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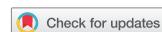
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Acoustic signalling in female fish: factors influencing sound characteristics in croaking gouramis

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ABSTRACT

The characteristics of sounds produced by fishes are influenced by several factors such as size. The current study analyses factors affecting structural properties of acoustic signals produced by female croaking gouramis *Trichopsis vittata* during agonistic interactions. Female sounds (although seldom analysed separately from male sounds) can equally be used to investigate factors affecting the sound characteristics in fish. Sound structure, dominant frequency and sound pressure levels (SPL) were determined and correlated to body size and the order in which sounds were emitted. Croaking sounds consisted of series of single-pulsed or double-pulsed bursts, each burst produced by one pectoral fin. Main energies were concentrated between 1.3 and 1.5 kHz. The dominant frequency decreased with size, as did the percentage of single-pulsed bursts within croaking sounds. The SPL and the number of bursts within a sound were independent of size but decreased significantly with the order of their production. Thus, acoustic signals produced at the beginning of agonistic interactions were louder and consisted of more bursts than subsequent ones. Our data indicate that body size affects the dominant frequency and structure of sounds. The increase in the percentage of double-pulsed bursts with size may be due to stronger pectoral muscles in larger fish. In contrast, ongoing fights apparently result in muscle fatigue and subsequently in a decline in the number of bursts and SPL. The factor 'order of sound production' points to an intra-individual variability of sounds and should be considered in future studies.

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Sound production; fish; sound level; dominant frequency; correlation

Introduction

Sound production in fishes has been described more frequently and in more detail in males than in females (see reviews: Myrberg 1981; Amorim 2006; Ladich and Myrberg 2006; Myrberg and Lugli 2006). The main reason for this sex-specific difference in reporting acoustic signalling in fishes is that vocal fish are typically substrate breeders, with males advertising and defending their nest sites acoustically and also vocalizing during courtship (Myrberg and Lugli 2006; Ladich 2014; Amorim et al. 2015; Kaatz et al. 2017). Female sound production was mainly reported during aggressive interactions (Myrberg et al. 1965;

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Hawkins and Rasmussen 1978; Schwarz 1980; Ladich 1990, 2007; Hawkins and Amorim 2000; Lagardere et al. 2005; Maruska and Mensinger 2009; Kéver et al. 2012) and on some occasions during mating (Ladich 2007; Oliveira et al. 2014).

Interestingly, sonic mechanisms are rarely absent in females, indicating that female sound production is widespread despite the few reports (reviewed in Ladich 2015a). Sexually dimorphic sonic mechanisms have been described in cods (family Gadidae) (Templeman and Hodder 1958), cusk-eels (Ophidiidae) (Kéver et al. 2012), European hakes (Merlucciidae) (Groison et al. 2011), toadfishes (Batrachoididae) (Fine et al. 1990), callichthyid catfishes (Callichthyidae) (Hadjiaghai and Ladich 2015), gouramis (Osphronemidae) (Kratochvil 1985) and croakers (Sciaenidae) (Hill et al. 1987, Connaughton and Taylor 1995). In gadi-forms, this sexual dimorphism is pronounced during the pre-spawning and spawning season due to hypertrophy of sonic muscles and higher vocal activity of males during the breeding season (Rowe and Hutchings 2004). Interestingly, the degree of sexual dimorphism may vary considerably among closely related species, including being absent in females such as among sciaenids (Hill et al. 1987). Within the osphronemid genus *Trichopsis*, the pectoral sonic mechanism is about one-third smaller in female *Trichopsis vittata* and absent in female pygmy gouramis *Trichopsis pumila* (Kratochvil 1985; Ladich 2015a).

