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„Sex-specific differences in sonic organs, agonistic behaviour and sound production in the Pygmy gourami (Teleostei)"

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D a n k e !

Contents

Abstract

Background: Sound production in fish was primarily described in males, because they have more developed sound generating mechanisms and vocalize during nest defence and courtship. But females in vocal species rarely lack sonic mechanisms and regularly produce sounds in agonistic contexts. Acoustic signalling is well studied in females of two out of three species of croaking gouramis (genus *Trichopsis*). The present study investigates sex-specific differences in sonic organs, vocalizing behaviour and sounds emitted in the third species, the pygmy gourami *T. pumila*, because based on our current knowledge, it is unclear if females are able to vocalize.

Methodology/principal findings: Croaking gouramis pluck two enhanced (sonic) pectoral fin tendons (ETs) during rapid fin beating, resulting in a series of double-pulsed bursts. The diameter of the first (ET1) and second (ET2) sonic tendon was measured in both sexes. In addition, the following behavioural and acoustic variables were determined: Duration of dyadic contests and of lateral displays, the number of sounds emitted and of buttings, the total number of bursts and the percentage of short bursts within a sound, the burst period, the dominant frequency and the sound pressure level (SPL). Twenty out of 21 males and ten out of 13 females possessed two ETs, but female ETs were less developed. The diameter of male ETs was twice as large as in females, and ET1 was 1.5 times larger than ET2 in both sexes. Sexes did not differ in behaviour (duration of contests and lateral displays, number of buttings and vocalizations), but in all sound characteristics. Male sounds consisted of twice as many bursts, a higher percentage of double-pulsed bursts (80 % vs. 7 % in females) and of a higher burst period. Additionally, male sounds had a lower dominant frequency (2090 Hz vs. 2280 Hz in females) and a higher SPL (114 dB vs. 99 dB in females).

Conclusions/Significance: In contrast to previous reports, the majority of female pygmy gouramis possessed sonic organs and were able to vocalize during dyadic contests. The sexual dimorphism in ETs is clearly reflected by sex-specific differences in sound characteristics, but not in agonistic behaviour.

Keywords: fish, *Trichopsis*, sexual dimorphism, sonic organs, agonistic behaviour, sound characteristics

1. Introduction

Since Aristotle (350 B.C.), it has been known that many fish are able to vocalize. Currently there are more than 32,000 extant species (Nelson et al. 2016), many of whom are assumed to be vocal. Unsurprisingly, there exists a vast knowledge on sound production in fish during different behavioural contexts, e.g. during agonistic behaviour or during courtship and spawning (Fine et al. 1977, Myrberg 1981, Ladich 1997a, Ladich and Myrberg 2006, Myrberg and Lugli 2006) as well as on the sound generating mechanisms (sonic organs) (Schneider 1961, Tavolga 1971, Fine et al. 1977, Schaller and Kratochvil 1981, Ladich and Fine 2006, Ladich and Bass 2011, Fine and Parmentier 2015). Contrary to the large number of studies on sound production in fish in general, there are only few studies describing sound production in females, although sonic organs are rarely absent, indicating that the latter are vocal as well (Ladich 2015a).

Among vertebrates, fish evolved a unique diversity in sound generating mechanisms (Ladich and Fine 2006, Fine and Parmentier 2015). Sonic organs are generally larger in males than in females (Ladich 2015a). This sexual dimorphism is found in swim bladder as well as pectoral mechanisms in several families such as toadfishes (Batrachoididae), cods (Gadidae), cusk-eels (Ophidiidae), croakers (Sciaenidae), callichthyid armoured catfishes (Callichthyidae) and labyrinth fishes (Osphronemidae). In several representatives of these families, sonic muscles grow larger in males than in females (e.g. oyster toadfish *Opsanus tau* - Fine et al. 1990 and Lusitanian toadfish *Halobatrachus didactylus* - Modesto and Canário 2003; haddock *Melanogrammus aeglefinus* - Templeman and Hodder 1958, Casaretto et al. 2016 and Atlantic cod *Gadus morhua* - Rowe and Hutchings 2004, 2006; some species of the cusk-eel subfamily Neobythitinae - Ali et al. 2016, Fine et al. 2018). In addition to males having larger and heavier swim bladder and sonic muscles, male cusk-eels *Ophidion rochei* have a mineralized structure (rocker bone) on the swim bladder, which is absent in females (Kéver et al. 2012). Amongst sciaenids, drumming muscles are either smaller or even absent in females (Fish and Mowbray 1970, Hill et al. 1987, Connaughton et al. 2000, Ueng et al. 2007). In callichthyid armoured catfishes, males possess relatively larger pectoral spines than females, e.g. peppered corydoras *Corydoras paleatus* (Pruzsinszky and Ladich 1998) or callichthyid armoured catfish *Megalechis thoracata* (Hadjiaghai and Ladich 2015).

Within the labyrinth fishes (Osphronemidae), representatives of the genus *Trichopsis* have a unique sound generating mechanism consisting of two enhanced pectoral fin tendons and an enlarged adductor muscle (Kratochvil 1978, 1980). Besides interspecific differences in

the sound producing apparatus between the croaking gourami *Trichopsis vittata* and the pygmy gourami *Trichopsis pumila*, sonic organs are always larger in males (Kratochvil 1985).

Fish typically vocalize during agonistic and reproductive interactions when courting females (Myrberg 1981, Ladich 1997a, Ladich and Myrberg 2006). Males frequently defend their territories and nest sites aggressively, and thus are typically more vocal than females. Nevertheless, investigations in several species revealed that both sexes vocalize during agonistic interactions. In representatives of cichlids (e.g. jewelfish *Hemichromis bimaculatus* - Myrberg et al. 1965 and flier cichlid *Archocentrus* (formerly *Cichlasoma*) *centrachus* - Schwarz 1980), sculpins (e.g. bullhead *Cottus gobio* - Ladich 1989, 1990) and gadids (e.g. *G. morhua* and *M. aeglefinus* - Hawkins and Rasmussen 1978), both sexes are found to vocalize when defending their territories, or after penetrating a holothurian host in which another cusk-eel was already situated (e.g. pinhead pearlfish *Encheliophis* (formerly *Carapus*) *boraborensis* - Lagardère et al. 2005).

Yet, only few studies compared sounds emitted by both sexes in the same behavioural context. They found only small sex-specific differences in sound characteristics of agonistic sounds. Male sounds might differ in temporal properties from female sounds, the latter being either longer (e.g. *E. boraborensis* - Lagardère et al. 2005; Japanese meagre *Argyrosomus japonicus* - Ueng et al. 2007; skunk clownfish *Amphiprion akallopisos* - Colleye et al. 2009), or shorter (e.g. zebra mbuna *Maylandia* (formerly *Pseudotropheus*) *zebra* - Simões et al. 2008), or they might utter different types of sounds. Male *M. thoracata* produced barks and thumps whereas females produced crackles, which had a different complex structure and frequency content (Hadjiaghai and Ladich 2015). Other studies, however, did not find any sex-specific differences in sound characteristics during distress situations, i.e. when hand-held (e.g. black drum *Pogonias cromis* - Tellechea et al. 2011; longsnout seahorse *Hippocampus reidi* - Oliveira et al. 2014; toadfish *O. tau* - Fine and Waybright 2015). One exception is the meagre *Argyrosomus regius*, in which male disturbance calls differed in spectral as well as temporal properties from females' (Pereira et al. 2020).

Within the osphronemid genus *Trichopsis*, all three species (*T. vittata*, the threestripe gourami *T. schalleri* and *T. pumila*) vocalize during agonistic interactions (Marshall 1966, Ladich et al. 1992a, 1992b, Bischof 1996, Ladich 1998, Ladich 2007, Ladich and Maiditsch 2018, Ladich and Schleinzer 2020). Croaking sounds always consisted of a series of mostly double-pulsed bursts, but differed between species (Ladich et al. 1992a). Sex-specific differences in agonistic sounds were described in *T. vittata* (Ladich 2007) and in *T. schalleri* (Ladich and Schleinzer 2020). Data on sound production in female pygmy gourami *T. pumila*

are contradictory. Marshall (1966) claimed that both males and females produce agonistic sounds whereas Kratochvil (1980) assumed that females are probably unable to vocalize due to their small sonic organs. Schleinzer (1992) mentioned that only 4 out of 26 *T. pumila* females vocalized.

The aim of the present study was to investigate sex-specific differences in sonic organ anatomy, agonistic behaviour and croaking sounds produced by *T. pumila.* Furthermore, it should be analysed if sex-specific differences in sonic organ anatomy within the genus *Trichopsis* are linked to sex-specific differences in sound properties.

2. Material and Methods

2.1. Animals

Seventeen male (body mass BM 0.3 - 0.61 g, standard length SL 24.46 - 30.97 mm) and 20 female pygmy gouramis (BM 0.33 - 0.63 g, SL 25.59 - 30.15 mm), obtained from a local pet supplier, were used for dyadic contests. Agonistic sounds of twelve males and 13 females were analysed. The other did not produce any sounds during dyadic contests.
Fish were kept in two community tanks (110 × 55 × 30 cm) equipped with sand, plants and flowerpots as hiding places, at a 12:12 h light:dark cycle. Water was maintained by external filters, and the temperature kept constant at 25 ± 1 °C. Fish were primarily fed food flakes five times a week (Tetramin).

2.2. Anatomy

I dissected the left side of 21 males (BM 0.28 - 0.59 g, SL 23.33 - 29.22 mm) and 13 females (BM 0.21 - 0.8 g, SL 21.08 - 30.19 mm) (Fig. 1A and 1B), previously fixed in 70 % ethanol. Sex of the fish was confirmed based on the gonads. To increase the visibility of the tendons, they were stained with methylene blue. The diameters of the first (Fig. 1C and 1E) and the second (Fig. 1D and 1F) enhanced tendon were measured using a digital microscope system (Leica DMS 1000). Fish used for dissections are not identical to those used for behavioural or acoustic analyses.

