation and which only occurred singly. They consisted of one to three parts and were therefore classified as being mono-, bi- or tripartite (Fig. 8A, B). The most common sound structure was bipartite, in which the second part was of higher amplitude than the first part (Fig. 9A, B). Sound duration ranged from 159 to 317 ms, and the SPL ranged from 101.2 to 125 dB re 1 µPa at a distance of 3 cm (Tab. 2). The main energies were found in the first, second or third harmonic. The dominant frequency of bipartite barks varied in the first part from 110 to 600 Hz, and in the second from 170 to 730 Hz.

Thumps were produced singly and showed no harmonic structure. They were mostly mono- seldom bipartite (Fig. 10A, B). The latter were only recorded in the adult subject. Sound duration ranged from 116 to 446 ms, with SPLs ranging from 107.07 to 137.5 dB re 1 µPa at a distance of 3 cm. The dominant frequency varied from 70 to 210 Hz.

3.3.2. Female agonistic sounds

Female crackles differed from male sounds in their complex structure and frequency content. They were of higher frequency and always consisted of series of sound elements (Fig. 11A, B). Crackles were built up of two to eight, and mostly of four sound elements. These series were characterized by a main element characterized by the highest peak-to-peak-amplitude and several elements of lower amplitude before and after the main element (Fig. 11A). Elements could be separated by intervals from each other and could consist of a substructure such as a train of pulses (= one element).

The duration of crackles ranged from 81 to 394 ms. Single elements (including train of pulses) ranged from 5.6 up to 192.9 ms and main elements varied from 15.3 to 57.6 ms in duration. SPLs were between 101.5 and 128.1 dB re 1 µPa at a distance of 3 cm (Tab. 2). Dominant frequencies of crackles varied from 370 to 830 Hz.

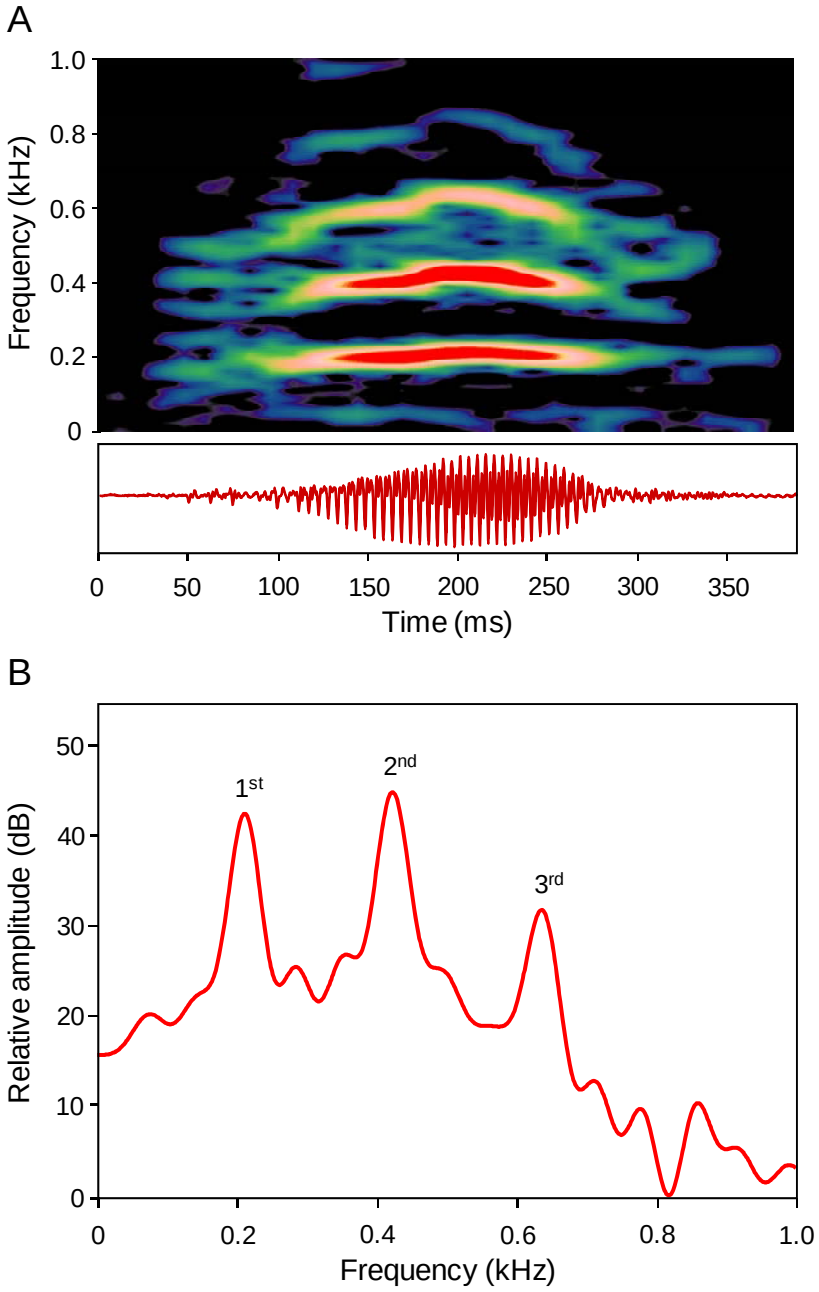

Fig. 8. (A) Sonogram (top) and oscillogram (below) and (B) cepstrum-smoothed power spectrum of a monopartite bark of a male *M. thoracata* produced during an aggressive encounter. The spectrum shows three harmonics (1^{st}, 2^{nd}, 3^{rd}) with the highest energy found in the second harmonic. Sampling rate 22 kHz. Hanning filter, overlap 75%, (A) filter bandwidth 20 Hz, (B) filter bandwidth 1 Hz, number of coefficients 350.

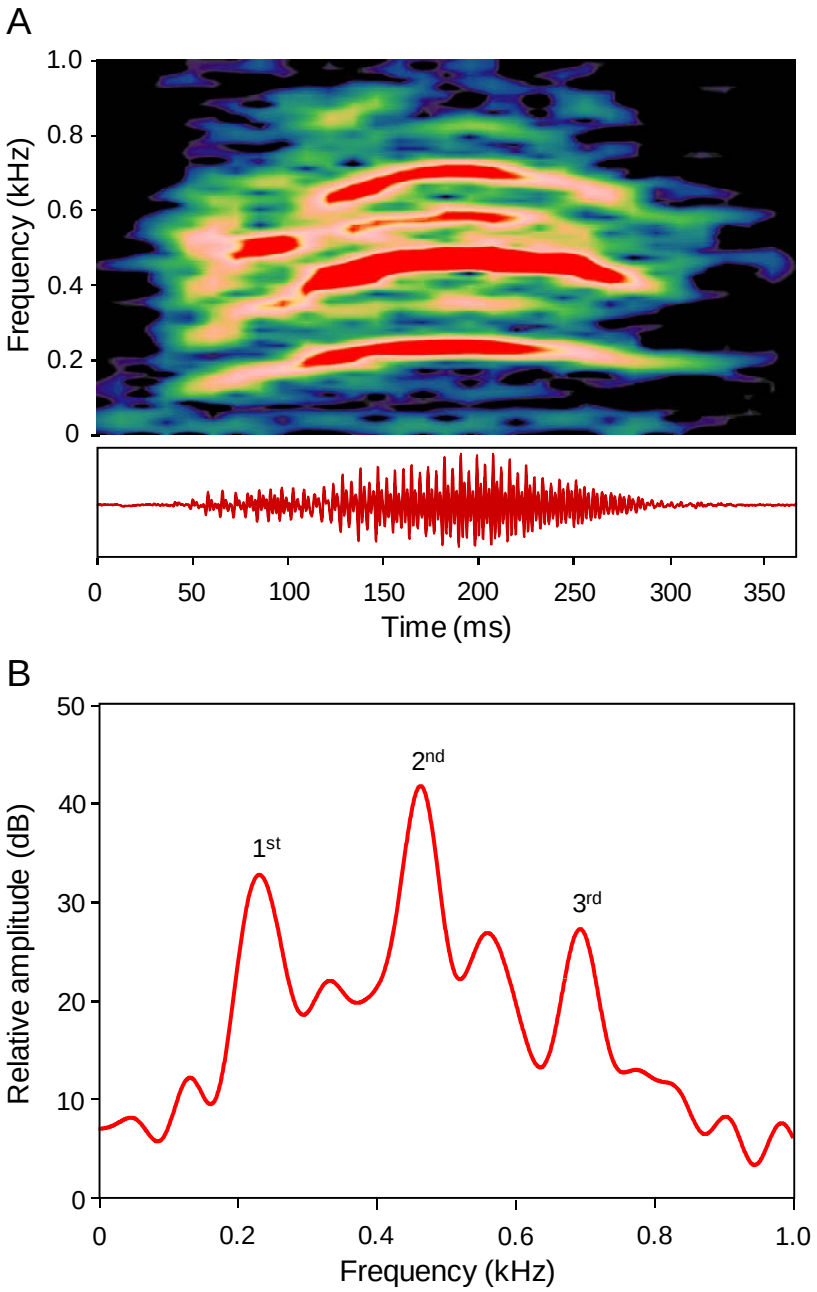

Fig. 9. (A) Sonogram (top) and oscillogram (below) and (B) cepstrum-smoothed power spectrum of the bipartite bark of a male *M. thoracata*. The spectrum reveals three harmonics (1^{st}, 2^{nd}, 3^{rd}) within the second sound part with the highest energy found in the second harmonic. The oscillogram shows lower amplitude in the first part. Sampling rate 11 kHz. Hanning filter, overlap 75%, (A) filter bandwidth 20 Hz, (B) filter bandwidth 1 Hz, number of coefficients 170.