Sound production in female fish has typically been described in comparison to males, but the behavioural contexts were not always described satisfactorily. This complicates statistical analysis of female sounds. Male and female fish have on a few occasions been recorded under similar conditions and analysed separately statistically (Lagardere et al. 2005; Ladich 2007; Fine and Waybright 2015; Ueng et al. 2007; Simoes et al. 2008; Tellechea et al. 2010b; Oliveira et al. 2014). For example, sound characteristics differ between sexes in the cusk-eel *Ophidion rochei* (Kéver et al. 2012) and in the pinhead pearlfish *Carapus boraborensis* (Carapidae) (Lagardere et al. 2005), but behavioural observations are missing in both studies. Ueng et al. (2007) claimed that both sexes of the Japanese croaker emit pre-spawning advertisement calls in single-sex groups and then spawning calls. The behavioural observations, however, were insufficiently detailed to support the interpretation that both sexes advertise their readiness to spawn acoustically. When females and males were recorded in the same behavioural context and both sexes were similarly sized, then the differences in sound characteristics were small (Ladich 2007; Simoes et al. 2008; Oliveira et al. 2014).

Nonetheless, analyses of female sound features in relationship to their body size or other factors are sparse (for an exception, see Tellechea et al. 2010b). Several characteristics of vocalizations depend on size and fish may use them to assess the fighting ability of opponents (Ladich 1998) or in mate choice (Myrberg et al. 1986; McKibben and Bass 1998; Amorim et al. 2015). Correlations between signal structure and size or age are evident in those ontogenetic studies in which size differs considerably between stages. Temporal patterns, dominant (peak) sound frequencies and sound levels were found to be correlated to age or size (Henglmüller and Ladich 1999; Wysocki and Ladich 2001; Amorim and Hawkins 2005; Lechner et al. 2010; Vasconcelos and Ladich 2008; reviewed in Ladich 2015b).

In adult fish the most common relationship was between size (body mass, length) and sound frequency. This correlation was negative in numerous non-related taxa possessing different sonic mechanisms. Examples include croaking gouramis (male *T. vittata*, *T. schalleri*, *T. pumila* – Ladich et al. 1992), damselfish (male *Stegastes partitus* – Myrberg et al. 1993; *Amphiprion* spp. – Colleye et al. 2009; Colleye and Parmentier 2012), catfishes (*Corydoras paleatus* both sexes pooled – Pruzsinszky and Ladich 1998; *Platydoras armatulus*

– Ladich 1997; doradids – Knight and Ladich 2014) and croakers (male *Cynoscion regalis* – Connaughton et al. 2000; *Micropogonias furnieri* – Tellechea et al. 2010a; *Pogonias cromis* both sexes – Tellechea et al. 2010b). A lack of a correlation between dominant frequency and size was reported in five out of six catfish species, but explained by the small size range of individuals recorded (Ladich 1997).

Sound (pressure) levels (SPL) have seldom been reported to depend on body size in adult fish but may be higher in males or winners of fights (Ladich 1998, 2007). An increase in SPL with body size was primarily reported in ontogenetic studies in *T. vittata*, the toadfish *Halobatrachus didactylus* and the catfish *Synodontis schoutedeni* (Wysocki and Ladich 2001; Vasconcelos and Ladich 2008; Lechner et al. 2010). No sound level – size dependency was determined for adult males within the genus *Trichopsis* (Ladich et al. 1992) but found in the croaker *C. regalis* (Connaughton et al. 2000) and the catfish *Hoplosternum thoracatum* (both sexes pooled – Hadjiaghai and Ladich 2015).

The temporal properties of sounds (duration, pulse/burst number and period, pulse duration) typically increased with size during ontogeny (eg *T. vittata* – Henglmüller and Ladich 1999; *H. didactylus* – Vasconcelos and Ladich 2008; *S. schoutedeni* – Lechner et al. 2010) and similarly in adults as they grew larger (Colley et al. 2009; Connaughton et al. 2000; Tellechea et al. 2010a; 2010b; Colley and Parmentier 2012; Hadjiaghai and Ladich 2015; Casaretto et al. 2016).