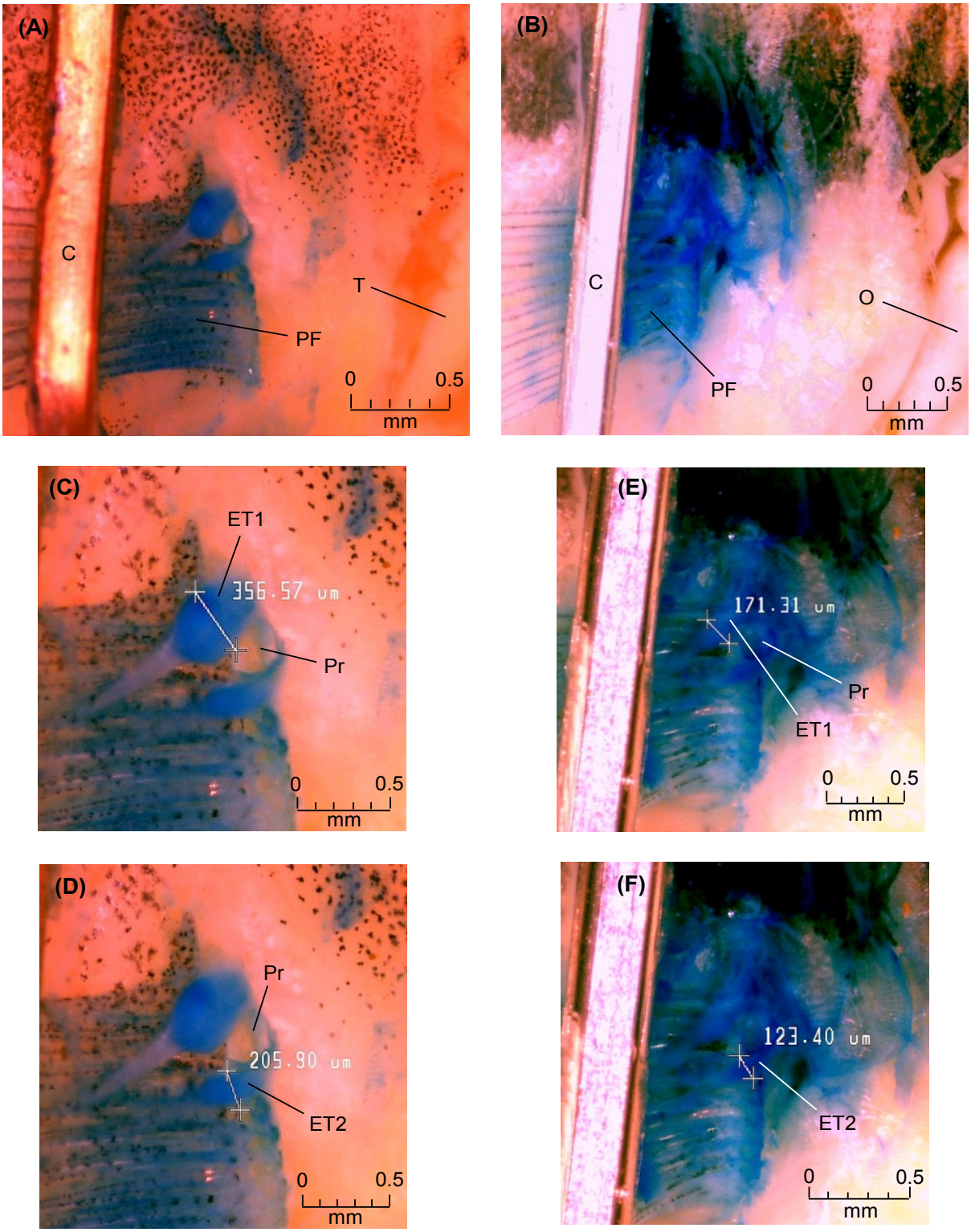

Fig. 1: Sonic organs of (A, C, D) male and of (B, E, F) female *T. pumila*. Pectoral fin rays were turned cranially and fixed by a clip to see enhanced tendons, which have been stained with methylene blue. (C, D) Male and (E, F) female tendons are shown on an expanded scale to illustrate measurement of the diameter. Abbreviations: C - clip, ET1 - first enhanced tendon, ET2 - second enhanced tendon, O - ovary, PF - pectoral fin rays, Pr - processus of second fin ray, T - testis.

2.3. Experimental setup for behavioural investigations

The test tank (50 × 30 × 27 cm) was placed on a vibration-isolated table in a walk-in soundproof room constructed as a Faraday cage. The bottom of the tank was covered with sand, and contained two half flowerpots. The light:dark cycle and the water temperature were identical to the community tanks. The walls inside the test tank, except for the front, were lined with bubble wrap in order to reduce reflection and resonance from the tank glass. To determine the position of the fish in the tank, the front glass was divided in 50 sectors by a grid. The hydrophone (Brüel & Kjær 8101, sensitivity -186 dB re 1 V/µPa) was placed close to the back wall and left next to the plastic plate, which divided the tank into two halves. It was connected to a power supply (Brüel & Kjær 2804), which was connected to the XLR microphone input of a 4-K video camera (Panasonic HC-X1000) as well as to a sound level meter (Brüel & Kjær Type 2250). The camera was additionally connected to a monitor (Sony PVM-1440QM) to control the video recordings. The equipment was positioned behind a curtain so that the experimenter could not be seen by the animals (Fig. 2).

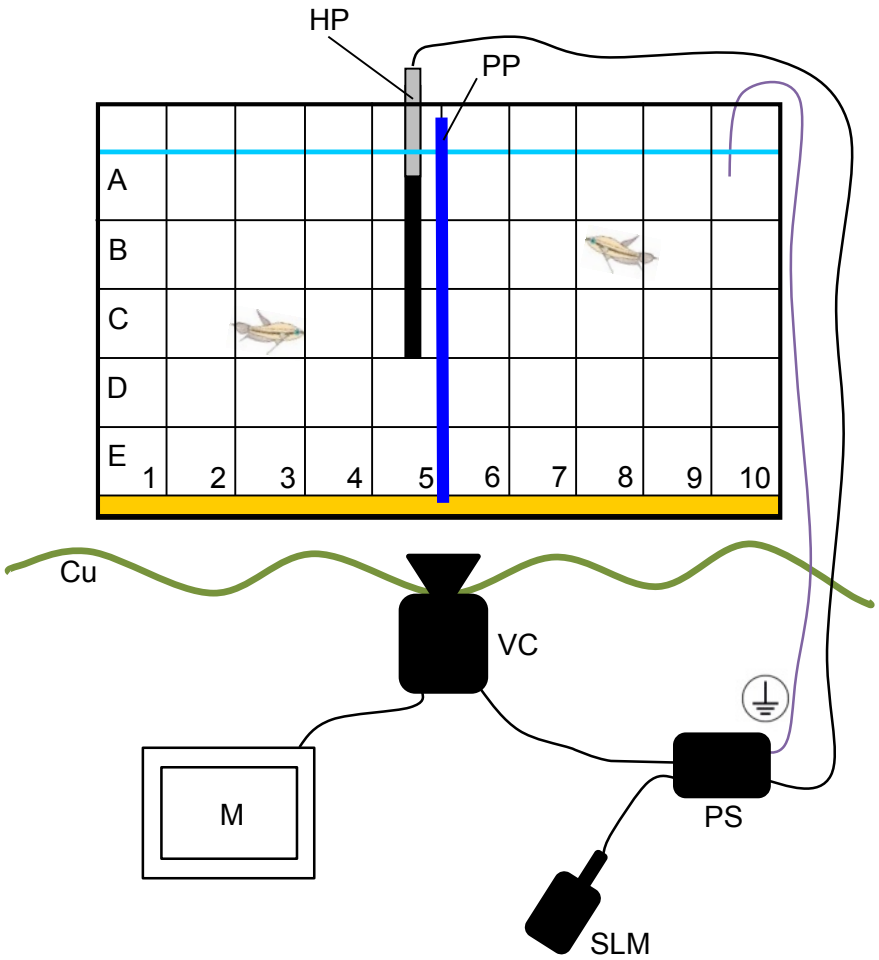

Fig. 2: Experimental setup of the test tank with one *T. pumila* in each half. Letters A to E and numbers 1 to 10 indicate the horizontal and vertical position of each sector. Abbreviations: Cu - curtain, HP - hydrophone, M - monitor, PP - plastic plate, PS - power supply, SLM - sound level meter, VC - video camera.

2.4. Behaviour and Sound Recordings

To reduce dominance experience, fish were isolated for five days in isolation tanks under conditions similar to the community tanks, except that fish were fed daily. After the isolation period, fish were marked at the caudal fin, and introduced for another day into the left and right halves of the test tank, which were separated by a plastic plate (Fig. 2). Sex determination of the fish was based on the presence or absence of the whitish ovaries, visible against bright light.

Before the experiments, the plants were removed and the hydrophone as well as the grounding cable was introduced into the test tank. Afterwards, I waited 15 min before starting the

recordings, and after 2 min I then removed the plastic plate. In order to avoid overloading, sound recording levels were adjusted on one track manually in the video camera, on the second one automatically.

After the experiments, I weighted and measured both fish before they were returned to the community tanks. Fish, which were going to be used in a second test later, were returned to another community tank. All experiments took place between 11 a.m. and 3 p.m.

2.5. Behaviour analysis

Behaviour was analysed using Sony Vegas Pro 13.0 (Sony Creative Software Inc.). I determined the following variables:

- Contest duration: time between the onset of the first and the end of the last agonistic behaviour including breaks, e.g. for air-breathing. The end of a contest was defined as the moment when one fish gave up and fled, and the other clearly emerged as winner.
- Lateral display duration: Lateral displays (LDs) consisted of erecting unpaired fins, head-to-tail circling and sound production. Such fight sequences were interrupted by air-breathing. LD duration constitutes the sum of all LD sequences excluding breaks.
- Number of sounds: constitutes the number croaking sounds produced by both fish during a dyadic contest. Sounds produced after the contest ended, i.e. from the winner only, were not included.
- Number of buttings: buttings are thrusts of the head towards the body of the other fish. The number constitutes all buttings of one opponent towards the other in the course of one contest.

2.6. Sound analysis

Sounds were rendered (44.1 kHz, 16 bit) to WAV-format using Sony Vegas Pro 13.0 and subsequently analysed using Cool Edit 2000 (Syntrillium Software Corporation, Phoenix, AZ, USA) and S_TOOLS-STX 3.7.8 (Acoustics Research Institute, Austrian Academy of Sciences, Vienna, Austria). The following sound characteristics were determined:

- Number of bursts: total number of long (double-pulsed) and short (single-pulsed) bursts per croaking sound (Fig. 3).
- Percentage of short bursts within a sound.
- Burst period: defined as the time between the maximum peaks of two successive bursts within a sound (Fig. 3).

- Dominant frequency (Fig. 4): defined as frequency of highest spectral level in a cepstrum-smoothed power spectrum (Noll 1967, Ladich 2007, Ladich and Maiditsch 2018) (settings STX: bandwidth 5 Hz, overlap 75 %, number of coefficients: 30 - 200, Hanning window). To avoid the resonance frequencies in small tanks (above 3.3 kHz) (Akamatsu et al. 2002, Ladich and Maiditsch 2018), all sounds were low pass (3.5 kHz) filtered.