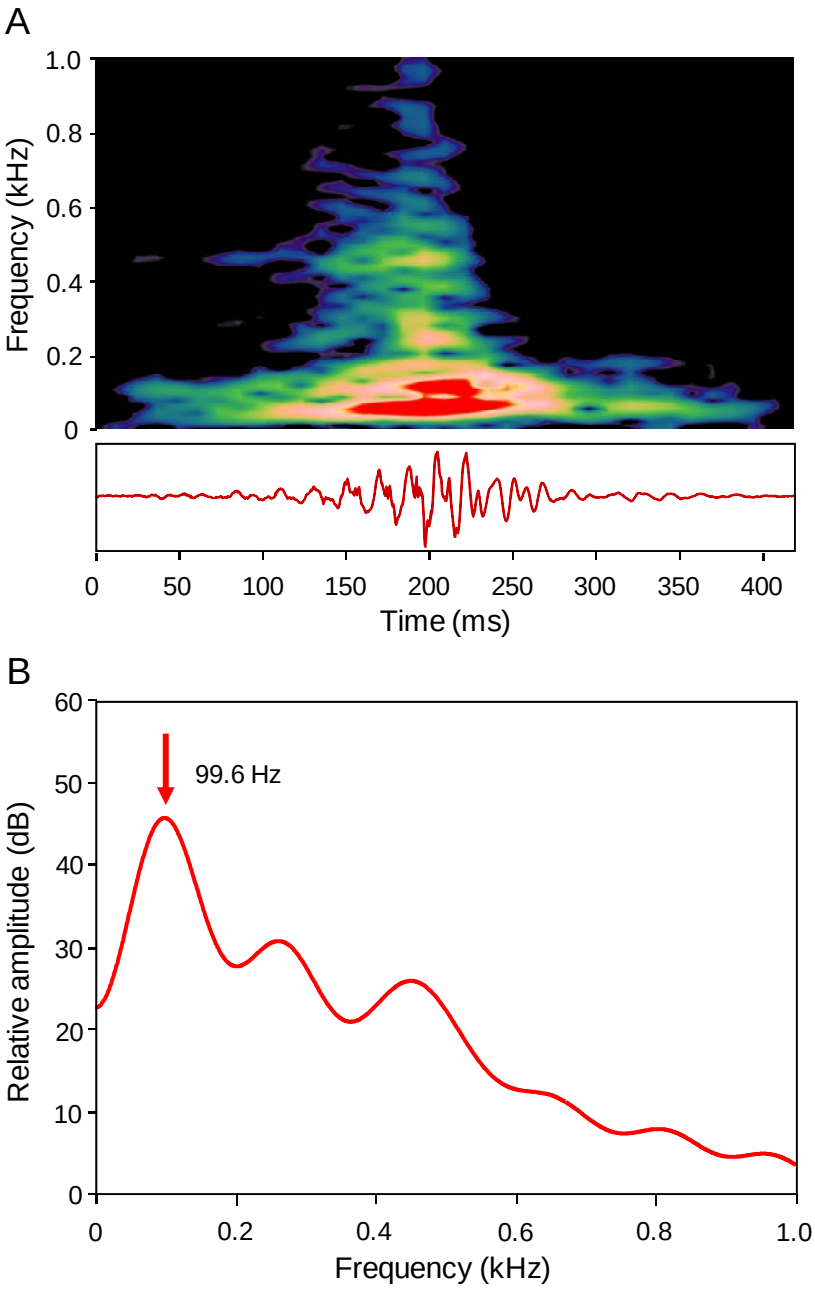

Fig. 10. (A) Sonogram (top) and oscillogram (below) and (B) cepstrum-smoothed power spectrum of a monopartite thump of a male *M. thoracata* uttered in an agonistic context. The dominant frequency is indicated in (B). Sampling rate 11 kHz. Hanning filter, overlap 75%, (A) filter bandwidth 20 Hz, (B) filter bandwidth 1 Hz, number of coefficients 80.

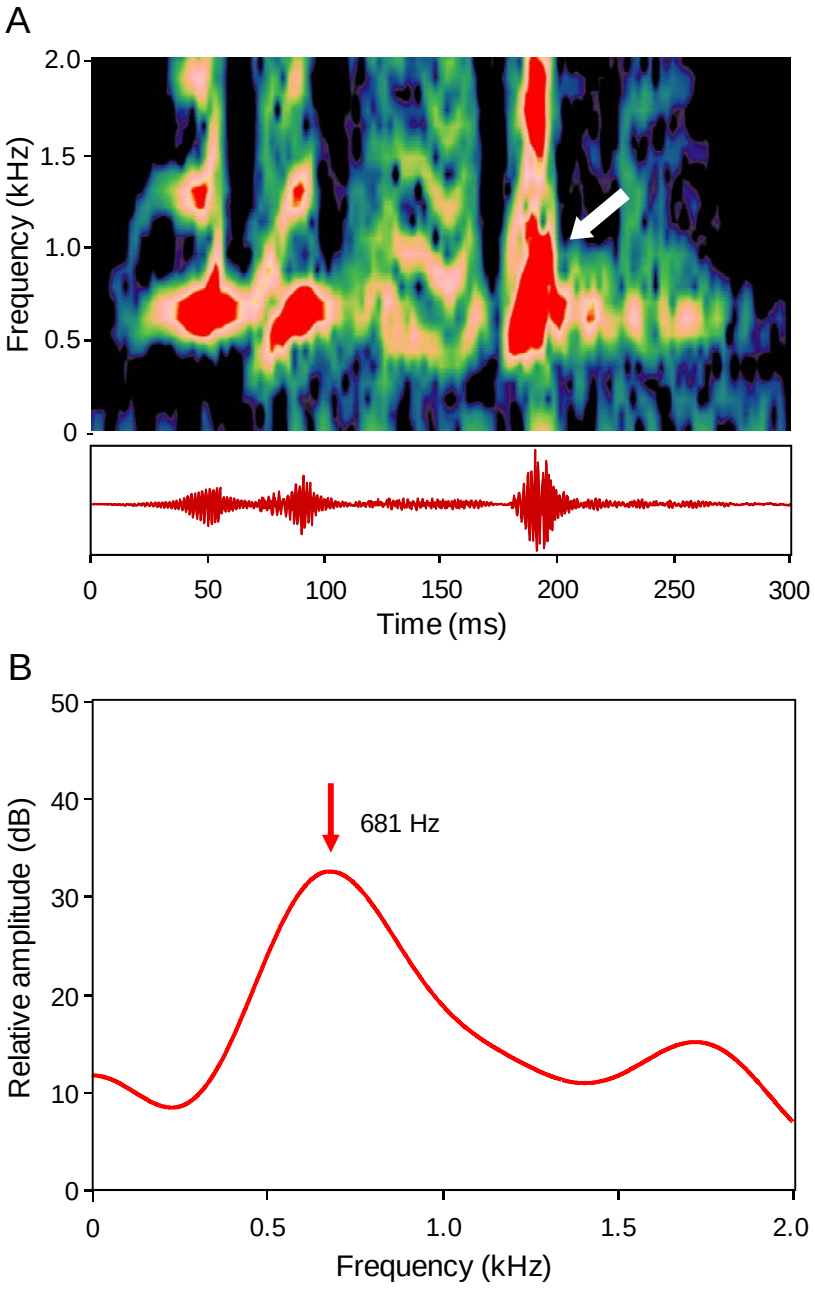

Fig. 11. (A) Sonogram (top) and oscillogram (below) and (B) cepstrum-smoothed power spectrum of crackles of a female *M. thoracata* produced in an agonistic context. The oscillogram shows five sound elements. The arrow indicates the main element, followed by a train of pulses. The dominant frequency is indicated in the cepstrum-smoothed power spectrum in (B). Sampling rate 11 kHz. Hanning filter, overlap 75%, (A) filter bandwidth 100 Hz, (B) filter bandwidth 1 Hz, number of coefficients 20.

Tab. 2. Mean (± SE) sound duration, sound pressure level and dominant frequency of the three sound types produced by *M. thoracata*. N - number of individuals.

Sound type	N	Sound duration (ms)	Sound pressure level (dB re 1 µPa)	Dominant frequency (Hz)	
				Bark Part 1	Bark Part 2
Bark	7	218.90 ± 0.01	110.73 ± 1.16	252.98 ± 23.03	403.22 ± 27.62
Thump	7	240.26 ± 0.02	119.97 ± 1.95	132.47 ± 8.26	
Crackle	8	167.08 ± 0.02	112.45 ± 1.80	561.62 ± 13.93	

3.3.3. Comparison between sound types

The sound duration differed between sound types (One-way ANOVA: $F_{2,19} = 8.06$, $p < 0.01$). Bonferroni post hoc test revealed that barks and thumps were similar in sound duration, but were significantly longer than crackles (Fig. 12). SPLs differed between sound types (One-way ANOVA: $F_{2,19} = 10.85$, $p \leq 0.001$) (Fig. 13). Thumps were significantly louder than barks and crackles, but no such difference was found between barks and crackles (Bonferroni post hoc test). Furthermore, the dominant frequencies varied between sound types (One-way ANOVA: $F_{3,25} = 33.95$, $p < 0.001$) (Fig. 14). Mean dominant frequencies of crackles were much higher than in the first and second bark parts and thumps. The first bark parts and thumps did not differ significantly (Bonferroni post hoc test).

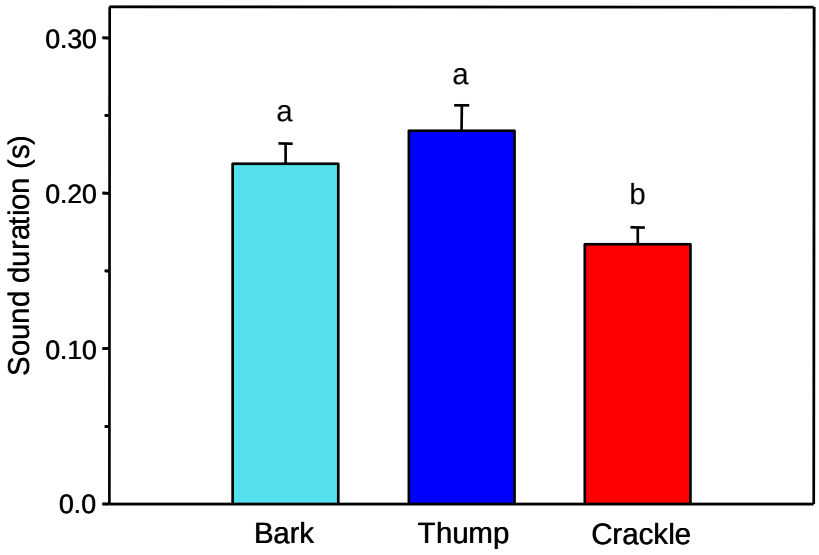

Fig. 12. Mean (+ SE) sound duration of male barks and thumps (N = 7) and of female crackles (N = 8). Different letters indicate statistically significant differences between sound types.