The present study measured the characteristics of sounds that female *T. vittata* produced during agonistic encounters (Ladich et al. 1992; Ladich 2007) to determine whether temporal and spectral characteristics as well as sound levels are indications of body size or whether they depend on other factors. Differences due to water temperature or behavioural contexts were not investigated because this has been done in two prior studies (Ladich 2007; Ladich and Schleinzer 2015). This study is the first entirely devoted to analysing acoustic signals in female fish and showing that female sounds can be used similar to males' to study factors affecting sound characteristics.

Material and methods

Animals

Eleven female *T. vittata* (body weight: 0.76–1.48 g, standard length: 35–41 g) obtained from local pet suppliers were investigated during this study. They were kept in community tanks (100 × 50 × 40 cm) at 25 ± 1 °C and in a 12-h light – 12 h dark cycle. Water was maintained by external filters. Tank bottoms were covered with sand and flowerpots; plants were provided as hiding places. Fish were primarily fed food flakes (Tetramin) five times a week. Sexing of fish was based on the presence of the whitish ovary in females. After experiments, fish were returned to the community tanks.

Behaviour and sound recordings

Prior to experiments, females were isolated for five days in tanks (50 × 27 × 30 cm) under conditions similar to the holding tanks in order to reduce dominance experience. On the fifth day, fish were introduced into the left and right halves of the test tanks (50 × 27 × 30 cm), which were separated by a plastic plate. The test tank was placed on a table that rested on a

vibration-isolated concrete plate. The entire set-up was enclosed in a walk-in sound-proof room, which was constructed as a Faraday's cage.

Agonistic behaviour started after the separating plate was removed. The agonistic interaction consisted of erecting unpaired fins, head to tail circling and sound production (see Figure 1 in Ladich 2007). Typically, both fish emitted sounds alternately. Such fighting sequences are interrupted by air-breathing. The sound-producing fish could be determined by the rapid pectoral fin beating during which the whole animal was shaking. The first 15 sounds emitted by each female were used for analysis (see Statistics).

Acoustic signals and behaviour were recorded using a hydrophone (Brüel and Kjaer 8101, sensitivity: -186 dB re 1 V/ μ Pa) connected to a microphone power supply (Brüel and Kjaer 2804) which was connected to the XLR mic input of a 4-K video camera (Panasonic HC-X1000). The entire setup was positioned behind a curtain so that animals could not see the experimenter. Recordings were controlled via the camera display and a video monitor (Sony PVM 4000).

Sound pressure level measurements

Sound pressure levels (LAFmax, broadband A frequency weighting, RMS Fast time weighting) were recorded using a sound-level meter (Brüel and Kjaer 2250) connected to the second output of the microphone power supply. The equipment was calibrated with the hydrophone calibrator (Brüel and Kjaer 4229). All dB values were referenced to 1 μ Pa.

Because of varying distances of the fish to the hydrophone, the test tank was divided into 50 sectors (5×5 cm) by a grid applied to the front glass of the aquarium, and the sector in which female produced croaking sounds was noted. To compensate for different distances between the hydrophone and the croaking fish, a correction factor was calculated (Ladich et al. 1992; Ladich 2007). For this correction factor, a typical croak was played back at a constant level from a small loudspeaker (Fuji 7G06) in each of the 50 sectors and the SPL noted. The SPL differences between the sector nearest to the hydrophone (10 cm away) and all other sectors were calculated and added to the SPL values measured, while the fish produced sounds in a particular sector. This yielded a distance-independent absolute SPL for each sound emission.

Sound analysis

The video camera recorded LPCM-coded sounds, which were afterwards rendered in Sony Vegas Pro 13.0 to wav-format (44.1 kHz, 16 bit). These sounds were analysed using CoolEdit 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: (1) total number of bursts (number of short single-pulsed and long double-pulsed bursts) within a croaking sound (Figure 1(a)); (2) percentage of short bursts within a sound, (3) burst period [sound duration/burst number] and (4) dominant frequency of sounds. Dominant frequency was determined by measuring the frequency at the highest spectral level in cepstrum-smoothed power spectra (filter bandwidth 50 Hz, number of coefficients: 30–40, overlap 75%, Hanning window, maximum frequency 3.5 kHz) (Figure 1(b)) (Noll 1967; Ladich 2007). Frequencies were not analysed above 3.5 kHz to avoid the resonance frequencies of our small tank, which are above 3.3 kHz according to Akamatsu et al. (2002).