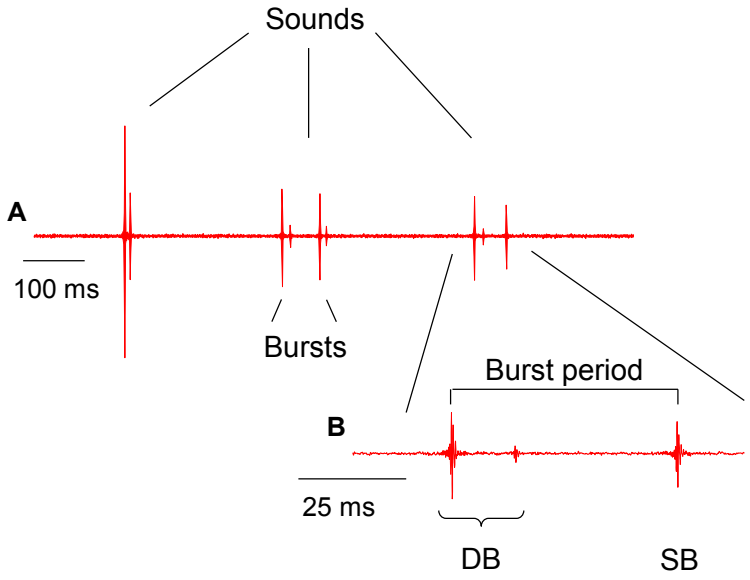

Fig.3: Oscillogram of (A) three croaking sounds of a male *T. pumila* consisting of one or two bursts respectively, and of (B) the expansion of the third sound consisting of one double-pulsed (DB) and one single-pulsed (SB) burst.

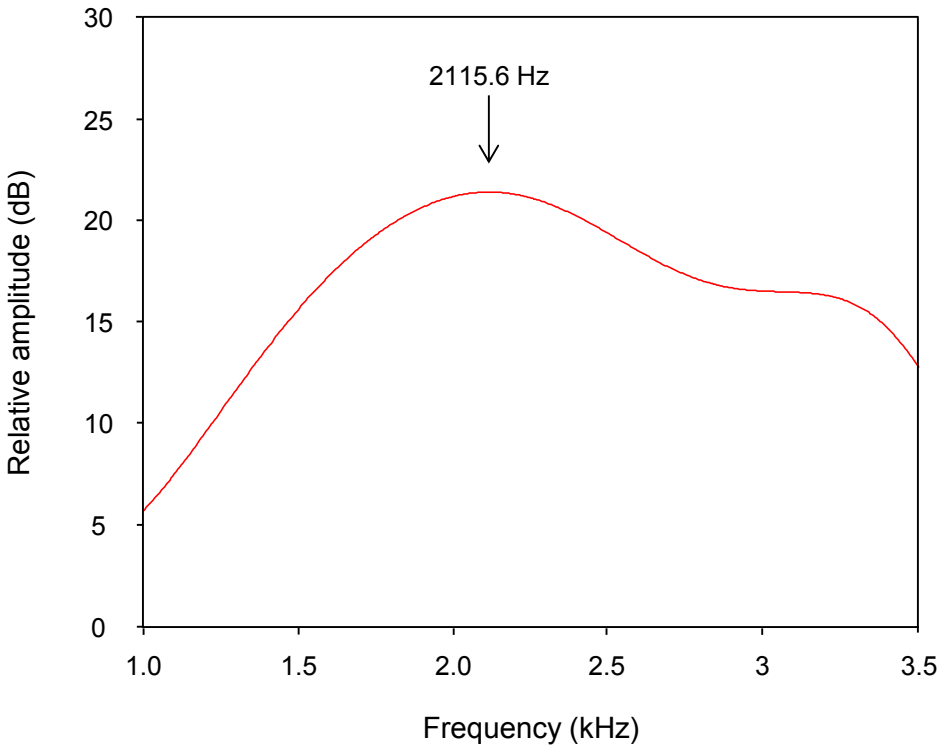

Fig. 4: Cepstrum-smoothed power spectrum of seven croaking sounds of a male *T. pumila*. Dominant frequency is indicated by the arrow. Sampling frequency 44.1 kHz, filter bandwidth 10 Hz, 75 % overlap, number of coefficients 38, Hanning window.

2.7. Sound pressure level measurement

I measured the sound pressure level SPL (LAFmax, broadband A and Z frequency weighting, RMS Fast time weighting) using a sound level meter (Brüel & Kjær Type 2250), which was connected to the second output of the hydrophone power supply (Fig. 2). All dB values were referenced to 1 µPa. Since the distance of the fish to the hydrophone varied, I divided the test tank into 50 sectors (5 × 5 cm) by a grid applied to the front glass of the tank (Fig. 2), and noted the sector in which the fish produced sounds. To compensate for the differences between the hydrophone and the croaking fish, I calculated a correction factor (Ladich et al. 1992a, Ladich 2007, Ladich and Maiditsch 2018, Ladich and Schleinzer 2020) by playing back a *T. pumila* croaking sound at a constant SPL from a small loudspeaker (Fuji 7G06) in each sector and noted the SPL. Subsequently, the differences in SPL between the sector nearest to the hydrophone (10 cm away) and the other 50 sectors were calculated, added to the SPL measured and thereby a distance-independent absolute SPL for each croaking sound was determined.

2.8. Statistical analysis

Behavioural analysis: In order to obtain a minimum number of dyadic contests per sex, some fish were used two times (males: n = 1; females: n = 8), but two individuals were never paired twice. Nine male-male contests and 14 female-female contests were analysed and a total of 17 males and 20 females were used.

Sound analysis: I only analysed sounds emitted in the first dyadic contest, but not when this individual was used for the second time. In total, I recorded and analysed sounds of twelve males and of 13 females (including sounds emitted after a contest ended).

Means of sound characteristics (number of bursts, percentage of short bursts, burst period, dominant frequency and SPL) were calculated for each individual (males: 1 - 17 sounds; females: 1 - 18 sounds) and used for further analyses. All data was tested for normal distribution using the Shapiro-Wilk test. When data was normally distributed, I used an independent samples T-test to analyse differences between sexes. Otherwise, I used the Mann-Whitney U-test. Burst period was normally distributed for both sexes, but given the small number of samples in females, nonetheless I used non-parametric tests to compare both sexes. For the comparison of ET diameters within sexes, the paired samples T-test was applied. Relationships between body measures and sound characteristics were calculated using Pearson's correlation coefficient, because all data were normally distributed. All statistical tests were run using IBM SPSS Statistics Version 23 and Version 26. The significance level was set at $p \leq 0.05$.

Ethical considerations

Pygmy gouramis produce visual as well as acoustic signals during dyadic contests. Physical contact between opponents only occurred during butting behaviour, but injuries were never observed in this study. All applicable national and institutional guidelines for the care and use of animals were followed (permit numbers BMWF-66.006/0038-II/3b/2013 and BMWFW-66.006/0011-WF/II/3b/2014).

3. Results

3.1. Anatomy of sonic organs

Twenty out of 21 males and ten out of 13 females possessed two enhanced sonic tendons (Tab. 1). In one female, I might accidentally have removed the second tendon while dissecting. The remaining fish (one male and two females) only had one enhanced tendon (controlled by dissecting the other side as well).

The diameter of both the first (ET1) and the second (ET2) enhanced tendons in males was on average twice as large as in females (ET1: T-test: $T = 6.734$, $df = 32$, $p < 0.001$; ET2: T-test: $T = 5.952$, $df = 28$, $p < 0.001$) (Fig. 5A and 5B). Within both sexes, ET1 was about 1.5 times larger than ET2 (males: paired T-Test: $T = 12.427$, $df = 19$, $p < 0.001$; females: paired T-test: $T = 3.467$, $df = 9$, $p < 0.05$) (Fig. 6A and 6B). The ratio between ET1 and ET2 diameters, however, was similar in both sexes (U-test: $U = 89$, $N_m = 20$, $N_f = 10$, n.s.).

Males and females did not differ in size (BM: T-test: $T = -0.413$, $df = 15.44$, n.s.; SL: T-test: $T = 0.817$, $df = 16.87$, n.s.). Thus, the sex-specific difference in ET diameters was not due to differences in body size.

Tab. 1: Mean (± S.E.) body mass, standard length, diameter of the first (ET1) and of the second (ET2) enhanced tendon and the ratio between ET1 and ET2 (RatioET1/ET2) of male and female *T. pumila*. The range and number of animals measured are given brackets.

Variable	Males	Females
Body mass (g)	0.43 ± 0.02 (0.28 - 0.59; 21)	0.45 ± 0.06 (0.21 - 0.8; 13)
Standard length (mm)	26.56 ± 0.35 (23.33 - 29.22; 21)	25.86 ± 0.79 (21.08 - 30.19; 13)
ET1 (mm)	0.36 ± 0.02 (0.19 - 0.52; 21)	0.17 ± 0.02 (0.11 - 0.3; 13)
ET2 (mm)	0.24 ± 0.01 (0.12 - 0.34; 20)	0.11 ± 0.01 (0.06 - 0.2; 10)
Ratio ET1/ET2	1.5 ± 0.04 (1.17 - 1.92; 20)	1.54 ± 0.15 (1.04 - 2.73; 10)