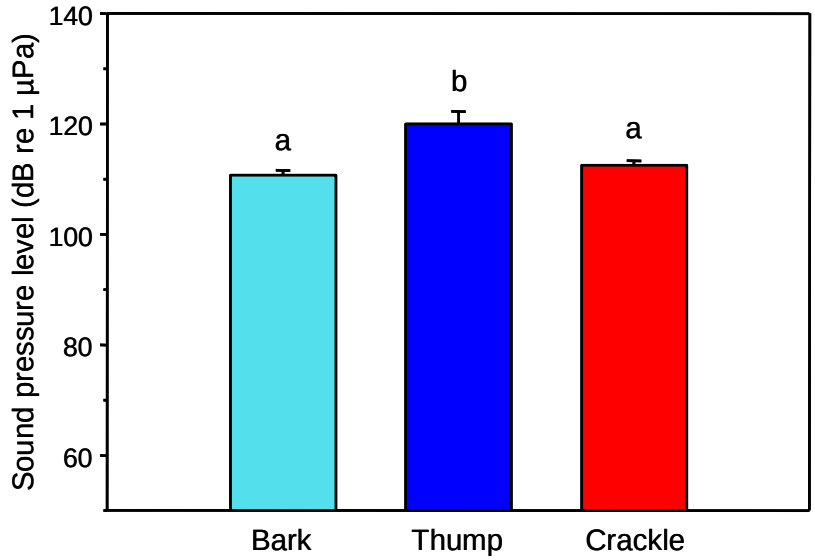

Fig. 13. Mean (+ SE) sound pressure level of male barks and thumps (N = 7) and of female crackles (N = 8). Different letters indicate statistically significant differences between sound types.

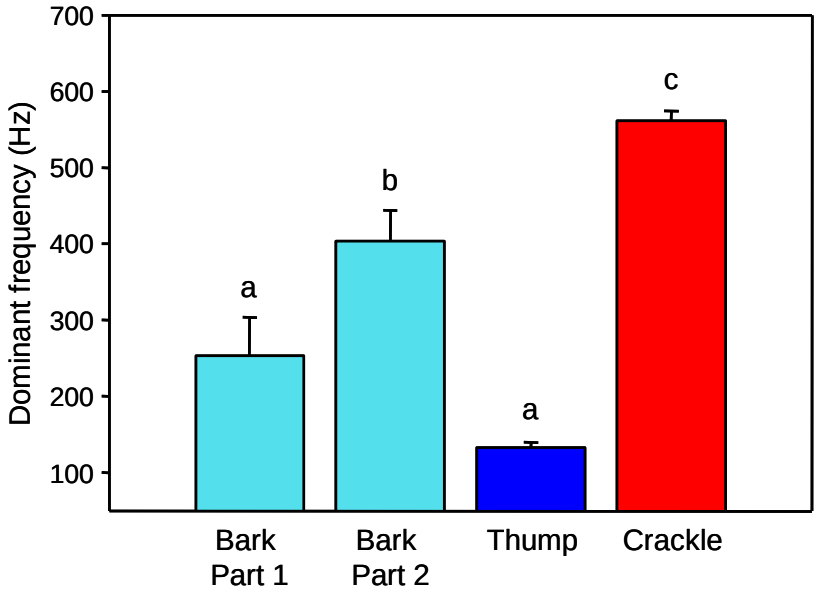

Fig. 14. Mean (+ SE) dominant frequency of male barks and thumps (N = 7) and of female crackles (N = 8). Different letters indicate statistically significant differences between sound types.

3.3.4. Correlations between morphological measures and sound characteristics

Larger fish produced longer calls than smaller ones. Duration of male thumps and female crackles combined increased with mean standard length ($r = 0.80$, $N = 15$, $p < 0.001$) (Fig. 15A) and pectoral spine length ($r = 0.84$, $N = 15$, $p < 0.001$) (Fig. 15B). In contrast, male barks (and female crackles) were only correlated to pectoral spine length ($r = 0.68$, $N = 15$, $p < 0.01$) (Tab. 3).

Mean SPLs of male thumps and female crackles were positively correlated with standard length ($r = 0.79$, $N = 15$, $p \leq 0.001$) (Fig. 16A) and the pectoral spine lengths ($r = 0.81$, $N = 15$, $p < 0.001$) (Fig. 16B). Such a correlation was not found for SPLs of barks and crackles (standard length: $r = -0.23$, $N = 15$, $p = 0.409$; pectoral spine length: $r = -0.38$, $N = 15$, $p = 0.165$; relative pectoral spine length: $r = -0.37$, $N = 15$, $p = 0.177$) (Tab. 3).

Individuals with larger pectoral spines emitted sounds of lower frequency. Mean dominant frequencies of the first part, or the second part of barks, or of thumps and with crackles combined were negatively correlated to pectoral spine lengths (Fig. 17A, B; 18), but not to standard length (first bark part: $r = -0.89$, $N = 15$, $p < 0.001$; second bark part: $r = -0.77$, $N = 15$, $p \leq 0.001$; thumps: $r = -0.96$, $N = 15$, $p < 0.001$) (Tab. 3).

Thus, mean sound characteristics were always correlated to relative pectoral spine lengths, except for SPLs of male barks. In contrast, only sound duration of thumps and crackles combined were correlated to standard length (Tab. 3).

Tab. 3. Correlations between mean sound characteristics (sound duration, dominant frequency and sound pressure level) of male and female sound types and morphological variables (standard length, pectoral spine length, relative pectoral spine length). N = 15. B - bark, BP - bark part, C - crackles, T - thumps. Pearson's correlation coefficients are given. Asterisks indicate statistically significant differences: * $p \leq 0.01$, ** $p \leq 0.001$.

Morphological variables	**Sound duration**		**Sound pressure level**		**Dominant frequency**		
Sound types	**B + C**	**T + C**	**B + C**	**T + C**	**BP 1 + C**	**BP 2 + C**	**T + C**
Standard length	0.375	0.795**	- 0.230	0.785**	- 0.369	- 0.333	- 0.449
Pectoral spine length	0.677*	0.842**	- 0.378	0.806**	- 0.885**	- 0.767**	- 0.957**
Relative pectoral spine length	0.667*	0.708*	- 0.368	0.639*	- 0.862**	- 0.741*	- 0.991**

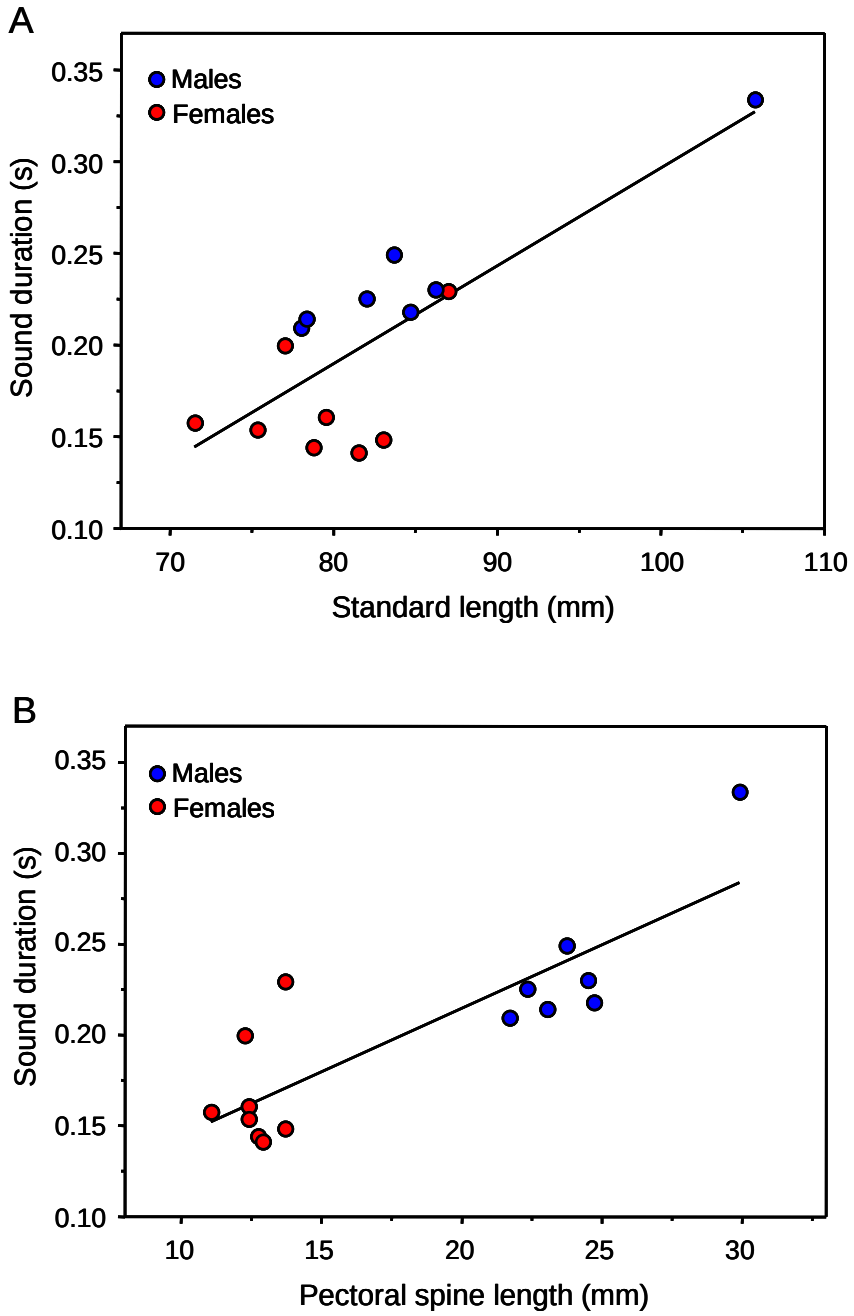

Fig. 15. Correlation between (A) standard length and (B) pectoral spine length and mean sound duration of male thumps and female crackles in *M. thoracata*. Regression equation: (A) Sound duration = standard length * 5.34 + 0.238, r = 0.795, $p < 0.001$; (B) Sound duration = pectoral spine length * 6.99 + 0.075, r = 0.842, $p < 0.001$.