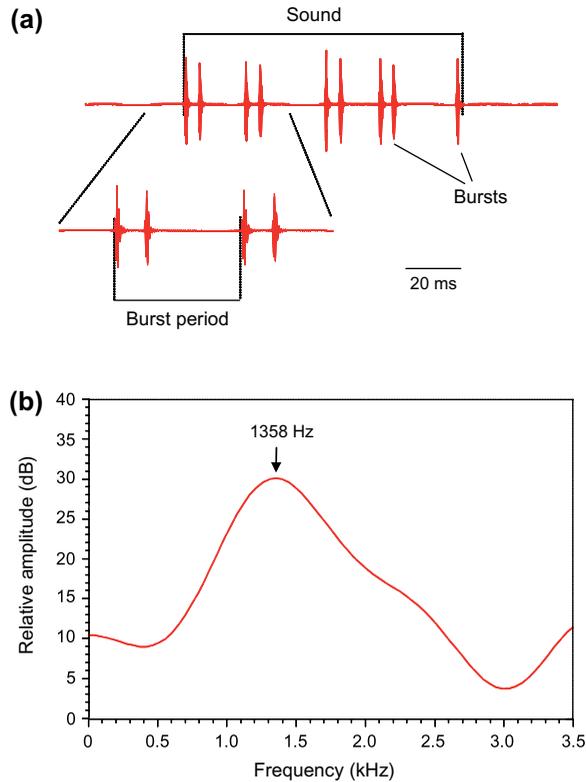


Figure 1. (a) Oscillogram of a female croaking sound consisting of four double-pulsed bursts and one single-pulsed burst and expansion of the first two bursts illustrating the burst period. (b) Cepstrum-smoothed power spectrum of a female sound. Arrow indicates the dominant frequency. Sampling frequency 48 kHz, filter bandwidth 50 Hz, number of coefficients 40, 75% overlap, Hanning window.

Statistical analysis

We recorded sounds emitted during agonistic interactions of 11 females and analysed 10–15 sounds per fish (except for 2 females, where 7 and 9 sounds were recorded). Means of sound characteristics (number of bursts, burst period, percentage of short bursts within a croaking sound, dominant frequency and SPL) were calculated for each individual ($N = 11$, SPL: $N = 9$). Individual means of sound characteristics were then correlated to body measures (body weight and standard length).

Second, we calculated means of characteristics of all sounds emitted first, second, third, etc. in agonistic encounters. A maximum of 11 sounds was analysed because most females produced at least 11 sounds. This calculation was done to determine whether sound features depend on the order of sound production besides body size. All calculations were done using SPSS 23 (IBM SPSS Statistics).

Ethical considerations

Both sexes of croaking gouramis produce visual and acoustic signals during the lateral display phase (Ladich 1998, 2007) without any physical contact between opponents. Contests

were stopped as soon as one fish won or as soon as the frontal display phase was reached. 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).

Results

Sound structure

Acoustic signals produced by female *T. vittata* during agonistic interactions consisted of series of bursts, each one produced by one pectoral fin. Bursts were typically built up of two pulses (long burst) and occasionally of single pulses (short burst) (Figure 1(a), 2(a, b)). The mean number of bursts was 4.5, the mean percentage of short bursts within sounds was 21.8, the mean burst period 42 ms, the mean dominant frequency 1.4 kHz and the mean SPL 119 dB (Table 1).