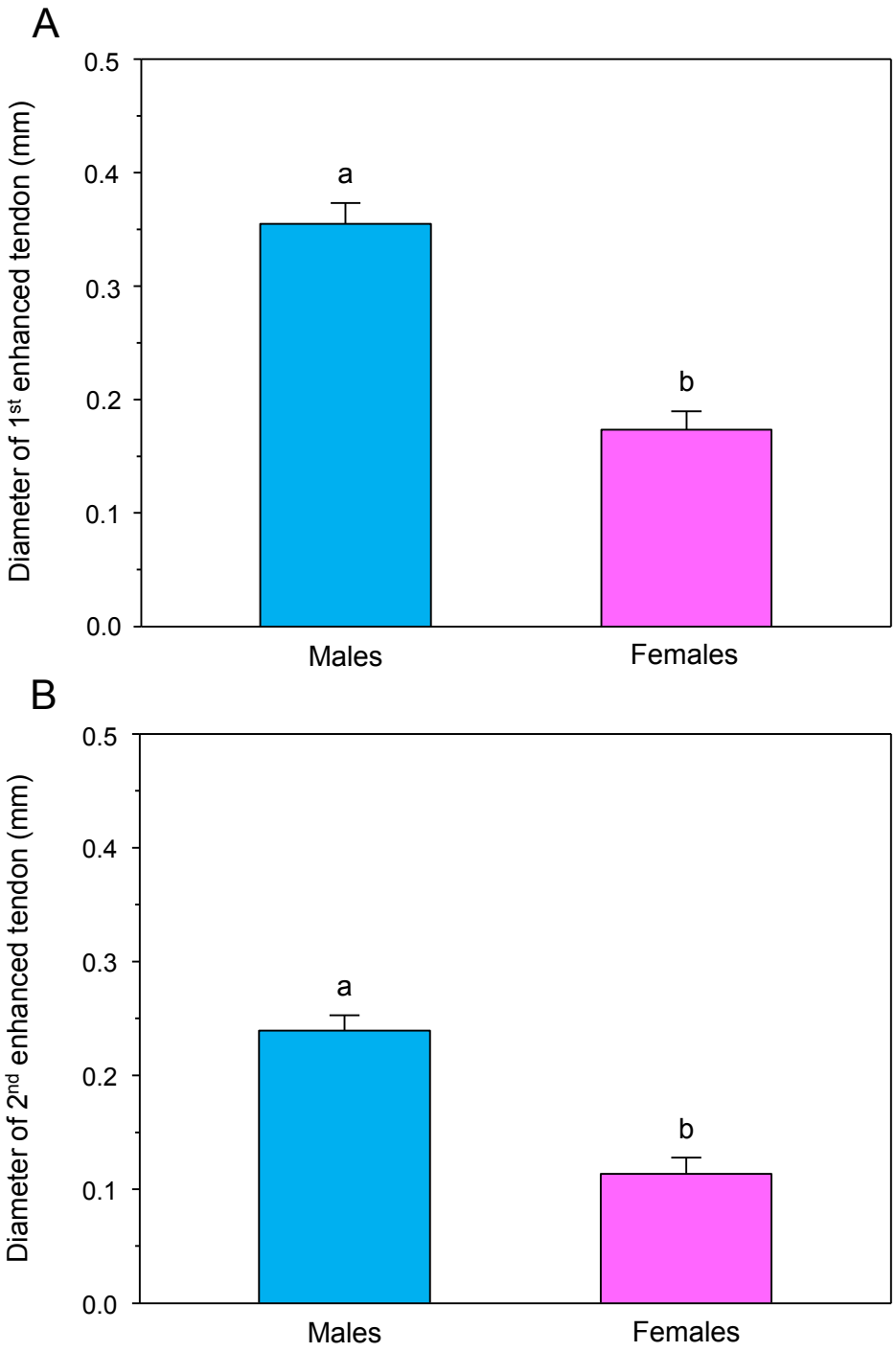

Fig. 5: Mean (+ S.E.) diameter of (A) the first and of (B) the second enhanced tendon in male and female *T. pumila*. Significant differences are indicated by different letters above bars.

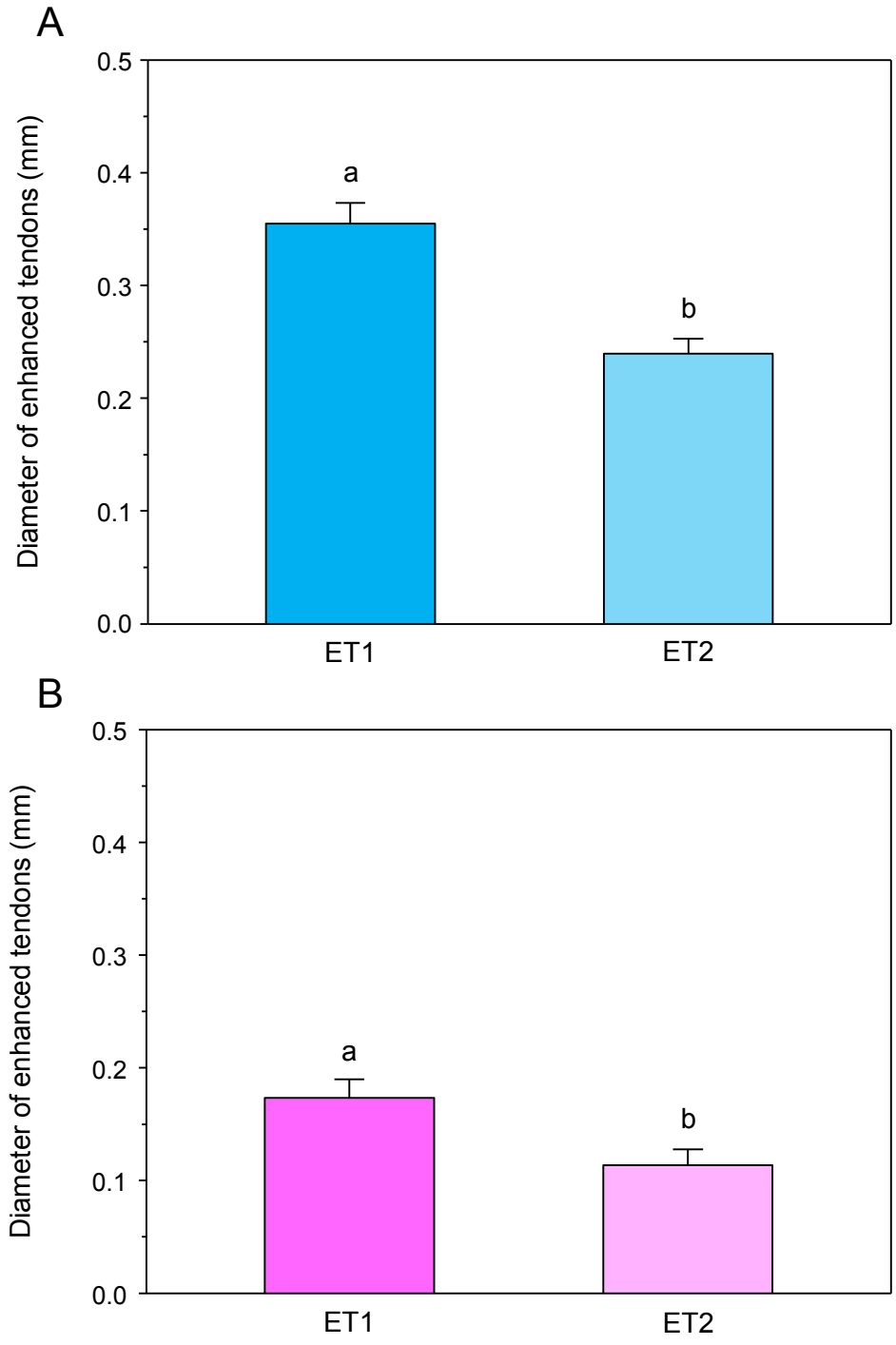

Fig. 6: Mean (+ S.E.) diameter of the first (ET1) and of the second (ET2) enhanced tendon in (A) male and in (B) female *T. pumila*. Significant differences are indicated by different letters above bars.

3.2. Agonistic interactions

In general, agonistic interactions started shortly after the separating plate was removed and one fish detected the other visually. They approached each other and started lateral displaying. Lateral display (LD) consisted of circling around each other in a head-to-tail position, spreading of unpaired fins, and sound production. Agonistic croaking sounds were produced by rapid pectoral fin beating, resulting in the fish's body shaking. In the beginning, contests consisted primarily of LD, which gradually decreased while the number of buttings increased, and finally ended by one fish retreating. Butting behaviour was observed in 20 out of 23 contests. In 17 out of these 20 contests, it already occurred within 5 min of the beginning of an encounter. As soon as butting behaviour started, fish stopped producing acoustical signals.

No sex-specific differences in agonistic behaviour were observed (Tab. 2). Dyadic contests lasted for approximately 8 minutes, and did not differ in total duration between sexes (U-test: $U = 60.5$, $N_m = 9$, $N_f = 14$, n.s.) nor in duration of LD (T-test: $T = 0.234$. $df = 21$, n.s.). Furthermore, males did not vocalize more than females during LDs (U-test: $U = 48.5$, $N_m = 9$, $N_f = 14$, n.s.) nor did sexes differ in the number of buttings (U-test: $U = 48$, $N_m = 9$, $N_f = 14$, n.s.).

Tab. 2: Mean (± S.E) contest duration, lateral display duration, number of sounds and number of buttings in male-male and female-female contests. The number of contests and the range are indicated in brackets.

Variable	Males	Females
Contest duration (s)	493 ± 172.57 (21 - 1710; 9)	485 ± 135.2 (21 - 1608; 14)
Lateral display duration (s)	95 ± 25.46 (10 - 204; 9)	89 ± 12.94 (11 - 165; 14)
Sound number	9.7 ± 3.49 (0 - 28; 9)	5.8 ± 1.75 (0 - 24; 14)
Butting number	13.7 ± 6.16 (0 - 55; 9)	24.1 ± 10.15 (1 - 141; 14)

3.3. Sound characteristics and differences between sexes

In general, croaking sounds of *T. pumila* were built up of one to four bursts, which were either single-pulsed or double-pulsed (Fig. 3, Fig. 7).

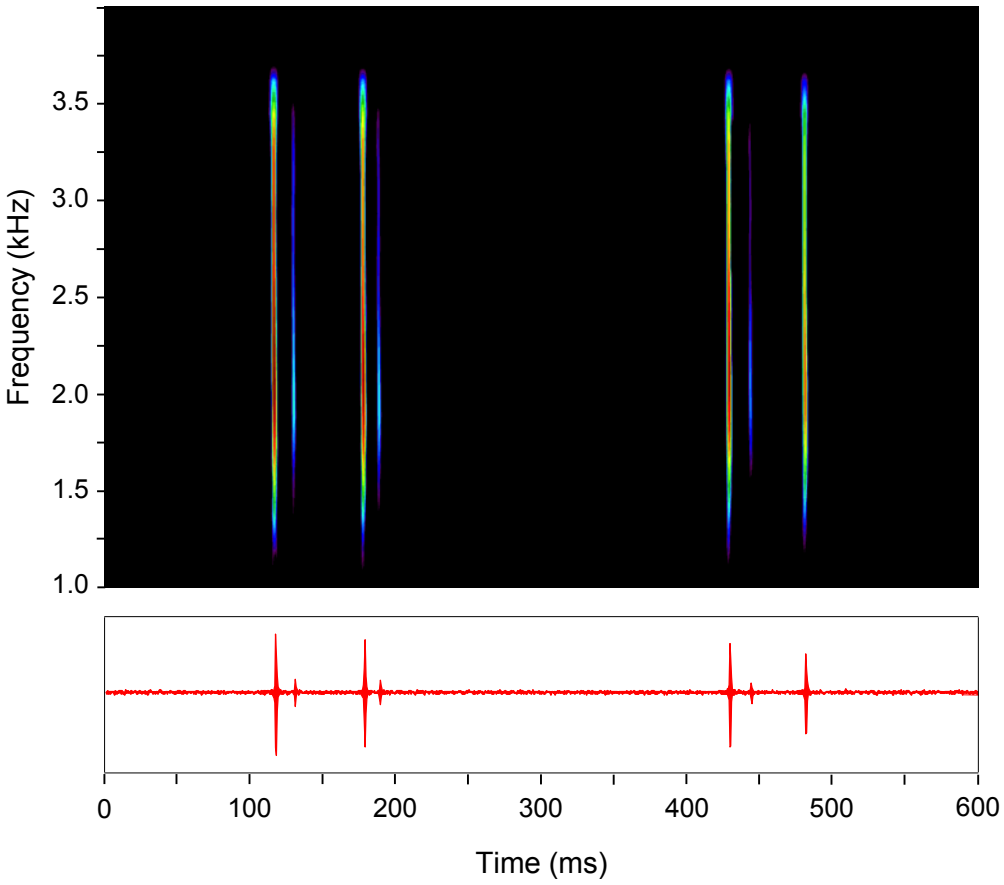

Fig. 7: Sonagram and oscillogram (below) of two agonistic sounds of a *T. pumila* male with the main energy concentrated between 1.75 and 3 kHz. The first croaking sound consists of two double-pulsed bursts, the second one of one double-pulsed and one single-pulsed burst. Sampling frequency 44.1 kHz, filter bandwidth 200 Hz, 75 % overlap, Hanning window.