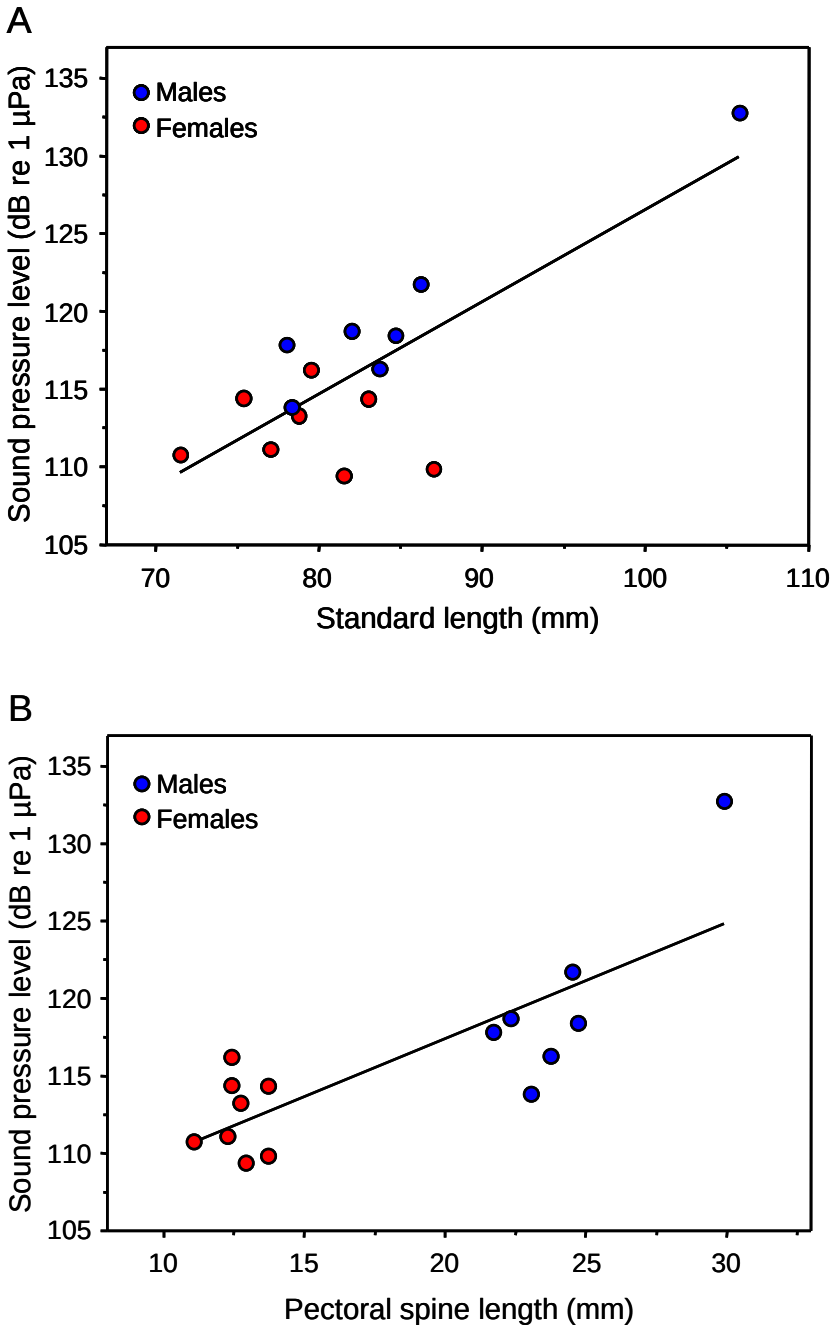

Fig. 16. Correlation between (A) standard length and (B) pectoral spine length and mean sound pressure level of male thumps and females crackles. Regression equation: (A) Sound pressure level = standard length * 0.59 + 67.3, $r = 0.785$, $p \leq 0.001$; (B) Sound pressure level = pectoral spine length * 0.75 + 102.4, $r = 0.806$, $p < 0.001$.

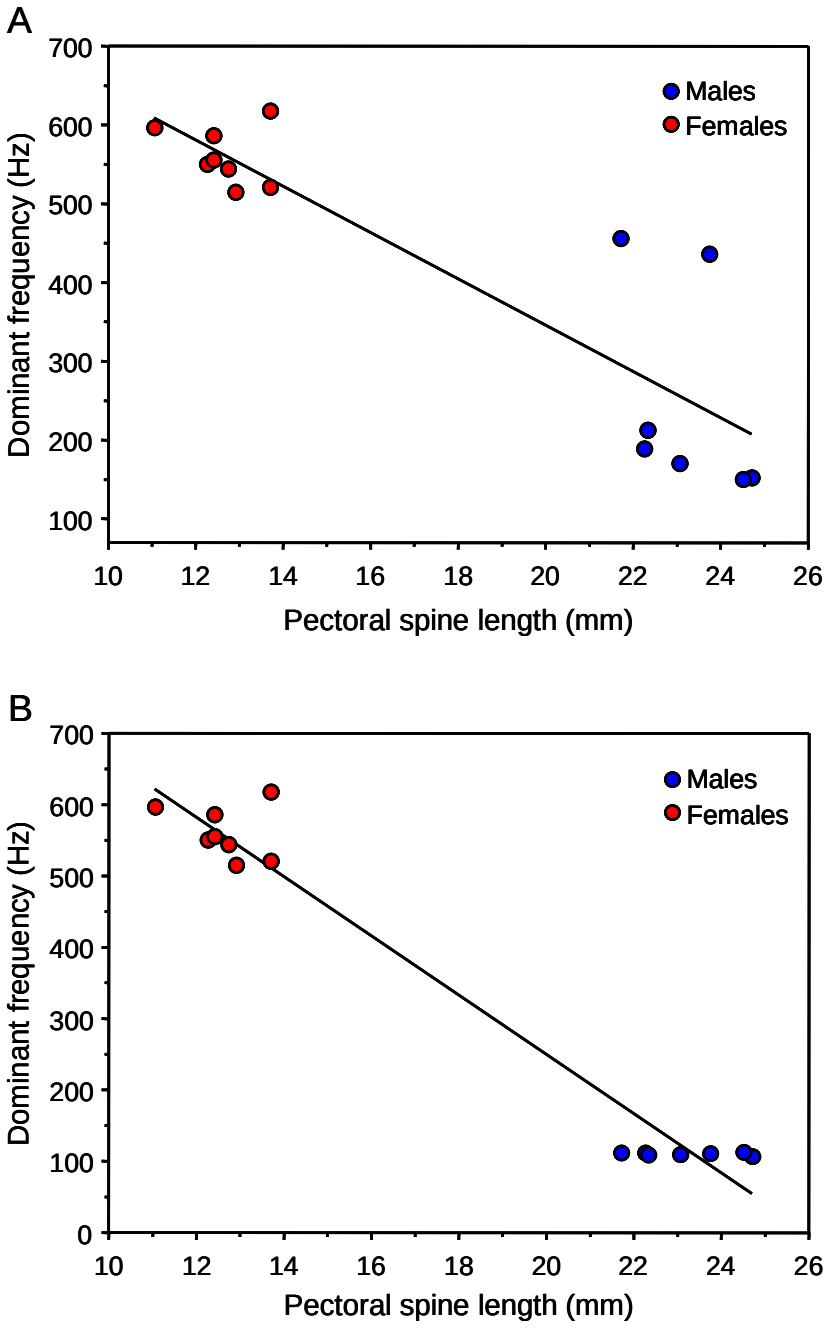

Fig. 17. Correlation between pectoral spine length and mean dominant frequency of (A) the first bark part and female crackles and (B) the second bark part and female crackles. Regression equation: (A) Dominant frequency = pectoral spine length * 29.4 + 933.75, r = - 0.885, $p < 0.001$; (B) Dominant frequency = pectoral spine length * 41.59 + 1081.48, r = - 0.767, $p \leq 0.001$.

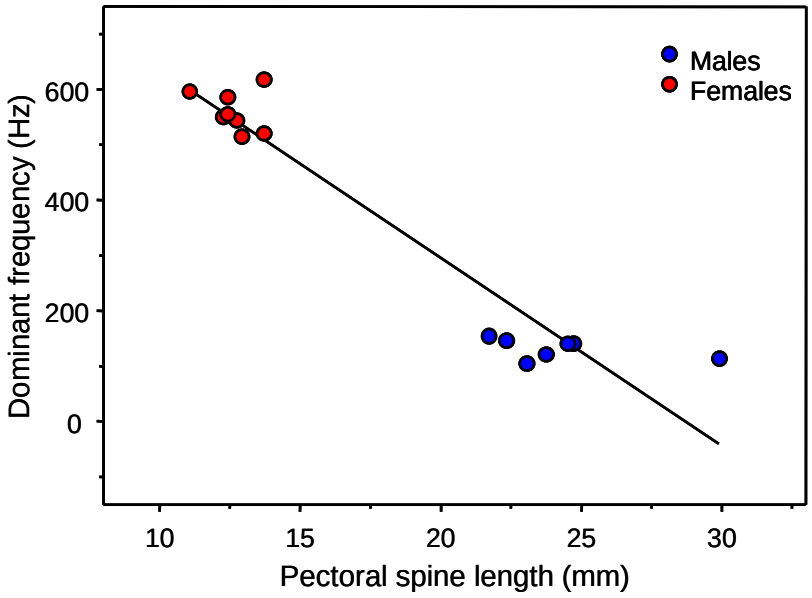

Fig. 18. Correlation between pectoral spine length and mean dominant frequency of male thumps and female crackles. Regression equation: Dominant frequency = pectoral spine length * 33.97 + 975.14, r = - 0.957, $p < 0.001$.