Sound characteristics and body size

Two out of five sound characteristics measured were correlated with body size. The dominant frequency was highly correlated to all morphological measures and decreased with increasing size (body weight: $r = -.87$, $n = 11$, $p < 0.001$; SL: $r = -.70$, $p < 0.02$) (Figure 3(a)). Standard length was negatively correlated to the percentage of short bursts within croaking sounds ($r = -.69$, $n = 11$, $p < 0.05$) and the correlation to body weight was close to significance ($r = -.59$, $n = 11$, $p = .056$). Thus, smaller females produced a higher percentage of short bursts compared to long bursts than larger females (Figure 3(b)). No relationship was found between size and SPL, total numbers of bursts and burst period.

Sound characteristics and order of sound production

Sound characteristics were also examined with respect to the order of their production to investigate whether their variability depended on this factor. The SPL declined with the order of production of sounds ($r = -.91$, $n = 11$, $p < 0.001$). Thus, the levels of the first sounds were higher than those of subsequent sounds (Figure 4(a)). Similarly, the mean number of bursts was higher in the beginning than in subsequent sounds ($r = -.67$, $n = 11$, $p < .05$) (Figure 4(b)). Accordingly, the SPL and the number of bursts were positively correlated to each other ($r = .783$, $N = 11$, $p < 0.01$).

Discussion

The present analysis of croaking sounds of female *T. vittata* revealed that sound characteristics are affected by different factors. While the factor body size explains some properties of sounds such as the dominant frequencies, it fails to affect others such as SPL in particular in adult fish. Therefore, a new factor – namely the order of production of sounds – has been investigated in the present study and its effect on sound characteristics is discussed in the following.

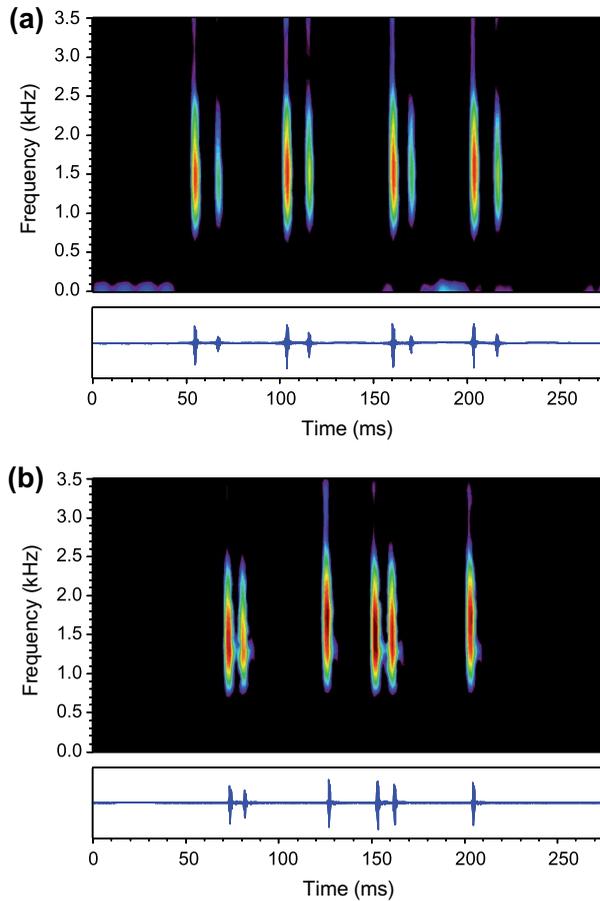


Figure 2. Sonograms (above) and oscillograms (below) of two sounds produced by females to illustrate the variability in the temporal structure of sounds. (a) A sound consisting of four long (double-pulsed) bursts, and (b) a sound consisting of two long and two short (single-pulsed) bursts produced alternately. Sampling frequency 44.1 kHz, filter bandwidth 150 Hz, 75% overlap, Hanning window.

Table 1. Mean, standard error of the mean (S.E.M.), minimum and maximum value of sound characteristics of female croaking sounds. Means of 11 females (SPL, $N = 9$) are shown.