Twelve out of 17 males and 13 out of 20 females produced sounds during agonistic interactions (Tab. 3). The remaining fish (five males and seven females) did not vocalize during LD. Male croaking sounds consisted of one to four bursts and were on average twice as long as female agonistic sounds, which were built up of one to two bursts (U-test: $U = 12$, $N_m = 12$, $N_f = 13$, $p < 0.001$) (Fig. 8A). Approximately 20 % of male bursts were single-pulsed whereas the percentage was more than four times higher in females (U-test: U = 15,

$N_m = 12$, $N_f = 13$, $p < 0.001$) (Fig. 8B). The burst period was larger in male than in female sounds (U-test: $U = 3$, $N_m = 11$, $N_f = 3$, $p < 0.05$) (Fig. 9). Male sounds were significantly lower in dominant frequency (T-test: $T = -4.959$, $df = 23$, $p < 0.001$) (Fig. 10A) and had a significantly higher sound pressure level (SPL) than female sounds (A frequency weighting: T-test: $T = 7.152$, $df = 23$, $p < 0.001$; Z frequency weighting: U-test: $U = 41$, $N_m = 12$, $N_f = 13$, $p < 0.05$) (Fig. 10B).

Tab. 3: Mean (± S.E.) body mass, standard length, number of bursts, percentage of short bursts within a sound, burst period, dominant frequency and sound pressure level (SPL LAF A frequency weighting and SPL LZF Z frequency weighting) of male and female *T. pumila*. The number of animals analysed and the range are indicated in brackets.

Variable	**Males**	**Females**
Body mass (g)	0.48 ± 0.02 (0.3 - 0.61; 12)	0.45 ± 0.02 (0.33 - 0.55; 13)
Standard length (mm)	28.25 ± 0.52 (24.46 - 30.97; 12)	27.32 ± 0.36 (25.59 - 29.88; 13)
Burst number	2.12 ± 0.19 (1 - 3; 12)	1.11 ± 0.06 (1 - 1.7; 13)
Percentage of short bursts (%)	20.87 ± 10.83 (0 - 100; 12)	93.66 ± 4.38 (50.93 - 100; 13)
Burst period (ms)	54.96 ± 1.71 (42.36 - 61.87; 11)	44.88 ± 0.33 (44.34 - 45.47; 3)
Dominant frequency (Hz)	2089.0 ± 22.6 (1954.1 - 2234.1; 12)	2281.8 ± 30.95 (2079.7 - 2411.7; 13)
Sound pressure level (dB, LAF)	113.46 ± 1.62 (100.46 - 121.72; 12)	98.83 ± 1.27 (91.9 - 107.62; 13)
Sound pressure level (dB, LZF)	116.26 ± 1.25 (107.67 - 121.33; 12)	113.82 ± 2.23 (105.01 - 137.7; 13)

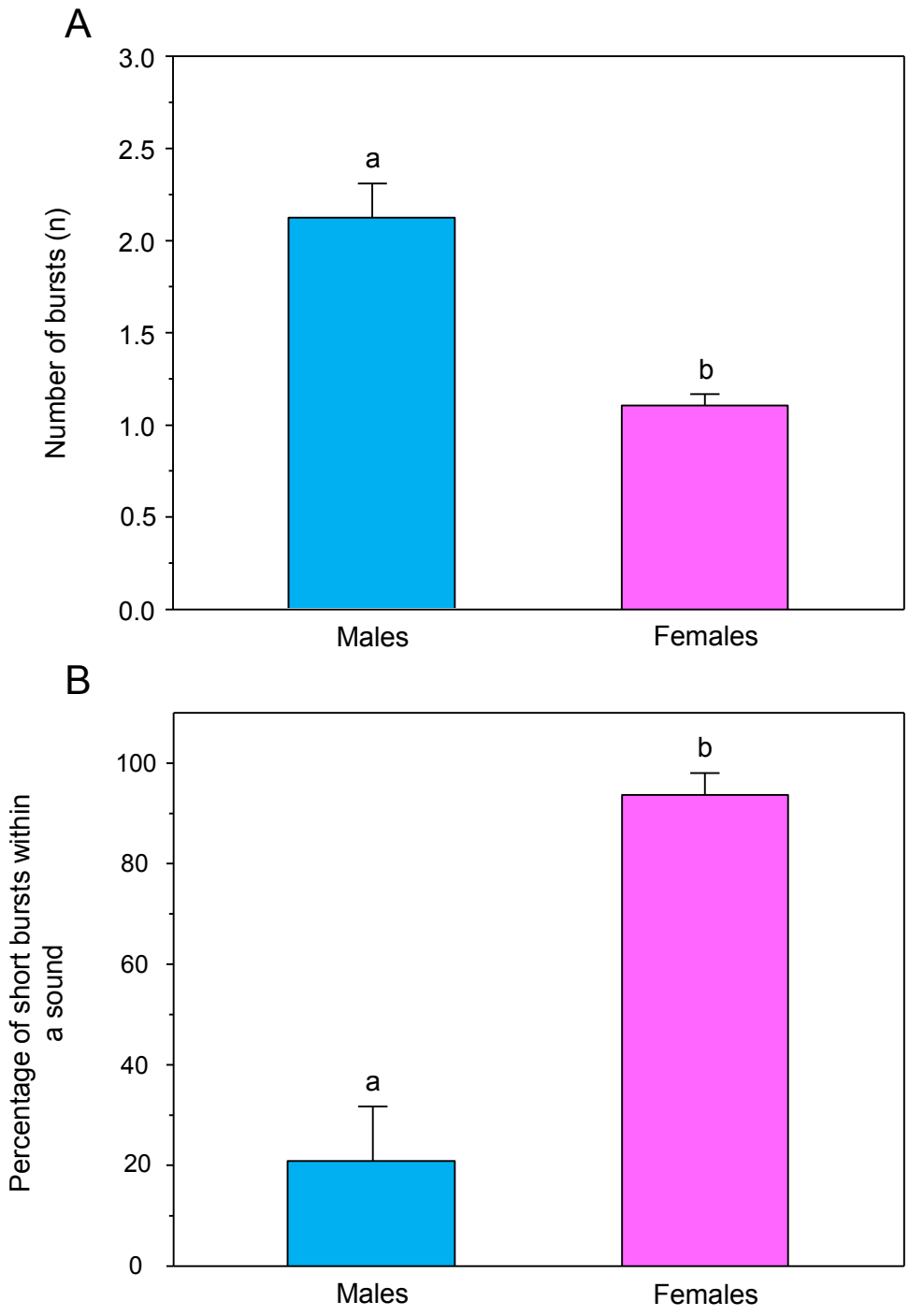

Fig. 8: Mean (+ S.E.) (A) number of bursts and (B) percentage of short bursts within an agonistic sound of male and female *T. pumila.* Significant differences are indicated by different letters above bars.

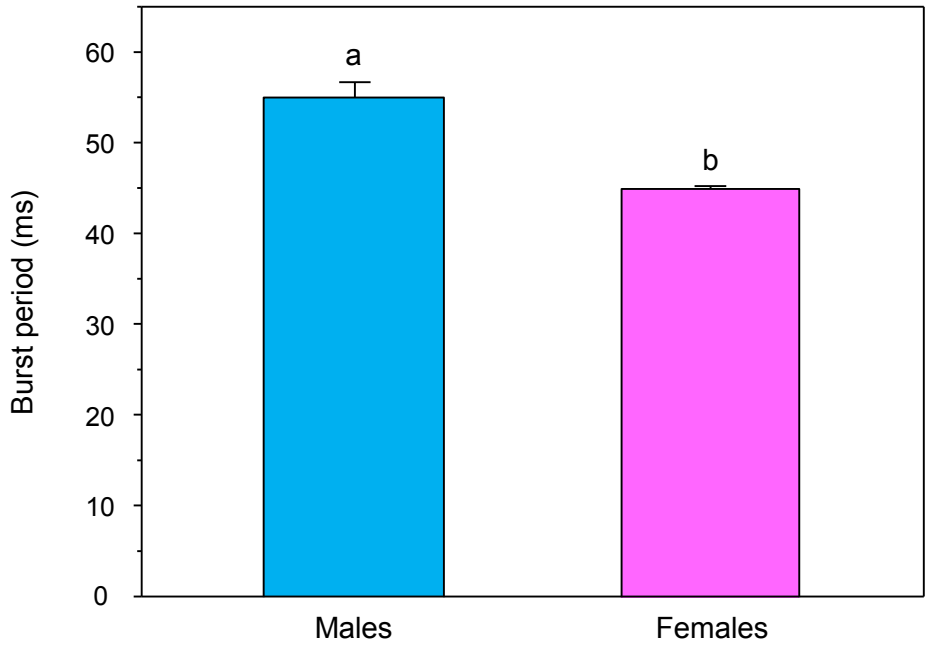

Fig. 9: Mean (+ S.E.) burst period of male and female *T. pumila* croaking sounds. Significant differences are indicated by different letters above bars.