3.4. Auditory sensitivities in males and females

All fish detected tone bursts between 100 Hz and 4 kHz. Hearing curves of both sexes were U-shaped with best auditory sensitivities between 0.2 and 1 kHz (Fig. 19). Hearing abilities decreased rapidly above 1 kHz. Thresholds increased by 41 dB between 1 and 4 kHz in males and females. Hearing thresholds did not differ between sexes (Two-way ANOVA: $F_{8, 89} = 1.2$, n. s.).

3.5. Comparison between hearing thresholds and sound spectra

Both sexes showed best auditory sensitivities in frequency ranges where main energies of sounds were concentrated (Fig. 20). The greatest energy of sounds was concentrated from 180 to 620 Hz in male barks, from 100 to 540 Hz in male thumps and from 470 to 750 Hz in female crackles 120 and 600 Hz.

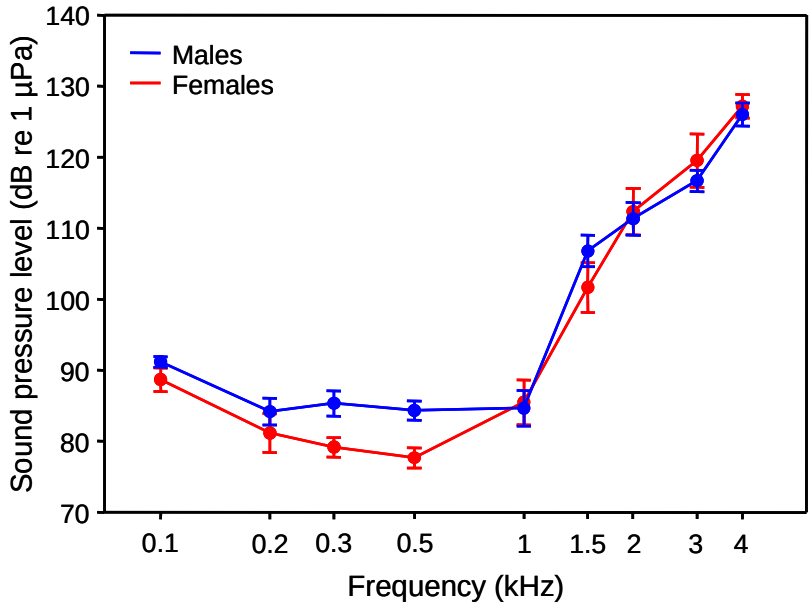

Fig. 19. Mean (± SE) auditory sensitivities of male (N = 6) and female (N = 6) *M. thoracata*.

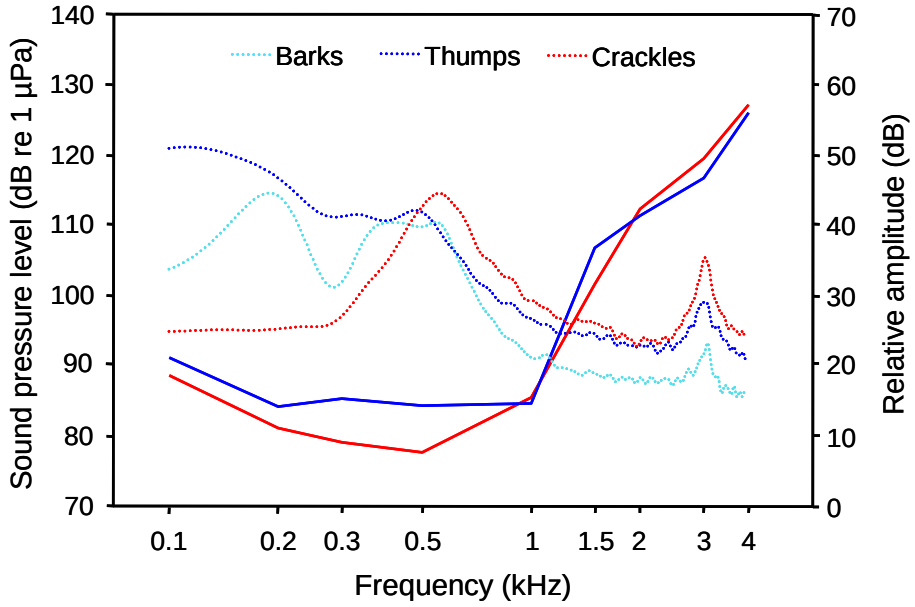

Fig. 20. Mean auditory sensitivities of male and female *M. thoracata* (solid lines) in relation to spectral and intensity characteristics of sounds (dotted lines). Power spectra of sounds were averaged of sounds of all individuals and are shown in relative amplitude values (right Y-axis).

4. Discussion

4.1. Sexual dimorphism and sound producing mechanism

Male *M. thoracata* possess relatively longer pectoral spines than females. This agrees with the general finding that typically males have larger sonic organs than females (Ladich and Fine 2006). This sexual dimorphism was found in pectoral sonic organs in Osphronemidae (genus *Trichopsis*; Kratochvil 1985) and in drumming muscles in toadfish (genus *Opsanus* and *Porichthys*; Fine et al. 1990, Brantley et al. 1993a), cods (genus *Melanogrammus*; Templeman and Hodder 1958), cusk-eels (genus *Ophidion*; Courtenay 1971, Kéver et al. 2012) and drums (genus *Argyrosomus*; Takemura et al. 1978, Ueng et al. 2007). However, in the specious order Siluriformes (approximately 3500 species) only one species is known having dimorphic sonic mechanisms. Males of the callichthyid catfish *C. paleatus* possess relatively longer pectoral fins than females (Pruzsinszky and Ladich 1998), which is in accordance with the current finding in *M. thoracata* and seems to be a family characteristic.

Video analysis revealed that both sexes of *M. thoracata* produced sounds during rapid pectoral fin movements. Therefore, it is assumed that sound production is based on a stridulatory mechanism, well known in numerous catfish families (Fine and Ladich 2003). While it was observed that male barks were produced during abduction of pectoral fins, the movement of pectoral spines during generation of thumps and crackles remains unclear due to faster movements of fins and technical limitation of a standard video recording system. Pruzsinszky and Ladich (1998) mentioned that *C. paleatus* produced sounds by abducting the pectoral fins alternately. Similarly, Heyd and Pfeiffer (2000) reported that in the callichthyid catfish *D. urostriatum* sounds were produced during abduction and it is very likely that all members of the family Callichthyidae generate sounds during abduction of pectoral fins. It is assumed that barks and thumps are generated by one pectoral fin abduction and crackles by several fin abductions depending on the number of elements within a crackle sound.

Interestingly, male barks showed low-frequency harmonic content, indicating the presence of a swimbladder drumming mechanism, similar to many other catfish families (Fine and Ladich 2003, Ladich and Fine 2006). However, dissection revealed that *M. thoracata* possesses tiny and paired bony encapsulated bladders, which lack any drumming muscles, a common characteristic of the family Callichthyidae (Lechner and Ladich 2008). Kaatz et al. (2010) revealed by scanning electron microscopy that members of the subfamily Callichthyinae, such as *Callichthys*, *Dianema*, *Megalechis* and *Hoplosternum*, lack ridges at

the dorsal process of the base of the pectoral spine, but possess convolutions instead. These may partly explain the low-frequency character of *Megalechis* sounds.

4.2. Sexual differences in agonistic behaviour

The current study revealed that agonistic behaviour of male and female *M. thoracata* differed from each other. Male agonistic behaviour mainly consisted of fin displays and jerks, whereas female behaviour was characterized by circling, head nodding, sneaking and striking. Agonistic sounds were produced by males and females in different behavioural contexts. While males uttered thumps during threatening displays and barks mostly during approaching and swimming, females, in contrast, emitted crackles mainly during chasing behaviour. Threatening displays in males consisted of a sequence of visual displays shown by both opponents during which both may produce sounds. In contrast, chasing behaviour in females was only shown in one individual, which vocalized when following or moving toward the other fish.

Acoustic signalling by females during agonistic interactions has been described in several families such as cichlids (Simões et al. 2008), gobiids (Ladich and Kratochvil 1989), gouramis (Ladich 2007), sculpins (Ladich 1989), and toadfish (Brantley and Bass 1994). However, sex-specific differences in agonistic behaviour and vocalizations have not been described in any family. E.g. both sexes of the bicolour damselfish *Stegastes partitus* (formerly *Pomacentrus partitus*) produced intense single-pulsed pops during aggressive interactions (Myrberg 1972). In *C. gobio*, both sexes produced knocks and growls while defending their territories with aggressive calling being mainly size and not sex dependent (Ladich 1989). Large females were as successful in defending territories as males were and produced more sounds than smaller males (Ladich 1990).

Based on the present data, males of *M. thoracata* seem to be more aggressive than females as revealed by the much higher number of attacks (40 in males versus four in females) observed during a similar number of same-sex contests. The vocalizing behaviour of *M. thoracata* differs remarkably from the closely related callichthyine subfamily member *C. paleatus*, in which only males produced trains of sounds and aggressive behaviour was absent during dyadic contests (Pruzsinszky and Ladich 1998). This is primarily due to the different mating system. Male *Megalechis* are territorial and defend nest sites, whereas *Corydoras* does not build nests or show parental care.

