Effect of temperature on acoustic communication: Sound production in the croaking gourami (labyrinth fishes)

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ABSTRACT

Sound communication comprising the production and detection of acoustic signals is affected by ambient temperature in ectothermic animals. In the present study we investigated the effects of temperature on sound production and characteristics in the croaking gourami *Trichopsis vittata*, a freshwater fish from Southeast Asia possessing a highly specialized sound-generating mechanism found only in a single genus. The croaking gourami produces pulsed sounds by stretching and plucking two enhanced pectoral fin tendons during rapid pectoral fin beating. Croaking sounds typically consist of a series of double-pulsed bursts with main energies between 1 and 1.5 kHz. Sounds were recorded during dyadic contests between two males at three different temperatures (25°, 30° and 35 °C). The mean dominant frequency increased with rising temperature from 1.18 to 1.33 kHz, whereas temporal characteristics decreased. The sound interval dropped from 492 to 259 ms, the burst period from 51 to 35 ms and the pulse period from 5.8 to 5.1 ms. In contrast, the number of sounds and number of bursts within a sound were not affected by temperature. The current study shows that spectral and temporal characteristics of sounds are affected in different ways by temperature in the croaking gourami, whereas the numbers of sounds and bursts remain unaffected. We conclude that acoustic communication in gouramis is affected by changes in ambient temperature.

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1. Introduction

Acoustic communication in ectothermic animals such as insects, fish and amphibians is affected by ambient temperature in different ways. Temperature can influence the general vocalizing activity as well as the temporal and spectral patterns of sounds. Second, temperatures can affect the auditory sensitivity and thus the detection of acoustic signals and their characteristics (Papes and Ladich, 2011). This is because temperature affects various physiological processes such as neuronal and muscular activities, including all sensory systems in ectothermic animals (Siegmund and Vogel, 1977; Bennett, 1985; Smotherman and Narins, 1998; Franz and Ronacher, 2002).

Fishes have evolved an incredible diversity of sound-generating mechanisms and communicate acoustically in various contexts such as agonistic and courtship behaviour (for reviews see Ladich and Fine, 2006; Ladich and Myrberg, 2006; Myrberg and Lugli, 2006; Kasumyan, 2008; Fine and Parmentier, in press). The occurrence of vocal organs in different species of fish does not follow any systematic pattern. Vocal organs may be absent in some taxa, whereas in others – such as doradid and pimelodid catfishes – even two different mechanisms

may be present in the same species. The most important mechanisms comprise structures entirely devoted to sound production, namely sonic (drumming) muscles which vibrate swim bladders. The drumming muscles can be completely attached to the bladder wall (intrinsic type, e.g. toadfishes) or they originate on structures outside the bladder (such as the skull, pectoral girdle, vertebral elements or ribs) and insert on the bladder (extrinsic type, e.g. pimelodid catfishes). They may also vibrate the bladder indirectly via thin bony plates (elastic springs in ariid or doradid catfishes) or via broad tendons (e.g. piranhas) (for reviews see Ladich and Bass, 2011). Swimbladder vibration results in the production of low-frequency harmonic sounds (with main energies below 500 Hz), whereby the fundamental frequency reflects the sonic muscle contraction rate (Ladich, 2014a).

The second major group of sonic mechanisms utilizes pectoral structures which then serve in sound production besides swimming and hovering. Numerous catfish families possess an enhanced first pectoral fin ray which can generate stridulatory sounds when pressing and rubbing ridges of its base against a groove of the shoulder girdle (Fine and Ladich, 2003). Entirely different is the pectoral mechanism in croaking gouramis. In contrast to catfishes where the pectoral mechanisms are known in hundreds of species, the vocal organs in croaking gouramis are found only in representatives of the genus *Trichopsis* (3 species) (Kratochvil, 1985). The mechanism consists of two enhanced pectoral fin tendons which are stretched and plucked by basal elevations of two fin rays similar to guitar strings during rapid fin beating.

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In *Trichopsis* spp., pectoral fins always beat alternately, each fin producing a double-pulsed burst. Sounds produced during territorial interactions typically consist of 4–8 bursts with main energies above 1 kHz (Ladich et al., 1992).

Prior studies on temperature dependence of fish sound production showed that temporal and spectral patterns are affected, although these effects may differ between taxa (Doradidae — Papes and Ladich, 2011; Gobiidae — Torricelli et al., 1990; Lugli et al., 1996; Sciaenidae — Connaughton et al., 2000; Triglidae — Amorim, 2005; and Batrachoididae — Fine, 1978; Brantley and Bass, 1994; Amorim et al., 2006; Maruska and Mensinger, 2009). Fundamental or dominant frequency typically increases, and pulse period (which is the inverse of fundamental frequency) decreases with rising temperature. Sound duration, in contrast, may increase, e.g. in the Lusitanian toadfish, or may decrease, e.g. in the Striped Raphael catfish with rising temperatures (Amorim et al., 2006; Papes and Ladich, 2011). Similarly, it is unclear if temperature affects vocalizing activity, specifically the number of sounds or pulses. Brawn (1961) observed an increase in the number of sounds produced in the cod *Gadus morhua* (formerly *G. callarias*). In contrast, Papes and Ladich (2011) observed no change in the number of pulses either in drumming or stridulation sounds in thorny catfishes. These differences may be due to different sound elements, sonic organs, recording conditions (field, laboratory) or behavioural contexts.