Sound characteristics	Mean	S.E.M.	Min	Max
Dominant frequency (kHz)	1396	20.2	1293	1508
Burst number (n)	4.55	0.24	3.8	5.9
Percent short bursts (%)	21.8	4.9	7.7	59.5
Burst period (ms)	42	0.51	37.9	44.1
Sound pressure level (dB)	118.9	1.48	112.5	124.5

Dominant frequency

The dominant frequency of sounds decreases with body size in female *T. vittata*, similar to males in all representatives of the genus *Trichopsis* (Ladich et al. 1992) and many non-related species investigated so far. The correlation is strong for both size measures, namely weight and length. Such a negative relationship has been shown in females of the drum

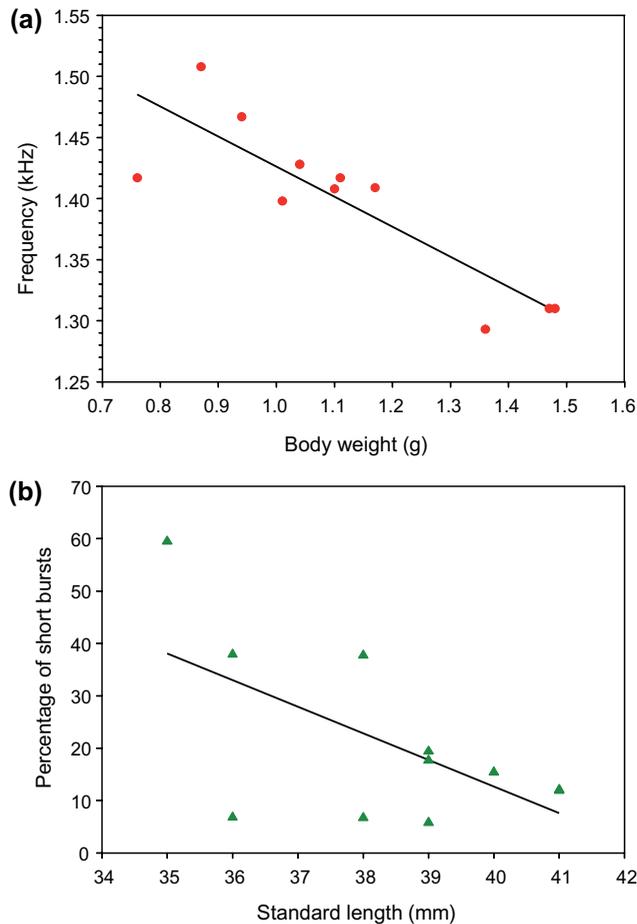


Figure 3. Correlation between (a) body weight and mean dominant frequency of female croaking sounds recorded during agonistic interactions. Regression equation: Frequency (kHz) = $1.67 - 246 * \text{body weight}$; $r^2 = 0.74$, and between (b) standard length and mean percentage of short bursts relative to the total number of burst within a sound. Regression equation: Percentage (%) = $216 - 5.08 * \text{SL}$; $r^2 = 0.36$.

P. cromis (Tellechea et al. 2010b). Data indicate that such correlations exist in females of other species. Strong negative correlations were described in studies in which females and males were pooled, such as in ontogenetic studies (reviewed in Ladich 2015b), as well as in adult fish (eg callichthyid catfish: Pruzsinszky and Ladich 1998; Hadjiaghai and Ladich 2015; clownfish: Colleye et al. 2009; Colleye and Parmentier 2012). In general, dominant frequencies do not differ between male and female *T. vittata* if both sexes are size-matched (see Figure 5(a) in Ladich 2007). Interestingly, the dominant frequency declined more rapidly in female disturbance calls of *P. cromis* than in male calls (Tellechea et al. 2010b). This is not the case in *T. vittata* (Ladich et al. 1992 and present study).