While male thumps and female crackles were only emitted at distances within one to two body lengths, male barks have also been emitted at much larger distances and in the

absence of opponents. For this reason, Mayr (1987) called male thumps aggressive sounds and male barks territorial sounds. Mayr's terms have not been used in the current study because they imply unproven functions. Interestingly, the present study showed that barks were only emitted after prior agonistic interactions. Thus, bark production in the absence of intruders might reflect a high level of arousal and less so territorial signalling. Therefore, it is assumed that *M. thoracata* does not produce territorial advertisement signals, similar to toadfish or damselfish, which vocalize without any stimuli from conspecifics (Gray and Winn 1961, Myrberg 1972). Furthermore, our study reveals that both sexes of *M. thoracata* start to defend territories at the age of at least ten months in contrast to the prior observations by Mayr (1987), who claimed that this species exhibit first agonistic behaviours at the age of one and a half years.

4.3. Sex-specific differences in sound characteristics

In this study, three different agonistic sound types (two in males, one in females) could be determined based on physical characteristics of sounds. Sound duration in *M. thoracata* differed between sexes with female crackles (167 ms) being shorter than both male barks (219 ms) and thumps (240 ms). SPLs of thumps (120 dB) were higher than those of barks (111 dB) and crackles (112 dB). Dominant frequency of female crackles (562 Hz) was much higher than of male sounds (132 - 403 Hz). In contrast, Mayr (1987) wrote that aggressive signals (= thumps) were shorter than territorial sounds (= barks). But there exists a lack of information, if male sounds differ from female sounds because sound characteristics have not been compared statistically between sexes. Differences between the current and the prior study by Mayr (1987) may be due to the fact that the present study investigated subadult fish and the former one adult reproductive fish. It can be excluded that our fish were mature because no reproductive behaviour was observed during this study.

Sound production and sound characteristics of male and female fish have seldom been described and much less compared statistically. In the osphronemid *T. vittata* male croaking sounds were louder, but temporal and spectral characteristics did no differ (Ladich 2007). Lagardère et al. (2005) revealed that females of *C. boraborensis* produced longer sound pulses than males. Similarly, Brantley and Bass (1994) reported that duration of agonistic grunts of type II sneaker males in *P. notatus* was shorter than those of females, but this observation was not compared to sounds of territorial type I males. In *O. rochei*, usually females emitted shorter calls that differed dramatically from male sounds (Kéver et al. 2012).

The most common intraspecific variation in fish sound characteristics is found in the dominant frequency (Amorim 2006). Decrease in dominant sound frequencies with increase in body size is a general phenomenon in animals, based largely on resonance (Ladich and Myrberg 2006). In the present study, differences in morphological measures such as body size and pectoral fin length explain differences in sound characteristics to some degree. Duration and intensity of sounds increased with pectoral spine length, whereas dominant frequency of sounds decreased. Body size was not correlated with sound features (except for the correlation between male thumps and female crackles versus sound duration and sound level), indicating that the size of the sound generating structures, namely the pectoral spine, determines sound characteristics primarily. This is in accordance with the findings in *C. paleatus*, in which sound duration of distress calls was positively correlated with the relative pectoral spine length (Pruzsinszky and Ladich, 1998). Similarly, Ladich (2007) argued that differences in levels of agonistic sounds of *T. vittata* might be due to the larger pectoral muscles in males. Parmentier and Vandewalle (2005) supposed that differences in duration of the pearlfish *C. boraborensis* sounds might be due to the fact that females lack a distinct swimbladder bulb (with yet unknown functional significance) at their posterior end which seems to influence sound characteristics. Furthermore, mature female pearlfish are longer than males (Parmentier and Vandewalle 2005), and differences in sound characteristics may be due to body size differences as well. Kéver et al. (2012) demonstrated in the cusk-eel *O. rochei* a tight relationship between morphology of sonic apparatus and sound characteristics with males showing more morphological modifications that may reflect a greater specialization for sound production.

4.4. Sex-specific differences in hearing abilities in fish

Hearing sensitivities in male and female of *M. thoracata* do not differ from each other. Sex-specific differences in hearing have rarely been studied in fish (Fay 1988, Ladich and Fay 2013). Similarly to the present finding, investigations on *C. paleatus* (Ladich 1999), *A. abdominalis* (Maruska et al. 2007) and the Atlantic Molly *Poecilia mexicana* (Schulz-Mirbach et al. 2010) did not reveal any differences between sexes. Only Maruska et al. (2012) described differences in hearing abilities depending on dominance and reproductive status of males and females of the cichlid *A. burtoni*, but did not compare sexes directly. Subordinate males had lower thresholds than dominant males between 600 and 800 Hz, whereas gravid females had about 5 to 15 dB lower thresholds at low frequencies between 100 to 600 Hz than mouth-brooding females (Maruska et al. 2012). The authors assumed that

higher levels of sex steroids could explain these differences. The lack of a difference in *Megalechis* corresponds to most of the previous studies. However, it cannot be excluded that adult males and females differ in their auditory sensitivities.

AEP audiograms of both sexes of *M. thoracat*a are very similar to hearing curves of other members of the family Callichthyidae investigated in the same lab (Fig. 21). All show best sensitivity between 0.3 and 1 kHz and a step decrease in sensitivity above 1 kHz (Ladich 1999, Lechner and Ladich 2008). This step decrease is certainly due to the tiny and encapsulated swimbladders in callichthyids. Lechner and Ladich (2008) showed that smaller swimbladders and lower number of Weberian ossicles results in a decrease in sensitivity at higher thresholds.

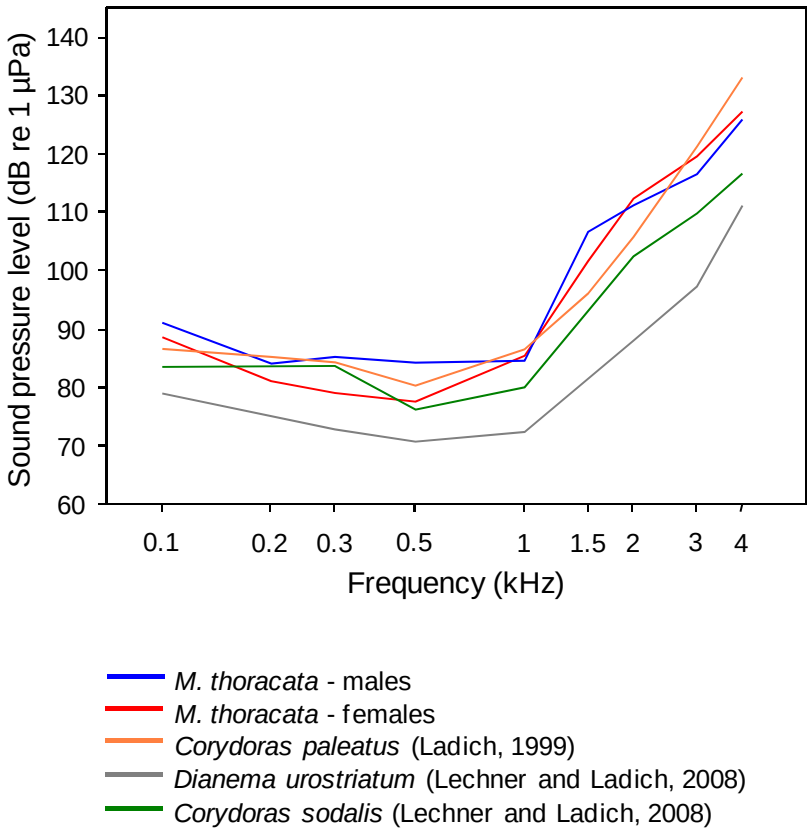

Fig. 21. Mean AEP- audiograms of all representatives of the family Callichthyidae investigated in the recent and in the prior studies (Ladich 1999, Lechner and Ladich 2008).

4.5. Acoustic communication

In *M. thoracata* main energies of sounds were found below 1 kHz at the most sensitive frequencies. Both sexes show a similar match between spectral content of sounds and best hearing ability. Based on the results of the present study, males and females of *Megalechis* are well adapted for acoustic communication. The relatively low level of sounds (mean SPLs: 111 - 120 dB) indicates that fish communicate at close distances to each other. Studies in several sound producing taxa revealed a fairly good match between main energies of sounds and the best hearing range (Cohen and Winn 1967, Myrberg and Spires 1980, Fine 1981, Stabentheiner 1988, Ladich and Yan 1998, Ladich 1999, Maruska et al. 2009, Lechner et al. 2010). Lechner et al. (2010) found even a match between spectral content of sounds and best hearing sensitivity in six different size groups in the mochokid catfish *Synodontis schoutedeni*. Ladich (1999) argued that these correlations suggest that sound-producing mechanisms did evolve in correlation with hearing abilities in fishes. Similar to the present study, Maruska et al. (2007) assumed that the damselfish *A. abdominalis* communicate at close distance which might be an explanation for the low sound intensity (mean SPLs: 105 - 130 dB). In contrast to the current data, Ladich (1999) revealed a mismatch in the closely related *C. paleatus*, in which the hearing ability decreased rapidly above 800 Hz, and the main energies of sounds were concentrated between 1 and 2 kHz.

In summary, this is the first investigation of sex-specific differences in agonistic behaviour, sound production and sound characteristics using same-sex agonistic contests. Data reveal clear differences in agonistic behaviour, which have not been shown in any fish species before. The study furthermore shows for the first time that differences in sound characteristics between sexes are mainly due to the dimorphism in the pectoral sonic organs.

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References

Amorim, M. C. P. (2006). Diversity of sound production in fish. In: F. Ladich, S. P. Collin, P. Moller and B. G. Kapoor (Eds.), Communication in Fishes. Enfield, NH: Science Publishers, pp. 71-105.

Bradbury, J. W. and Vehrencamp, S. L. (1998). Principles of Animal Communication. Sunderland, Massachusetts: Sinauer.

Bradbury, J. W. and Vehrencamp, S. L. (2011). Principles of Animal Communication, 2nd edition. Sunderland, Massachusetts: Sinauer Associates.