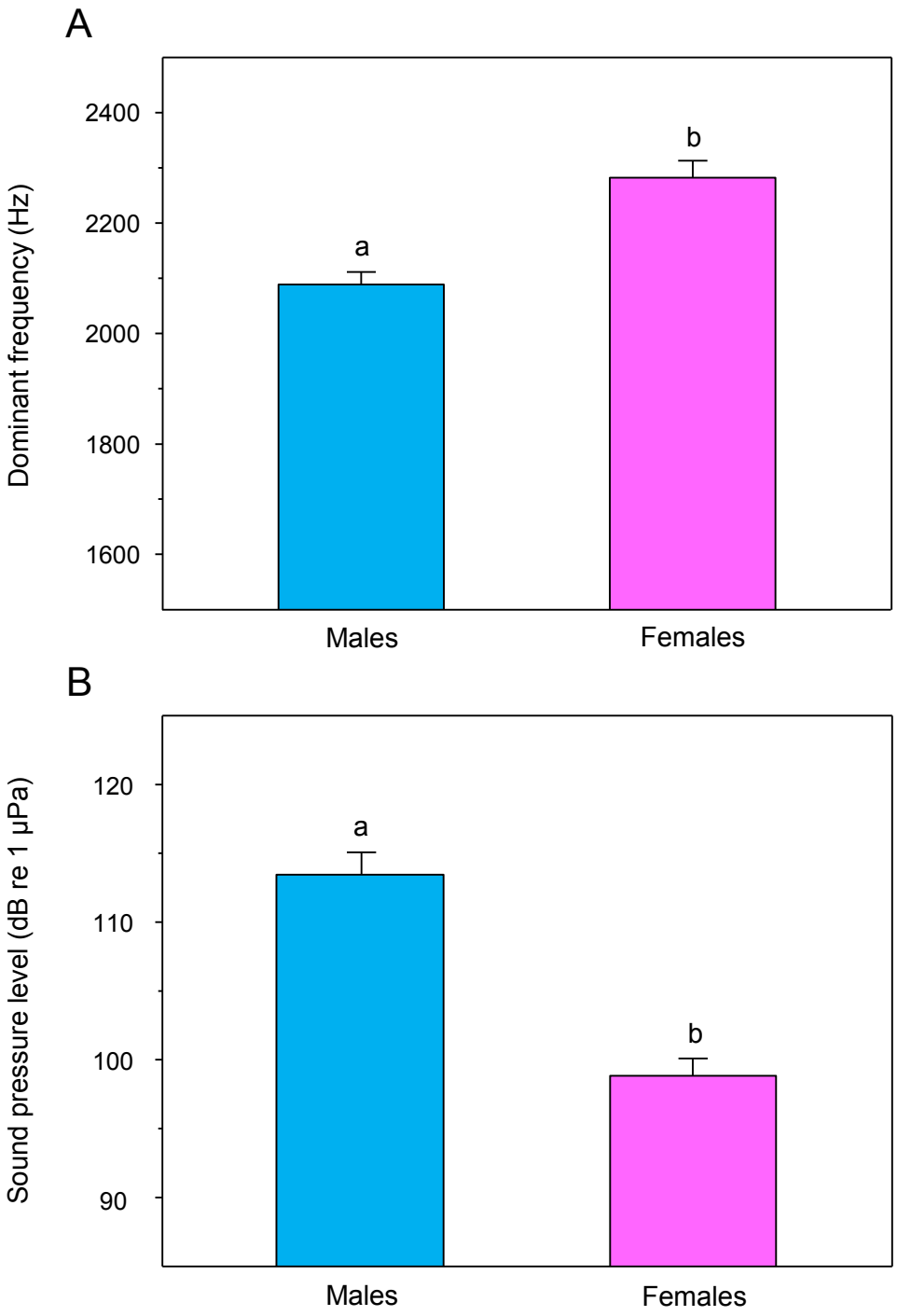

Fig. 10: Mean (+ S.E.) (A) dominant frequency and (B) sound pressure level (LAF) of male and female *T. pumila* agonistic sounds. Significant differences are indicated by different letters above bars.

3.4. Sound characteristics and body size

In males, body mass was negatively correlated with dominant frequency ($r = -0.505$, $N_m = 12$, $p < 0.05$, one-tailed) (Fig. 11A) and positively correlated with SPL (LAF) ($r = 0.544$, $N_m = 12$, $p < 0.05$, one-tailed) (Fig. 11B). Neither dominant frequency ($r = 0.111$, $N_f = 13$, n.s., one-tailed) nor SPL (LAF) ($r = 0.387$, $N_f = 13$, n.s., one-tailed) was correlated with body weight in females. Burst period did not correlate with body mass in either sex (males: $r = - 0.258$, $N_m = 12$, n.s.; females: $r = 0.498$, $N_f = 13$, n.s.).

Vocalizing males and females did not differ in BM (T-test: $T = 1.045$, $df = 23$, n.s.) nor in SL (T-test: $T = 1.492$, $df = 23$, n.s.). Thus, differences in sound characteristics were not due to any difference in body size.

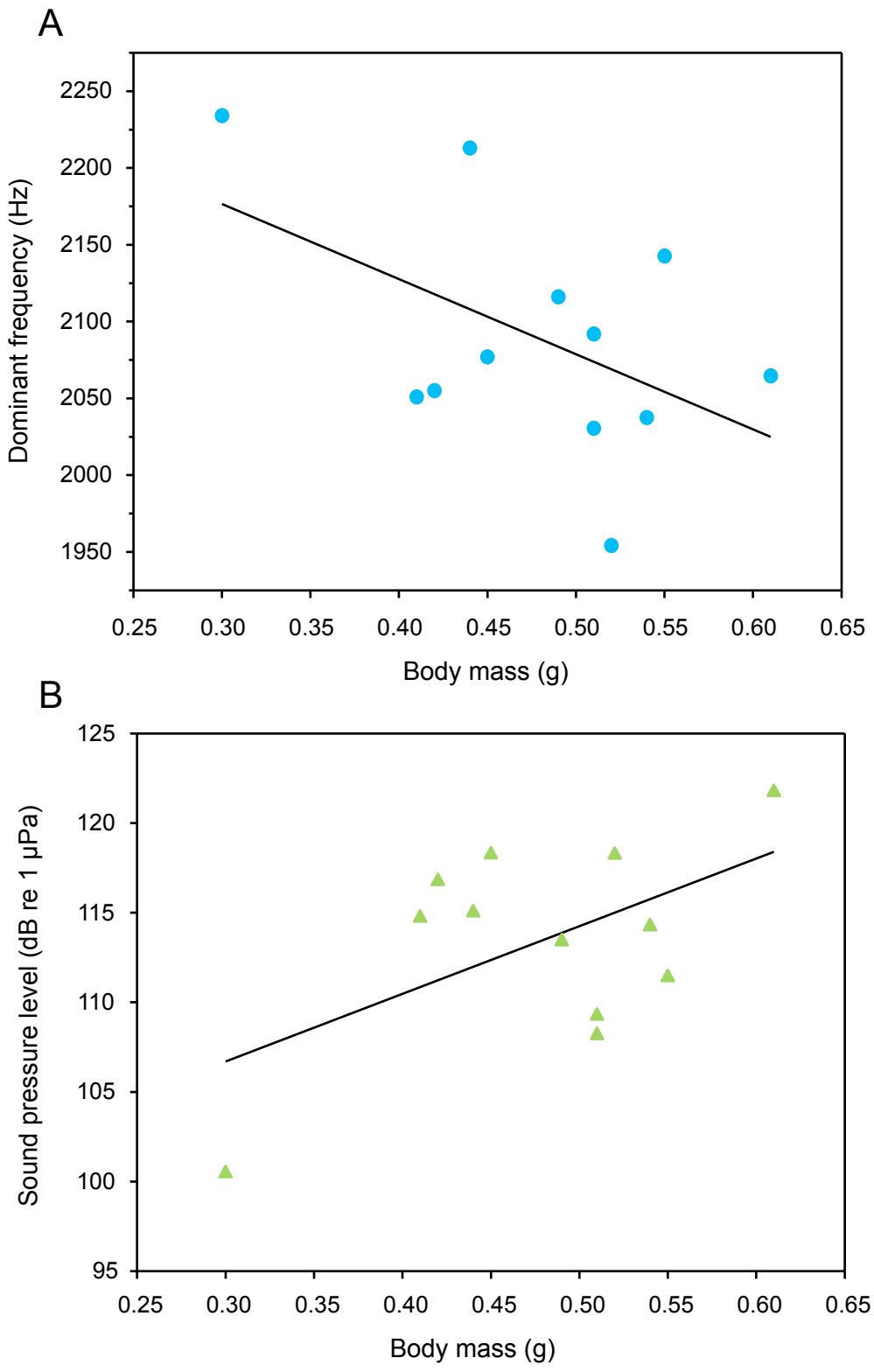

Fig. 11: Correlation between sound characteristics and body mass (BM) in male *T. pumila*. Regression equation: (A) dominant frequency = 2323 - BM * 488.57; $r^2 = 0.255$ and (B) sound pressure level (LAF) = 95 + BM * 37.76; $r^2 = 0.296$.

4. Discussion

Sound production during agonistic interactions in females within the genus *Trichopsis* has been shown in the croaking gourami *Trichopsis vittata* (Marshall 1966, Ladich 2007, Ladich and Maiditsch 2018) and in the threestripe gourami *Trichopsis schalleri* (Schleinzer 1992, Ladich and Schleinzer 2020), but remained unclear in the pygmy gourami *Trichopsis pumila* (Marshall 1966, Kratochvil 1980, Schleinzer 1992). This study provides evidence that despite having smaller sonic organs than males, two third of female *T. pumila* vocalized during agonistic interactions and that sex-specific differences in agonistic sound characteristics are most likely based on sex-specific differences in the sound generating mechanism.

4.1. Sex-specific differences in sonic organs

I measured and compared for the first time the key sonic structures (enhanced tendons) in both sexes of *T. pumila*. The enhanced sonic tendons were twice as large in males as in females whereas the ratio between the first and second sonic tendon was similar in both sexes. Within the genus *Trichopsis*, a sexual dimorphism in sound producing organs has also been described in the largest species *T. vittata* (Kratochvil 1978), but it is less pronounced than in *T. pumila* (Kratochvil 1980). Kratochvil (1985) estimated that sonic organs are about a third smaller in female than in male *T. vittata*. This is in contrast to *T. pumila*, where the tendon diameter is approximately twice as large in males as in females. A sexual dimorphism is also postulated for the third species *T. schalleri*, though anatomical data are lacking so far (Ladich and Schleinzer 2020).

Sound generating mechanisms are rarely absent in females, although males have in general more developed sonic organs (Ladich 2015a). Many studies showed that sonic organs in males are larger than in females, but sex-specific differences have rarely been analysed statistically before. In the oyster toadfish *Opsanus tau* (Batrachoididae), both swim bladder and sonic muscles grow larger and faster in males than in females (Fine 1975, Fine et al. 1990). Mean sonic muscle weighted 3.67 g in males and were significantly larger than in females, where sonic muscle weighted 2.55 g on average (Fine et al. 1990). Likewise, in type I males of the Lusitanian toadfish *Halobatrachus didactylus*, swim bladder and sonic muscles weighted 3.24 g and 2.67 g and were 25 % and 30 % heavier than in females (2.59 g and 2.05 g respectively) during breeding season (Modesto and Canário 2003). In the plainfin midshipman *Porichthys notatus*, drumming muscles are also larger in type I males in

comparison to females or type II males (Brantley et al. 1993, Brantley and Bass 1994). In type I males, relative to body weight, sonic muscles accounted for 1.2 % in contrast to 0.12 % or 0.16 % in females or type II males, respectively (Brantley and Bass 1994). Within cods (e.g. haddock *Melanogrammus aeglefinus*), drumming muscles hypertrophy during the spawning season in males (Templeman and Hodder 1958, Rowe and Hutchings 2004, 2006, Casaretto et al. 2016). But even outside the breeding season, drumming muscles in male *M. aeglefinus* were at least 50 % larger than in same-sized females (e.g. fish 44 cm in length: average volume of immature male sonic muscles 1.4 cc versus 0.9 cc in mature females versus 3.4 cc in matures males - Templeman and Hodder 1958). Similarly, in non-spawning European hake *Merluccius merluccius* (family Merluciidae), dry weight of male drumming muscles were approximately 3 times higher outside the spawning season (10.15 versus 3.12 mg in females). During spawning season, dry weight of sonic muscles was up to 10 times larger (225.7 mg in males versus 23.27 mg in females) (Groison et al. 2011). Additionally to size differences in sonic muscles, some structures might be missing in females. Female cusk-eels *Ophidion rochei* (family Ophidiidae) lack a rocker bone at the rostral end of the swim bladder, which is present in males. Furthermore, in females there is no neck formation at the anterior region and no internal tube at the posterior region of the swim bladder (Kéver et al. 2012). The majority of sciaenid species possess sexually dimorphic sonic muscles. In the Atlantic croaker *Micropogonias undulatus*, the adjusted weight of sonic muscles was larger in males than in females (1.92 g versus 1.4 g per 150 g fish) (Hill et al. 1987). Similarly, Ueng et al. (2007) found that in male Japanese meagre *Argyrosomus japonicus*, sonic muscles were larger (27.5 % versus 23.6 %), thicker (5.1 % versus 3.6 %), wider (4.3 % versus 3.5 %) and heavier (2.08 % versus 0.97 %) than in females. A sexual dimorphism is also found in pectoral mechanisms in callichthyid armoured catfishes. Male peppered corydoras *Corydoras paleatus* possess longer pectoral spines than females (Pruzsinszky and Ladich 1998). Likewise, in male armoured catfish *Megalechis thoracata*, pectoral spines (relative to body size) were 1.7 times longer than in females (Hadjiaghai and Ladich 2015).