The relationships between size and dominant (peak) frequency of acoustic signals are mainly but not exclusively found in species generating short-pulsed sounds. Myrberg et al. (1993) argued that differences in the peak frequencies of chirp sounds produced by male bicour damselfish *Stegastes* (*Eupomacentrus*) *partitus* are constrained by the volume of

their swim bladder. In *Trichopsis*, the suprabranchial organ (SBO), an air-breathing cavity dorsal to gills (Bader 1937), may be responsible for the dominant frequency together with the pectoral sound-generating mechanism close by. The relatively high dominant frequency above 1 kHz reflects the small SBO and corresponds well with the most sensitive frequency shown in auditory measurements (Ladich and Yan 1998). In contrast, Torricelli et al. (1990) reported that structural parameters of both aggressive and courtship sounds are not affected by the size of male Padanian gobies (*Padogobius bonelli*). Similarly, dominant frequencies of click sounds were not correlated to seahorse height in *H. reidi* (Oliveira et al. 2014). This may be due to a different sonic mechanism in which resonance properties of air-filled cavities do not determine dominant frequencies of sounds. The fundamental frequency of sounds may be related to size in some fish species possessing drumming muscles such as sciaenids or doradid catfishes (Connaughton et al. 2000; Tellechea et al. 2010a; 2010b; Knight and Ladich 2014). Connaughton et al. (2000) argued that larger muscles with longer fibres would take longer to complete a contraction, resulting in a lower frequency in drumming muscles in larger sciaenids.

Sound level

An increase in sound amplitudes with growth has been shown in several ontogenetic studies in non-related taxa such as tigerfish *Therapon jarbua* (Schneider 1961), gouramis, toadfish and catfish (Ladich 2015b). In contrast, a size-dependent increase in sound level has seldom been described in adult fish except in male *Cynoscion regalis* (Connaughton et al. 2000). In catfish species, it was demonstrated when both sexes and several species were pooled (Knight and Ladich 2014; Hadjiaghahi and Ladich 2015). In both female and male seahorse *H. reidi*, (Oliveira et al. 2014) such a relationship is lacking. Similarly, neither male nor female *T. vittata* show a size-dependent change in sound level (males: Ladich et al. 1992; females: present study).

Interestingly, the current detailed analysis of female *T. vittata* revealed a decrease in the SPL of acoustic signals produced later than at the beginning of agonistic interactions. Such a decline most likely reflects pectoral muscle fatigue in ongoing fights and may partly explain the lack of a size – amplitude relationship (Figure 4(a)).

Temporal characteristics of sounds

Temporal characteristics such as sound duration, number of burst/pulses within sounds, pulse duration and burst/pulse periods typically increased with growth or size in all species studied (eg Amorim and Hawkins 2005; Connaughton et al. 2000; Colleye et al. 2009; Tellechea et al. 2010a; 2010b, Knight and Ladich 2014; Hadjiaghahi and Ladich 2015), The few exceptions include the toadfish *H. didactylus*, in which the number of pulses within a sound and thus sound duration decreased as size increased during ontogeny (Vasconcelos and Ladich 2008). Ladich (1997) and Pruzsinszky and Ladich (1998) showed that sound duration depended on the size of the sound-generating mechanisms, namely the length of the pectoral spine in 7 catfish species from 4 families.

We found no relationship between body size and temporal patterns of sounds such as pulse period in female *T. vittata*. A correlation between pulse period and size was also lacking in males (Ladich et al. 1992). We did, however, observe a negative correlation