Brantley, R. K. and Bass, A. H. (1994). Alternative male spawning tactics and acoustic signals in the plainfin midshipman fish *Porichthys notatus* Girard (Teleostei, Batrachoididae). Ethology 96, 213-232.

Brantley, R. K., Tseng, J. and Bass, A. H. (1993a). The ontogeny of inter- and intrasexual vocal muscle dimorphisms in a sound-producing fish. Brain, Behavior and Evolution 42, 336-349.

Burgess, W. E. (1989). An Atlas of Freshwater and Marine Catfishes: A Preliminary Survey of the Siluriformes. T.F.H. Publications, Neptune City, New Jersey.

Cohen, M. J. and Winn, H. F. (1967). Electrophysiological observations on hearing and sound production in the fish *Porichthys notatus*. Journal of Experimental Zoology 165, 355-370.

Connaughton, M. A., Fine, M. L. and Taylor, M. H. (2002). Weakfish sonic muscle: influence of size, temperature and season. The Journal of Experimental Biology 205, 2183-2188.

Courtenay, W. R. J. (1971). Sexual dimorphism of the sound producing mechanism of the striped cusk-eel, *Rissola marginata* (Pisces: Ophidiidae). Copeia 1971 (2): 259-268.

Fay, R. R. (1988). Hearing in Vertebrates: A Psychophysics Databook. Winnetka, Ill.: Hill-Fay Associates.

Fine, M. L. (1981). Mismatch between sound production and hearing in the oyster toadfish. In: W. N. Tavolga, A. N. Popper and R. R. Fay (Eds.), Hearing and Sound Communication in Fishes. Springer, New York, pp. 257-263.

Fine, M. L., Burns, N. M. and Harris, T. M. (1990). Ontogeny and sexual dimorphism of the sonic muscle in the oyster toadfish. Canadian Journal of Zoology 68, 1374-1381.

Fine, M. L., Friel, J. P., McElroy D., King, C. B., Loesser, K. E. and Newton, S. (1997). Pectoral spine locking and sound production in the channel catfish *Ictalurus punctatus*. Copeia 1997, 777-790.

Fine, M. L. and Ladich, F. (2003). Sound production, spine locking and related adaptations. In: Arratia, G., Kapoor, B. G., Chardon, M. and Diogo, R. (Eds.), Catfishes. Enfield, NH: Science Publishers, pp. 248-290.

Gee, J. H. and Graham, J. B. (1978). Respiratory and hydrostatic functions of the intestine of the catfishes *Hoplosternum thoracatum* and *Brochis splendens* (Callichthyidae). The Journal of Experimental Biology 74, 1-16.

Gray, G. A. and Winn H. E. (1961). Reproductive ecology and sound production of the toadfish, O*psanus tau*. Ecology 42(2): 274-282.

Heyd, A. and Pfeiffer, W. (2000). Über die Lauterzeugung der Welse (Siluroidei, Ostariophysi, Teleostei) und ihren Zusammenhang mit der Phylogenie und der Schreckreaktion. Revue Suisse de Zoologie 107, 165-211.

Hill, G. L., Fine, M. L. and Musick, J. A. (1987). Ontogeny of the sexually dimorphic sonic muscle in three sciaenid species. Copeia, 1987, 709-713.

Kaatz, I. M., Stewart, D. J., Rice, A. N. and Lobel, P. S. (2010). Differences in pectoral fin spine morphology between vocal and silent clades of catfishes (Order Siluriformes): Ecomorphological implications. Current Zoology 56, pp. 73-89.

Kenyon, T. N., Ladich, F., and Yan, H. Y. (1998). A comparative study of hearing ability in fishes: the auditory brainstem response approach. Journal of Comparative Physiology A 182, 307-318.

Kéver, L., Boyle, K. S., Dragičević, B., Dulčić, J., Casadevall, M. and Parmentier, E. (2012). Sexual dimorphism of sonic apparatus and extreme intersexual variation of sounds in *Ophidion rochei* (Ophidiidae): first evidence of a tight relationship between morphology and sound characteristics in Ophidiidae. Frontiers in Zoology 9, 34.

Kratochvil, H. (1985). Beiträge zur Lautbiologie der Anabantoidei - Bau, Funktion und Entwicklung von lauterzeugenden Systemen. Zoologische Jahrbücher (Physiologie) 89, 203-255.

Ladich, F. (1989). Sound production by the river bullhead *Cottus gobio* L. (Cottidae, Teleostei). Journal of Fish Biology 35, 531-538.

Ladich, F. (1990). Vocalization during agonistic behaviour in *Cottus gobio* (Cottidae): an acoustic threat display. Ethology 84, 193-201.

Ladich, F. (1997a). Agonistic behaviour and significance of sounds in vocalizing fish. Marine and Freshwater Behaviour and Physiology 29, 87-108.

Ladich, F. (1999). Did auditory sensitivity and vocalization evolve independently in otophysan fishes? Brain, Behavior and Evolution 53, 288-304.

Ladich, F. (2007). Females whisper briefly during sex: context- and sex-specific differences in sounds made by croaking gouramis. Animal behaviour 73, 379-387.

Ladich, F. (2013). Diversity in hearing in fishes: Ecoacoustical, communicative, and developmental constraints. In: C. Köppl et al. (Eds). Insights from Comparative Hearing Research. New York: Springer Science+Business Media. DOI 10.1007/2506_2013_26.

Ladich, F. and Bass, A. H. (2003). Audition. In: G. Arratia, B. G. Kapoor, M. Chardon and R. Diogo (Eds.), Catfishes, Volume 2. Enfield, NH: Science Publishers, pp. 701-730.

Ladich, F. and Fay (2013). Auditory evoked potential audiometry in fishes. Reviews in Fish Biology and Fisheries 23, 317-364.

Ladich, F., and Fine, M. L. (2006). Sound-generating mechanisms in fishes: a unique diversity in vertebrates. In: F. Ladich, S. P. Collin, P. Moller and B. G. Kapoor (Eds.), Communication in Fishes. Enfield, NH: Science Publishers, pp. 3-43.

Ladich, F., and Kratochvil, H. (1989). Sound production by the marmoreal goby, *Proterorhinus marmoratus* (Pallas) (Gobiidae, Teleostei) Zoologisches Jahrbuch, Physiologie 93, 501-504.

Ladich, F. and Myrberg, A. A. (2006). Agonistic behavior and acoustic communication. In: F. Ladich, S. P., Collin, P. Moller and B. G. Kapoor (Eds.), Communication in Fishes. Enfield, NH: Science Publishers, pp. 121-148.

Ladich, F. and Popper, A. N. (2004). Parallel evolution in fish hearing organs. In: G. Manley, R. R. Fay, A. N. Popper (Eds.), Evolution of the Vertebrate Auditory System. New York: Springer. pp. 95-127.

Ladich, F. and Yan, H. Y. (1998). Correlation between auditory sensitivity and vocalization in anabantoid fishes. Journal of Comparative Physiology A 182, 737-746.

Ladich, F., Brittinger, W. and Kratochvil, H. (1992a). Significance of agonistic vocalizations in the croaking gourami (*Trichopsis vittatus*, Teleostei). Ethology 90, 307-314.

Lagardère, J. P., Millot, S. and Parmentier, E. (2005). Aspects of sound communication in the pearlfish *Carapus boraborensis* and *Carapus homei* (Carapidae). Journal of Experimental Zoology 303 A, 1066-1074.

Lechner, W., and Ladich, F. (2008). Size matters: diversity in swimbladders and Weberian ossicles affects hearing in catfishes. The Journal of Experimental Biology 211, 1681-1689.

Lechner, W. and Ladich, F. (2010). How do albino fish hear? Journal of Zoology 283, 186-192.

Lechner, W., Wysocki, E. L. and Ladich, F. (2010). Ontogenetic development of auditory sensitivity and sound production in the squeaker catfish *Synodontis schoutedeni*. BioMed Central Biology 8, 10.

Lechner, W., Heiss, E., Schwaha, T., Glösmann, M. and Ladich, F. (2011). Ontogenetic development of Weberian ossicles and hearing abilities in the African bullhead catfish. PLoS ONE, 6, e18511.

Lobel, P. S. and Mann, D. A. (1995). Spawning sounds of the domino damselfish, *Dascyllus albisella* (Pomacentridae), and the relationship to male size. Bioacoustics 6, 187-198.

Luczkovich, J. J., Sprague, M. W., and Krahforst, C. S. (2011). Acoustic behavior. Encyclopedia of fish physiology: from genome to environment. Vol. 1, 311-320.

Maruska, K. P., Boyle, K. S., Dewan, L. R., and Tricas, T. C. (2007). Sound production and spectral hearing sensitivity in the Hawaiian sergeant damselfish, *Abudefduf abdominalis*. Journal of Experimental Biology 210, 3990-4004.

Maruska, K. P., Ung, U. S. and Fernald, R. D. (2012). The African cichlid fish *Astatotilapia burtoni* uses acoustic communication for reproduction: sound production, hearing, and behavioural significance. PLoS ONE, 7, e37612.

Mayr, M. (1987). Verhaltensbeobachtungen an *Hoplosternum thoracatum*, Cuvier & Valenciennes (1840), mit besonderer Berücksichtigung des Lautverhaltens. Ph.D. thesis, University of Vienna, Vienna. 103 pp.

Mol, J. H. A. (1993). Structure and function of floating bubble nests of three armoured catfishes (Callichthyidae) in relation to the aquatic environment. In: P. E. Ouboter (Ed.), Freshwater Ecosystems of Suriname. Netherlands, Kluwer, pp. 167-197.

Myrberg, A. A. (1972). Ethology of the bicolor damselfish *Eupomacentrus partitus* (Pisces: Pomacentridae). A comparative analysis of laboratory and field behaviour. Animal Behaviour Monographs 5, 199-283.

Myrberg, A. A. (1981). Sound communication and interception in fishes. In: W. N. Tavolga, A. N. Popper and R. R. Fay (Eds.), Hearing and Sound Communication in Fishes. Springer, New York, pp. 395-425.