4.2. Sex-specific differences in agonistic behaviour

Agonistic behaviour in representatives of the genus *Trichopsis* has been described by Marshall (1966) and Bischof (1996) revealing interspecific differences between males. However, sex-specific differences were neither mentioned by Marshall (1966) nor Ladich (2007) in *T. vittata* based on observations without statistical analysis. The current study also revealed no differences in agonistic behaviour between male and female *T. pumila* with

regard to duration and intensity of agonistic encounters. This indicates that males and females are similarly territorial.

Several studies reported sound production during agonistic interactions in both sexes across different fish families mostly without detailed analysis. In Atlantic cod *Gadus morhua* (formerly *Gadus callarias*), grunting sounds were produced by both males and females during threat display (Brawn 1961a, 1961b, Hawkins and Rasmussen 1978). Likewise, male and female *M. aeglefinus* produce repeated 'knocks' during agonistic interactions (Hawkins and Rasmussen 1978, Hawkins and Amorim 2000). Among cichlids, both sexes of the jewelfish *Hemichromis bimaculatus* (Myrberg et al. 1965) and of the flier cichlid *Archocentrus* (formerly *Cichlasoma*) *centrachus* (Schwarz 1980) vocalized before attacking an intruder or when behaving aggressively towards each other. Ladich and Kratochvil (1989) observed both sexes in the tubenose goby *Proterorhinus marmoratus* producing sounds during agonistic interactions. Male and female bullhead *Cottus gobio* produced two types of sounds during threat displays, but with males vocalizing more often than females (Ladich 1989, 1990). However, since large females vocalized more than smaller males and defended their territories as successful as males, this difference in sound production was mainly size dependent (Ladich 1990). Both sexes of *O. tau* emitted grunts during agonistic interactions (Fish 1954, Gray and Winn 1961, Maruska and Mensinger 2009). Lagardère et al. (2005) found that both sexes of the pinhead pearlfish *Encheliophis* (formerly *Carapus*) *boraborensis* vocalized when entering a holothurian host already occupied by another fish. On the other hand, a study in the catfish *M. thoracata* revealed sex-specific differences during dyadic encounters (Hadjiaghai and Ladich 2015). Sounds by males (barks and thumps) accompanied different agonistic behaviour patterns than sounds emitted by females (crackles).

4.3. Sex-specific differences in sound characteristics

Sex-specific differences in sound properties vary within the genus *Trichopsis*. In *T. vittata*, agonistic sounds only differ in SPL between sexes, but not in temporal and spectral properties (Ladich 2007). Croaking sounds were significantly louder in same-sized males, which is probably due to their larger sound generating mechanism (Kratochvil 1978, Kratochvil 1985). Sex-specific differences in agonistic vocalizations are more pronounced in *T. schalleri*. Male sounds are louder and longer than in females (Ladich and Schleinzer 2020). Due to a lack of anatomical data, it is assumed that males possess larger sonic organs. In the smallest species *T. pumila*, the sex-specific difference is even more pronounced. Male sounds were longer

(more bursts, which were mostly double-pulsed, higher burst period), louder (higher SPL) and lower in dominant frequency.

Differences in SPL between sexes can be explained by the difference in size of sound generating mechanism. According to Kratochvil (1980), the sex-specific difference in pectoral muscles is much larger in *T. pumila* than in *T. vittata*. Analogous to *T. vittata*, this would enable male *T. pumila* to produce a higher tension on enhanced tendons resulting in louder pulses when plucking tendons during sound production than females (sex-specific difference: 14 dB in *T. pumila* versus 5 dB in *T. vittata*).

Interestingly, a sex-specific difference in dominant frequency could neither be found in *T. vittata* nor in *T. schalleri* (Ladich 2007, Ladich and Schleinzer 2020) in contrast to *T. pumila* in same-sized animals.

In contrast to *T. vittata* (Ladich 2007), but similar to *T. schalleri* (Ladich and Schleinzer 2020), male *T. pumila* emitted longer sounds than females. This is due to a larger number of bursts and a higher burst period. Additionally, bursts in male *T. pumila* were mostly double-pulsed (there is no data on *T. schalleri* regarding this variable). The higher number of double-pulsed bursts in male sounds of *T. pumila* is probably due to the larger tendons in males than in females. Thus, it could be that the small size of the second tendon in females did not result in a second sound pulse when pectoral fins are beaten rapidly.

In general, only a few studies reported sex-specific differences in sounds characteristics in the same behavioural context. In the zebra mbuna *Maylandia* (formerly *Pseudotropheus*) *zebra*, male agonistic sounds were longer and consisted of more pulses as compared to females (Simões et al. 2008). On the other hand, in *E. boraborensis*, male sounds were shorter due to the shorter pulse length as well as shorter pulse period than female sounds (Lagardère et al. 2005). Neither of these two studies reported sex-specific differences in spectral properties of sounds. In the skunk clownfish *Amphiprion akallopisos*, females emitted agonistic sounds, which had a higher pulse period than males (Colleye et al. 2009). However, pulse period was positively correlated with standard length (SL) as well as pulse duration, which in return was highly correlated to SL. Thus, this difference in pulse period might rather be size dependent than related to sex since female clownfish are always larger than males. There was also a highly negative correlation between dominant frequency and SL, which is why dominant frequency did not differ between sexes when taking into account the body size. However, Ueng et al. (2007) found that in *A. japonicus*, female sounds differed in spectral properties from males', the latter having a higher main frequency (686 Hz versus 589 Hz in females). In addition, female sounds were longer in duration due to a higher number of

pulses and larger interpulse-intervals (although pulse period as well as pulse duration were shorter) compared to male sounds. Similarly, in the meagre *Argyrosomus regius*, males also emitted sounds with a higher peak frequency (305 Hz versus 243 Hz in females). Female sounds had a shorter pulse period, but they were also shorter in sound duration compared to males (Pereira et al. 2020). A recent study in the haddock revealed that female sounds have larger pulse intervals, higher pulse frequencies and a higher amplitude ratio between the two successive pulses (Casaretto et al. 2016). However, sounds were emitted in different behavioural contexts in both sexes, making a comparison of sound characteristics difficult. In *C. paleatus*, both sexes vocalized when hand-held, and distress calls only differed in dominant frequency (1466 Hz in males versus 1235 Hz in females) most likely due to the fact that females are much larger, but they did not differ in temporal properties (sound duration, pulse period and number of pulses) (Pruzsinszky and Ladich 1998). In contrast, other studies did not find any sex-specific differences neither in the spectral nor in temporal characteristics of sounds when hand-held (e.g. black drum *Pogonias cromis* - Tellechea et al. 2011; longsnout seahorse *Hippocampus reidi* - Oliveira et al. 2014; toadfish *O. tau* - Fine and Waybright 2015).

4.4. Correlations between sound characteristics and size

In general, dominant frequency of pulsed sounds is negatively correlated with body size in fish and may convey reliable information about the fighting ability of opponents or fitness of mates (Myrberg et al. 1986, Ladich 1998). A negative relationship between dominant frequency and body weight was found in both sexes of *T. vittata* and *T. schalleri* as well as in male *T. pumila* (Ladich et al. 1992a, Ladich and Maiditsch 2018, Ladich and Schleinzer 2020). No such significant correlation was found in the present study in female *T. pumila*. This could be due to the small size range used (see Tab. 3) or to the small sonic organs in females. A negative relationship between size and main sound frequencies has been shown in representatives of several bony fish families such as pomacentrids (the bicolor damselfish *Stegastes* (formerly *Pomacentrus) partitus* - Myrberg et al. 1993; both sexes of the clownfish *A. akallopisos* - Colleye et al. 2009), sciaenids (black drum *P. cromis* - Tellechea et al. 2011; Squeteague *Cynoscion regalis* - Connaughton et al. 2000; whitemouth croaker *Micropogonias furnieri* - Tellechea et al. 2010; meagre *A. regius* - Pereira et al. 2020) and catfish (*C. paleatus* - Pruzsinsky and Ladich 1998; the Raphael catfish *Platydoras costatus* - Ladich 1997b; mochokid catfish *Synodontis schoutedeni* (when larger than 37 mm SL) - Lechner et al.

2010). In other studies, however, no such relationship was found neither for males nor for females, e.g. in *H. reidi* (Oliveira et al. 2014) or in *O. tau* (Fine and Waybright 2015).

Furthermore, in the present study, SPL increased with body mass in males, but not in females. A positive correlation was found in females, but not in males of *T. schalleri* (Ladich et al. 1992a, Ladich and Schleinzer 2020). In *T. vittata*, SPL increased with body weight during ontogeny, but not in adult fish of either sex (Ladich et al. 1992a, Henglmüller and Ladich 1999, Ladich and Maiditsch 2018). In *H. reidi* no such correlations were observed in either sex (Oliveira et al. 2014). However, besides *T. vittata*, it has been shown that SPL increased during ontogenetic development in *S. schoutedeni* and in *H. didactylus* (Vasconcelos and Ladich 2008, Lechner et al. 2010, reviewed in Ladich 2015b). Moreover, in *C. regalis*, SPL correlated positively with size (Connaughton et al. 2000). SPL increased rapidly with size up to 200 g in *O. tau* and up to 60 mm SL in *S. schoutedeni* respectively before levelling off (Lechner et al. 2010; Fine and Waybright 2015).