Parallel to sound production, sound detection in fishes depends on temperature. A few investigations in fishes possessing enhanced hearing abilities (Ladich and Popper, 2004: Ladich, 2014b) show that hearing sensitivity increases with temperature in eurythermal (temperate regions) as well as stenothermal (tropical regions) species (Wysocki et al., 2009; Papes and Ladich, 2011).

The current study was designed to determine the way in which temperature affects production and characteristics of sounds in *Trichopsis vittata*, a small representative of labyrinth fishes from Southeast Asia. *T. vittata* was chosen because both sexes regularly emit sounds during agonistic interactions (Ladich, 1998, 2007).

2. Material and methods

2.1. Animals

Eleven male *T. vittata* (1.1 to 2.5 g) purchased from a local pet supplier were investigated. They were kept in 50 to 300 l community tanks before introducing them into a test tank. All aquaria were planted but not aerated or filtered because gouramis possess air-breathing organs (suprabranchial organs or labyrinths) (Bader, 1937). The temperature was kept at 28 ± 1 °C and a 12 h:12 h light:dark cycle was maintained. Fish were fed chironomid larvae, *Tubifex* worms or *Daphnia* spp.

2.2. Experimental setup and sound recordings

The experimental tank was $50 \times 27 \times 30$ cm in size and similarly equipped as the holding tank. Temperature was changed using a heating cable submersed into the sand on the bottom. A male was introduced to the left and another male to the right half of the test tank, which was divided by a plastic sheet. Fish were allowed to adapt to the experimental temperature and their territory for 2 days. Males were never paired twice with the same male.

Acoustic signals and vocalizing behaviour were recorded on HiFi-video tapes using a hydrophone (Brüel & Kjær 8106, sensitivity −172.5 dB re 1 V/μPa; placed close to the back wall in the centre of the aquarium) and a video camera (Panasonic CCD-V800E). Both the hydrophone and the video camera were connected to a HiFi S-VHS video cassette recorder (JVC HRD 4700 EG). Thus, HiFi audio and S-video signals were both stored synchronously on video tapes. The hydrophone was connected via a microphone power supply (Brüel & Kjær 2804) to the microphone input of the VCR. Recordings started as soon as

the plastic sheet, which separated both parts of the test tank, was removed.

2.3. Sound analysis

The recorded sounds were analyzed using a Gould 1602 storage oscilloscope and S-TOOLS, the Integrated Workstation for Acoustics, Speech and Signal Processing developed by the Acoustics Research Institute of the Austrian Academy of Sciences in Vienna. All sounds were digitized using a sampling rate of 16 kHz.

The following acoustic variables were determined for each male and temperature (see also methods in Ladich et al., 1992; Ladich, 2007).

(1) The number of sounds produced within a sound series. Sounds were defined as being part of a sound series when the interval between sounds was less than 800 ms. (2) Sound interval was defined as the time between end of a sound and the onset of the following sound within a series; (3) number of bursts (either double or single pulsed) within a sound; (4) burst period, defined as the time interval between the onset of two successive bursts (Fig. 1); and (5) pulse period, defined as the time between the onsets of two successive pulses within a double-pulsed burst. (6) The dominant frequency of sounds was determined by calculating the cepstrum smoothed power spectrum using S-Tools.

2.4. Statistical analysis

An average of 23.5 sounds was analyzed per male at each experimental temperature (25 °C: 12–30; 30 °C: 13–30; 35 °C: 5–30). Means of sound characteristics were calculated for each individual and used to calculate differences between temperatures. Data were normally distributed. A repeated measures analysis of variance (RM-ANOVA) was calculated followed by a least significant difference (LSD) post hoc test.

2.5. Ethical note

Agonistic interactions between croaking gouramis consist of two stages — a lateral display phase and a frontal display phase following one another (Ladich, 1998, 2007). Lateral displays consist of visual and acoustic displays without any physical contact between opponents. As the intention of this study was to record sounds, agonistic interactions were stopped as soon as enough sounds were recorded. Fights were
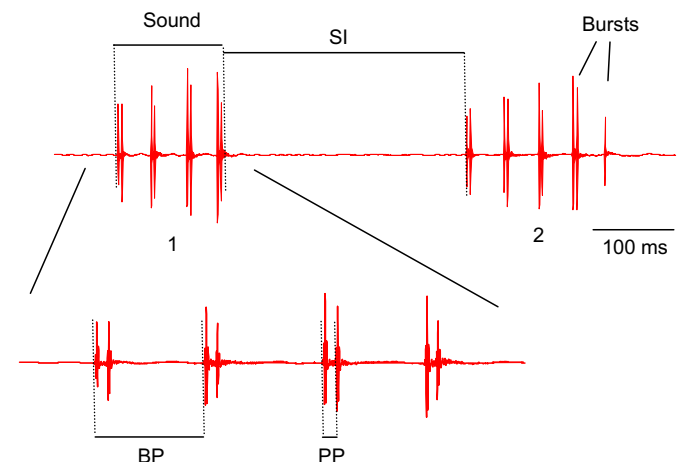

Fig. 1. Oscillograms of a sound series consisting of two croaking sounds (above) and expansion of the first sound (below) illustrating the temporal characteristics analyzed. Each sound consists of series of bursts which are mostly built up of two pulses. Note that the first sound (1) consists of four double pulsed bursts and the second sound (2) of four double-pulsed bursts and one short single-pulsed burst. BP — burst period, PP — pulse period, SI — sound interval.