Myrberg, A. A. and Lugli, M. (2006). Reproductive behaviour and acoustical interactions. In: F. Ladich, S. P. Collin, P. Moller, B. G. Kapoor (Eds.), Communication in Fishes. Enfield, NH: Science Publishers, pp. 149-176.

Myrberg, A. A. and Riggio, R. J. (1985). Acoustically mediated individual recognition by a coral reef fish (*Pomacentrus partitus*). Animal Behaviour 33, 411-416.

Myrberg, A., Kramer, E. and Heinecke, P. (1965). Sound production by cichlid fishes. Science 149, 555-558.

Myrberg, A. A., Mohler, M. & Catala, J. (1986). Sound production by males of a coral reef fish (*Pomacentrus partitus*): its significance to females. Animal Behaviour 34, 913-923.

Myrberg, A. A. and Spires, J. Y. (1980). Hearing in damselfishes: an analysis of signal detection among closely related species. Journal of Comparative Physiology 140, 135-144.

Parmentier, E. and Vandewalle, P. (2005). Further insight on carapid-holothuroid relationships. Marine Biology 146, 455-465.

Pruzsinszky, I. and Ladich, F. (1998). Sound production and reproductive behavior of the armoured catfish *Corydoras paleatus* (Callichthyidae). Environmental Biology of Fishes 53, 183-191.

Raffinger, E. and Ladich, F. (2009). Acoustic threat displays and agonistic behavior in the red-finned loach *Yasuhikotakia modesta*. Journal of Ethology 27, 239-247.

Rigley, L. and Muir, J. (1979). The role of sound production by the brown bullhead *Ictalurus nebulosus*. Proceedings of the Pennsylvania Academy of Science 53, 132-134.

Rowe, S. and Hutchings, J. A. (2004). The function of sound production by Atlantic cod as inferred from patterns of variation in drumming muscle mass. Canadian Journal of Zoology 82, 1391-1398.

Schulz-Mirbach, T., Ladich, F., Riesch, R. and Plath, M. (2010). Otolith morphology and hearing abilities in cave- and surface-dwelling ecotypes of the Atlantic molly, *Poecilia mexicana* (Teleostei: Poeciliidae). Hearing Research 267, 137-148.

Schwarz, A. (1980). Sound production and associated behavior in a cichlid fish, *Cichlasoma centrarchus*. II Breeding pairs. Environmental Biology of Fishes 5, 335-342.

Simões, J. M., Duarte, I. G., Fonseca, P. J., Turner, G. F. and Amorim, M. C. (2008). Courtship and agonistic sounds by the cichlid fish *Pseudotropheus zebra*. Journal of the Acoustical Society of America 124, pp. 1332-1338.

Stabentheiner, A. (1988). Correlations between hearing and sound production in piranhas. Journal of Comparative Physiology A 162, 67-76.

Takemura, A., Takita, T. and Mizue, K. (1978). Underwater calls on the Japanese marine drum fishes (Sciaenidae). Bulletin of the Japanese Society for the Science of Fish 44, 121-125.

Templeman, W. and Hodder, V. M. (1958). Variation with fish length, sex, stage of sexual maturity, and season in the appearance and volume of the drumming muscle of the swim-bladder in the haddock, *Melanogrammus aeglefinus* (L.). Journal of Fisheries Research Board of Canada 15, 355-390.

Ueng, J.-P., Huang, B.-Q. and Mok, H.-K. (2007). Sexual differences in the spawning sounds of the japanese croaker, *Argyrosomus japonicus* (Sciaenidae). Zoological studies 46 (1), 103-110.

Wysocki, L. E. and Ladich, F. (2005a). Effects of noise exposure on click detection and the temporal resolution ability of the goldfish auditory system. Hearing Research 201, 27-36.

Wysocki, L. E. and Ladich, F. (2005b).Hearing in fishes under noise conditions. Journal of Association for Research in Otolaryngology 6, 28-36.

Zusammenfassung

Daten zu geschlechtsspezifischen Unterschieden hinsichtlich Lautbildung, Lautverhalten und Hörvermögen bei Fischen sind spärlich. Vertreter zahlreicher Welsfamilien sind dafür bekannt während agonistischer Auseinandersetzungen Laute zu produzieren. Das Ziel der vorliegenden Arbeit war es das agonistische Verhalten, die Lautbildung und das Hörvermögen bei Männchen und Weibchen eines Schwielenwelses zu untersuchen. Dazu wurden ein adultes Männchen, sieben subadulte Männchen und neun subadulte Weibchen des Gemalten Schwielenwelses *Megalechis thoracata* untersucht. Das im Zuge von Männchen-Männchen und Weibchen-Weibchen-Konfrontationen gezeigte Aggressionsverhalten und die dabei produzierten Laute wurden auf Video aufgenommen, Lautmerkmale analysiert und das Hörvermögen mittels Ableitung von akustisch evozierten Potentialen (AEPs) gemessen. Der Brustflossenstachel der Männchen war durchschnittlich 1,7-fach länger als bei Weibchen. Visuelle und akustische Drohanzeigen unterschieden sich zwischen den Geschlechtern. Männchen produzierten niederfrequente ‚Barks' aus weiterer Entfernung und ‚Thumps' aus geringerer Entfernung, wohingegen Weibchen breitbandige, gepulste ‚Crackles' in unmittelbarer Nähe zum Artgenossen äußerten. Aggressionslaute der Weibchen waren signifikant kürzer als die der Männchen (167 ms versus 219 bis 240 ms) und wiesen eine merklich höhere dominante Frequenz auf (562 Hz versus 132 bis 403 Hz). Die Lautlänge und -stärkepegel nahmen mit zunehmender Körper- und Brustflossenstachellänge zu, während die Hauptfrequenz mit zunehmender Stachellänge abnahm. Beide Geschlechter zeigten ähnliche U-förmige Hörkurven mit der niedrigsten Hörschwelle zwischen 0,2 und 1 kHz und einer Abnahme der Hörempfindlichkeit über 1 kHz. Die Hauptenergien der Laute lagen im Bereich der höchsten Frequenzempfindlichkeit. Die aktuellen Daten veranschaulichen, dass beide Geschlechter in *M. thoracata* Aggressionslaute produzieren, sich jedoch in den Verhaltenskontexten und in den Lautmerkmalen voneinander unterscheiden. Männchen und Weibchen zeigen keinen Unterschied im Hörvermögen, aber es bedarf weiterer Untersuchungen, ob dies ein allgemeines Muster bei Fischen darstellt. Diese Studie beschreibt erstmals geschlechtsspezifische Unterschiede im Aggressionsverhalten einer Fischart.

Schlagwörter: Callichthyidae, geschlechtsspezifische Unterschiede, agonistisches Verhalten, akustische Signale, Lauteigenschaften, Auditorisch Evozierte Potentiale (AEP), Hören

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Appendix

TABLE I. Morphometric data of males (M10 - M17) and females (M1 - M9). BM - body mass, SL - standard length, TL - total length, PSL - pectoral spine length, rPSL - relative pectoral spine length.

Fish	BM (g)	SL (mm)	TL (mm)	PSL (mm)	rPSL
M1	13.5	77.0	90.5	12.3	0.200
M2	13.3	78.8	91.5	12.7	0.139
M3	14.4	83.0	100.0	13.7	0.137
M4	13.5	79.5	93.5	12.4	0.133
M5	9.8	71.5	83.5	11.1	0.132
M6	14.6	81.5	96.0	12.9	0.134
M7	10.0	71.3	84.7	11.4	0.135
M8	11.0	75.3	88.7	12.4	0.140
M9	17.1	87.0	101.7	13.7	0.135
M10	12.2	78.0	91.0	21.7	0.238
M11	16.2	84.7	100.3	24.7	0.246
M12	14.4	83.7	97.0	23.7	0.245
M13	19.1	86.2	104.0	24.5	0.236
M14	13.2	78.3	92.7	23.1	0.249
M15	14.0	79.0	94.5	22.3	0.235
M16	14.7	82.0	97.0	22.3	0.230
M17	32.9	105.8	126.0	29.9	0.237

TABLE II. Mean sound characteristics of males (M10 - M17) and females (M1 - M9).

Fish	Sound type	Sound duration (ms)	Dominant frequency (Hz)		Sound pressure level (dB)
			Bark part 1	Bark part 2	
M1	crackle	200	551.3		111.1
M2		144	545.0		113.3
M3		149	618.7		114.4
M4		161	587.1		116.2
M5		158	597.6		110.8
M6		142	515.7		109.4
M8		154	556.2		114.4
M9		230	521.3		109.9
M10	bark	209	456.8	557.9	112.3
M11		192	153.1	350.8	107.0
M12		243	436.9	486.0	111.3
M13		250	150.5	327.8	113.2
M14		264	170.8	338.9	109.8
M15		206	189.8	266.2	112.4
M16		169	213.0	495.0	109.2
M10	thump	210	155.2		117.9
M11		218	141.5		118.5
M12		249	121.7		116.3
M13		230	141.1		121.8
M14		214	105.8		113.8
M16		226	147.0		118.7
M17		334	114.9		132.8

TABLE III. Hearing thresholds of males (M10 - M16) and females (M1 - M9). n.m. - not measured.

Fish	Frequency (kHz)								
	0.1	**0.2**	**0.3**	**0.5**	**1**	**1.5**	**2**	**3**	**4**
M1	85	85	77	74	84	94	114	113	123
M3	92	80	79	76	90	105	112	111	126
M4	85	74	76	75	72	90	100	116	122
M6	92	90	81	82	88	103	111	115	131
M8	93	73	77	77	95	104	112	129	130
M9	85	85	85	82	84	114	125	133	131
M10	92	86	88	85	87	100	108	119	129
M11	92	85	89	86	85	104	116	115	120
M12	88	82	85	89	87	111	115	118	128
M13	92	87	83	81	85	107	111	119	128
M14	90	76	78	80	73	n.m.	102	110	122
M16	93	89	89	85	91	112	116	119	129