No correlation was found between burst period and body weight in this study, neither for males nor for females. But, since burst period could only be analysed for three females and the investigated size range for both sexes could have been too small, these results should be interpreted cautiously. Ladich et al. (1992a) did report that burst period correlated positively with body mass in male *T. pumila*, but not in male *T. vittata* nor male *T. schalleri*. Interestingly, in female *T. schalleri*, burst period increased significantly with size. In general, temporal properties of sounds seem to increase with size in fish. A positive correlation was found between pulse duration and size in *A. akallopisos* (Colleye et al. 2009) as well as in *C. regalis* (Connaughton et al. 2000). In *P. cromis*, both pulse duration and the interpulse interval increased with size (Tellechea et al. 2011). In *A. regius*, sound duration as well as number of pulses increased with increasing body size, but pulse period decreased (Pereira et al. 2020).

4.5. Conclusion

The present study revealed that about two third of female *T. pumila* are vocal during agonistic encounters. This higher percentage of vocalizing females compared to a prior study (Schleinzer 1992) might be due to improved recording methodology or due to differences between populations studied. This confirms that females in all representatives of the genus *Trichopsis* defended their territories similarly using visual and acoustic displays. Sex-specific differences in vocalizations are most likely based on sexual dimorphism of sonic organs. Because sound production and the involved mechanism are well investigated in *Trichopsis*

spp., this allowed further exploration to what extent sound characteristics are influenced by differences in sound generating mechanisms not only between sexes, but also within closely related species.

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Appendix

Table I: Number of fish used for anatomical, behavioural and acoustical analyses.

Anatomy	**Males**	**Females**
Total no. fish	21	13
No ET2	1	3
Behaviour	**Male contests**	**Female contests**
Total no. contests	9	14
Total no. fish analysed	18	28
Fish used twice	1	8
Contests without sounds	1	4
Acoustics	**Males**	**Females**
Total no. fish	12	13

Table II: Body mass (BM), standard length (SL), diameter of first (ET1) and of second (ET2) enhanced tendon for each *T. pumila* male (M1 - M21) and each *T. pumila* female (F1 - F13).

Fish	BM (g)	SL (mm)	ET1 (mm)	ET2 (mm)
M1	0.59	26.66	0.35	0.23
M2	0.57	29.11	0.28	0.24
M3	0.38	25.5	0.36	0.21
M4	0.47	26.57	0.36	0.23
M5	0.28	23.33	0.21	0.17
M6	0.54	26.95	0.39	0.20
M7	0.34	24.12	0.28	0.17
M8	0.28	26.8	0.49	0.32
M9	0.4	24.83	0.43	0.29
M10	0.52	29.15	0.42	0.27
M11	0.51	27.31	0.40	0.30
M12	0.36	25.58	0.36	0.22
M13	0.45	26.9	0.36	0.24
M14	0.38	27.09	0.52	0.34
M15	0.44	26.95	0.23	0.16
M16	0.45	27.45	0.44	0.32
M17	0.51	29.22	0.36	0.28
M18	0.39	27.79	0.37	0.24
M19	0.53	27.04	0.31	-
M20	0.34	24.88	0.19	0.12
M21	0.28	24.62	0.35	0.25

Table II (contd.)

Fish	BM (g)	SL (mm)	ET1 (mm)	ET2 (mm)
F1	0.78	30.19	0.30	0.11
F2	0.8	28.4	0.23	-
F3	0.55	26.65	0.21	-
F4	0.31	23.37	0.13	0.11
F5	0.57	28.12	0.24	0.18
F6	0.36	24.93	0.13	0.09
F7	0.28	26.17	0.14	-
F8	0.31	22.9	0.15	0.12
F9	0.26	22.35	0.12	0.08
F10	0.31	25.16	0.21	0.20
F11	0.21	21.08	0.12	0.07
F12	0.66	29.28	0.18	0.12
F13	0.5	27.56	0.11	0.06

Table III: Contest duration (CD), lateral display duration (LD), number of sounds (NS) and number of buttings (NB) for each male-male (cM1 - cM9) and each female-female (cF1 - cF14) contest. *) Individual used twice

Contest	CD (s)	LD (s)	NS (n)	NB (n)	BM (g)	
					Fish 1	Fish 2
cM1	21	18	14	0	0.55	0.51
cM2	1710	103	6	0	0.51	0.54
cM3	398	200	5	27	0.54	0.61
cM4	556	204	28	22	0.41	0.42
cM5	198	165	1	7	0.3	0.33
cM6	65	48	25	1	0.45	0.49
cM7	344	66	0	0	0.34	0.37
cM8	820	44	1	11	0.52	0.52 *)
cM9	326	10	7	55	0.44	0.41

Table III (contd.)

Contest	CD (s)	LD (s)	NS (n)	NB (n)	BM (g)	
					Fish 1	Fish 2
cF1	228	120	8	12	0.53	0.51
cF2	603	146	24	11	0.43	0.45
cF3	83	43	0	6	0.38	0.42
cF4	21	11	0	1	0.42	0.42
cF5	290	142	4	8	0.46	0.41
cF6	274	158	12	19	0.37	0.33
cF7	210	78	8	6	0.54 *)	0.52
cF8	355	55	5	6	0.58	0.55
cF9	125	68	0	4	0.63	0.59
cF10	211	165	0	1	0.43 *)	0.42 *)
cF11	953	65	4	68	0.36	0.38
cF12	350	89	2	22	0.55 *)	0.55 *)
cF13	1608	63	10	33	0.52 *)	0.51
cF14	1481	47	4	141	0.45 *)	0.42 *)

Table IV: Body mass (BM), standard length (SL), number of sounds (NS), mean number of bursts (Nob), percentage of short bursts within a sound (PerSB), burst period (BP), dominant frequency (DF), sound pressure level SPL frequency A weighting (LAF) and SPL frequency Z weighting (LZF) for each male (acM1 - acM12) and each female (acF1 - acF13).

Fish	BM (g)	SL (mm)	NS (n)	Nob (n)	PerSB (%)	BP (ms)	DF (Hz)	LAF (dB)	LZF (dB)
acM1	0.55	28.73	10	2.8	0	55.12	2143	111.4	113.9
acM2	0.51	29.47	6	2.3	100	61.87	2030	108.2	111.5
acM3	0.51	29.97	6	3	8.33	49.89	2092	109.3	112.4
acM4	0.54	28,29	3	1.3	0	50.66	2038	114.2	114.4
acM5	0.61	30.97	2	3	0	57.57	2065	121.7	121.3
acM6	0.41	26.76	12	2	16.67	55.53	2051	114.7	117.4
acM7	0.42	26.98	15	1.7	0	56.89	2055	116.8	117.8
acM8	0.3	24.46	1	1	100	-	2234	100.5	107.7
acM9	0.45	27	8	2.4	0	58.33	2077	118.2	120.1
acM10	0.49	29.73	17	1.5	8.82	54.45	2116	113.4	117.2
acM11	0.52	29.02	1	2	0	42.36	1954	118.2	121.3
acM12	0.44	27.61	7	2.4	16.67	61.84	2213	115.0	120.1

Table IV (contd.)

Fish	BM (g)	SL (mm)	NS (n)	Nob (n)	PerSB (%)	BP (ms)	DF (Hz)	LAF (dB)	LZF (dB)
acF1	0.53	28.43	2	1	100	-	2359	101.2	115.0
acF2	0.51	28.2	6	1	100	-	2327	96.2	114.2
acF3	0.43	27.68	18	1.7	50.93	45.47	2367	104.0	117.0
acF4	0.45	27.52	6	1	100	-	2229	101.9	115.2
acF5	0.46	26.96	3	1	66.67	-	2080	93.1	105.0
acF6	0.41	26.25	1	1	100	-	2121	95.2	116.4
acF7	0.37	26.17	2	1	100	-	2377	100.4	109.2
acF8	0.33	25.77	10	1.2	100	44.34	2273	99.3	109.7
acF9	0.52	28.89	2	1	100	-	2382	98.6	106.9
acF10	0.55	29.88	6	1	100	-	2412	101.4	111.0
acF11	0.36	26.17	2	1	100	-	2342	91.9	111.1
acF12	0.38	25.59	2	1	100	-	2272	94.1	111.1
acF13	0.51	27.65	2	1.5	100	44.84	2124	107.6	137.7

Zusammenfassung

Trotz zahlreicher Studien über Lautproduktion bei Fischen allgemein, ist die Zahl der Untersuchungen der Lautproduktion bei Weibchen überschaubar. Dies liegt vor allem daran, dass Männchen besser ausgebildete lautproduzierende Organe besitzen und häufiger Laute erzeugen. Dabei sind Weibchen sehr wohl zur Lautbildung befähigt, da die Organe hierfür selten fehlen. In zwei von drei Arten innerhalb der Gattung *Trichopsis* ist die Lautproduktion gut untersucht, allerdings gibt es Widersprüchlichkeiten, was die letzte und kleinste Art *T. pumila* betrifft. Diese Studie dient dazu, die Frage bezüglich der Lautproduktion in weiblichen Zwergguramis zu klären. Desweitern soll untersucht werden, ob es geschlechtsspezifische Unterschiede im agonistischen Verhalten, in den Lautmerkmalen sowie in dem zugrunde liegenden Mechanismus bestehen. Hierfür wurde die Anatomie der verstärkten Sehnenpolster (SPs), das agonistische Verhalten sowie die agonistischen Laute von weiblichen und männlichen Zwergguramis (*T. pumila*) untersucht. Folgende Variablen wurden ausgewertet: Durchmesser vom ersten (SP1) sowie vom zweiten (SP2) verdickten Sehnenpolster, Kampf- und Lateraldisplay-Dauer, Anzahl von Lauten sowie von Stossen innerhalb einer Auseinandersetzung, Anzahl von Bursts, Prozentanzahl von Einzelbursts innerhalb eines Lautes, Burstperiode, Hauptfrequenz und Schalldruckpegel (SDP). Die SPs hatten bei Männchen einen doppelt so großen Durchmesser wie bei Weibchen. Bei beiden Geschlechtern waren die SP1-Durchmesser rund 1.5-mal größer als der SP2. Es gab keine geschlechtsspezifischen Unterschiede in Kampf- und Lateraldisplay-Dauer, der Anzahl von Lauten sowie des Stossens innerhalb einer Auseinandersetzung. Dafür haben sich die Geschlechter jedoch in allen fünf untersuchten Lautmerkmalen unterschieden. Männliche Laute bestanden aus doppelt so vielen Bursts, welche hauptsächlich aus Doppelimpulsen (um 80 %) bestanden und einer höheren Burstperiode. Desweiteren waren männliche Laute mit einer Hauptfrequenz um 2090 Hz sowie einem SDP um 114 dB wesentlich tieffrequenter und lauter als die der Weibchen. Im Gegensatz zu früheren Annahmen produzieren rund zwei Drittel der weiblichen Zwergguramis Laute während agonistischen Auseinandersetzungen. Dabei reflektiert der Sexualdimorphismus in den Sehnenverdickungen die Unterschiede in den Lautmerkmalen zwischen Männchen und Weibchen.

Schlagwörter: Fische, *Trichopsis*, Sexualdimorphismus, lautproduzierende Organe, agonistisches Verhalten, Lautmerkmale