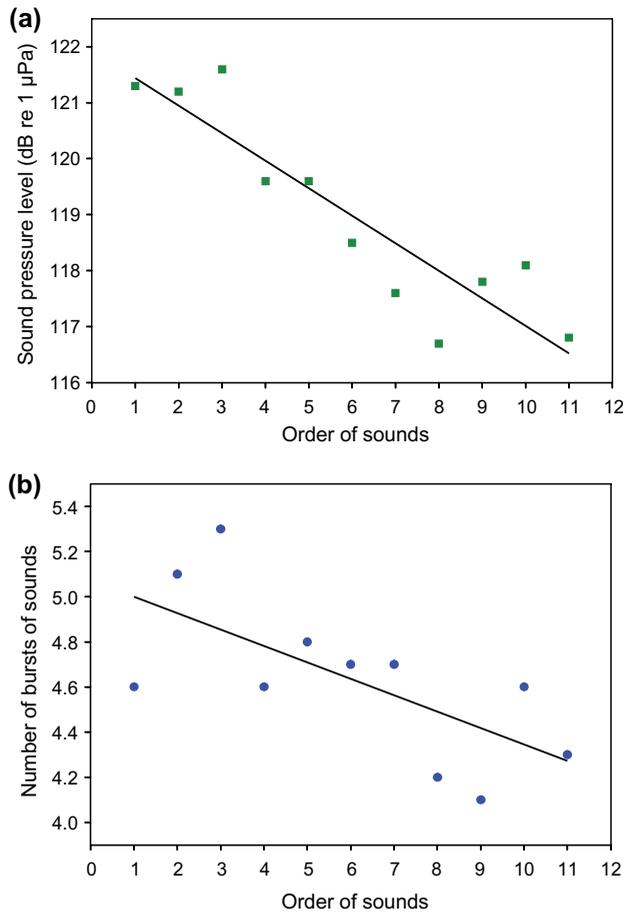


Figure 4. Correlation between (a) the mean SPL of sounds versus the order of production of sounds during agonistic interactions. Regression equation: $\text{SPL (dB re 1 } \mu\text{Pa)} = 122 - 0.49 * \text{order}$; $r^2 = 0.83$, and (b) between the mean number of bursts of sounds and the order of production of sounds during agonistic interactions. Regression equation: $\text{Number of bursts} = 5.07 - 0.07 * \text{order}$; $r^2 = 0.45$.

between body length and sound structure, namely the percentage of short bursts. This can be explained by the unique sound-generating mechanism in croaking gouramis (Kratovichil 1985; Ladich and Fine 2006). They produce two-pulsed bursts when two thickened pectoral fin tendons are stretched and plucked during rapid pectoral fin beating (similar to guitar strings). Smaller fish may not be able to stretch both tendons strongly enough to produce two pulses during forward movement of pectoral fins. An increase in the number of double-pulsed bursts within sounds also occurred during ontogeny (Henglmüller and Ladich 1999).

In addition, the number of bursts within croaking sounds, which is independent of body size, decreased in the course of fights. Sounds produced at the beginning are built up of more bursts than sounds emitted later. Muscle fatigue is the most likely explanation. A relationship between burst number and sound amplitude is clear when comparing the burst number of agonistic and courtship sounds in female *T. vittata* (Ladich 2007). Female pre-spawning purrs consist of fewer bursts and they had lower SPL than agonistic sounds.

While Ladich (2007) argued that short, low-amplitude pre-spawning sounds are advantageous to avoid being intercepted by conspecific males, a decrease in amplitude may be an unwanted side effect during prolonged agonistic interaction. For example, Ladich (1998) observed that males producing higher amplitude sounds had a higher chance of winning.

Conclusion

Several factors affect the sound characteristics in female *T. vittata*. Body size is negatively correlated to the dominant frequency of sounds, similar to many other fish studies in which males or both sexes were investigated. Size also affects the temporal structure of sounds to some degree: the number of two-pulsed bursts increases with size. Two sound characteristics are independent of size and correlated to the order of the production of sounds, namely sound level and sound duration (number of bursts). This decrease in level and duration most likely reflects muscle fatigue as fights progress. This points to an intra-individual variability of sounds besides inter-individual variability and should be considered in future studies.

A similar distinction between sound characteristics has been described by Gerhardt (1991) in male advertisement calls of tree frogs. He classified call properties as static or dynamic based on within-male variability during bouts of calling. Gerhardt (1991) assumed that call properties are important in female mate choice. This is in contrast to croaking gouramis, which do not produce advertisement calls. Nevertheless, different characteristics of agonistic sounds may be important in assessing opponents in female, male and juvenile *T. vittata* and other species.

Finally, our study indicates that sounds of female fish – although seldom analysed separately from males – can successfully be used to investigate factors influencing the structural properties of sounds.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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