# RESEARCH ARTICLE

## Sound production in red-bellied piranhas (*Pygocentrus nattereri*, Kner): an acoustical, behavioural and morphofunctional study

Sandie Millot\*, Pierre Vandewalle and Eric Parmentier

Laboratoire de Morphologie Fonctionnelle et Evolutive, Institut de Chimie–B6C, 4000 Liège, Belgium

\*Author for correspondence (sandiemillot@yahoo.fr)

### SUMMARY

Piranhas are known to be sound-producing animals. Nevertheless, the biological significance of piranha calls remains unclear because sounds have been recorded only when specimens were held by hand or trapped in a gill net. These sounds are generated by rapid contractions of sonic muscles that insert on a broad tendon surrounding ventrally the cranial sac of the swimbladder. The piranha swimbladder is thought to play an important role in sound production as an impedance-matching device and as a resonator. However, the vibratory capacities of the cranial and caudal sacs and the exact role of both sacs in sound production remain poorly understood. In this study, three sounds were each associated to a specific behaviour. The first sound (type 1) was produced during frontal display; it had numerous pulses and lasted 140±17 ms, with a fundamental frequency of 120±4 Hz. It corresponded to the sound made by hand-held fishes. The second sound (type 2) was produced during circling and fighting behaviour; it was a single pulse lasting 36±8 ms, with a fundamental frequency of 43±10 Hz. The third sound (type 3) corresponded to chasing behaviour and comprised three to four pulses, each lasting 3±1 ms, with a fundamental frequency of 1739±18 Hz. Using a laser vibrometer to study the swimbladder displacement when stimulated at different frequencies, it was demonstrated that the first two sounds corresponded to the swimbladder mechanism. By contrast, the third sound was associated with the jaw mechanism. The vibrometer indicated that the swimbladder is a highly damping structure, simply copying the sonic muscle contraction rate. This study provides two interesting insights. First, it shows the relationships between three kinds of piranha sound and three specific behaviours. Second, using muscle stimulation at different rates, it shows which simultaneous conditions are required for production of sound in this species. Swimbladder calls were produced by a muscle contraction rate of approximately 100 Hz because this periodicity allowed the swimbladder to vibrate. At this frequency range, the contraction–relaxation cycles of the swimbladder muscles engendered wall displacements that had short amplitudes and with only a small variability between them.

Key words: sound production, behaviour, swimbladder, sonic muscle, laser vibrometer.

## INTRODUCTION

Few species have attracted greater notoriety than the voracious red-bellied piranha (*Pygocentrus nattereri*), a common predatory fish of the Amazon and other South American rivers (Fowler, 1950; Goulding, 1980). There have, however, been few investigations into piranha behaviour, probably because of the perceived difficulties involved in handling these animals. Nevertheless, Sazima and Machado (Sazima and Machado, 1990) made direct underwater observations of the feeding and social interactions of red-bellied piranhas; Uetanabaro and colleagues examined breeding behaviour (Uetanabaro et al., 1993); Foxx (Foxx, 1972) described how individual piranhas attack goldfish (*Carassius auratus*, Linnaeus); and Magurran and Queiroz investigated piranha shoaling behaviour in a controlled environment (Magurran and Queiroz, 2003). In addition, Pauly summarised published information on foraging, growth and related aspects of the species (Pauly, 1994).

Piranhas are also known to be sound-producing animals (Meschkat, 1957; Markl, 1971; Kastberger, 1981a; Kastberger, 1981b). Nevertheless, the biological significance of piranha calls remains unclear because sounds have been recorded only when specimens were held by hand or trapped in a gill net. Markl (Markl, 1971) and Kastberger (Kastberger, 1981a) found that drumming calls

of hand-held specimens consisted of low-frequency harmonic sounds with several pulses and with a period of 7–10 ms. These sounds are generated by rapid contractions of sonic muscles, which originate on transverse expansions at the base of the second rib and insert on a broad tendon that ventrally surrounds the cranial sac of the swimbladder (Ladich and Bass, 2005). The sonic muscles are round in shape, extend between the first and third ribs (Ladich and Bass, 2005) and are innervated by branches of the third, fourth and fifth spinal nerves (Onuki et al., 2006). Sounds result from fast-contracting sonic muscles, whose contraction rate determines the pulse rate of the drumming sounds (Kastberger, 1981a), which also showed harmonics (Kastberger, 1981b). The piranha swimbladder is thought to play an important role in sound production as an impedance-matching device and as a resonator (Tavolga, 1971; Demski et al., 1973).

Although sound production apparently evolved independently among several distantly related groups, many species have a sonic mechanism dependent on fast-contracting sonic muscles that vibrate the gas-filled swim bladder (e.g. Osteoglossomorpha, Batrachoidiformes, Scorpaeniformes). However, species exhibit a wide range of variation in the origin and insertion of the sonic muscles. In this kind of mechanism, sound production stops after
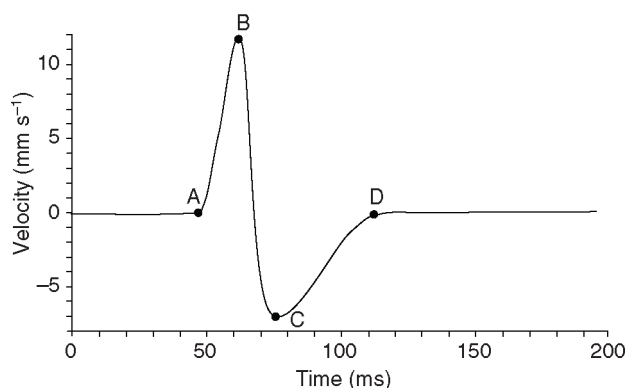
Fig. 1. Velocity of swimbladder wall displacement (twitch): A corresponds to the start of the movement, B to the maximal velocity and the half of swimbladder displacement, C to maximal velocity through the return of the swimbladder to its resting position, and D to the end of the movement. The A–B segment represents the velocity increase that corresponds to the main peak sound energy, and the C–D segment represents the recovery phase.

deflation or removal of the swimbladder (Tower, 1908). Moreover, as the swimbladder can undergo volume changes, the organ has been considered as an efficient radiator of sound. Consequently, the swimbladder has been modeled as an underwater resonant bubble, an acoustic monopole that radiates sound omnidirectionally (Bergeijk, 1964; Harris, 1964). However, few studies have directly studied the mechanism by which movement of the swimbladder could produce sound. The role of the swimbladder has been directly studied in only one Batrachoidiform species (*Opsanus tau*), which is non-related to the piranha. In the toadfish *Opsanus tau*, the bladder is a low-Q resonator, which follows muscle contraction rates independently of its natural frequency (Fine et al., 2009).

Here, our goals were to record sounds in a free-swimming group of piranhas and to be able to associate their sounds with given behaviours (e.g. aggression, intimidation, food competition, chasing). Moreover, different methods (vibrometer laser, muscle stimulation, etc.) were used to identify precisely the role of the cranial and caudal sacs of the swimbladder in the sound-producing mechanism.

## MATERIALS AND METHODS

Piranhas (*Pygocentrus nattereri* Kner) were purchased from a specialised store (Aqua Garden Centre, Liège, Belgium) and kept in two 300 litre tanks. The water temperature was maintained at 26±2°C, and the oxygenation level kept above 90%. The fish were fed three times a week with mussels and smelts.

### Recording and analysis of sounds and behaviour

The experiment was performed on three groups of 10 fish [18±5 g; 9±1 cm standard length (SL)]. Each group of fish was transferred to a 160 litre experimental tank (90 cm length, 35 cm breadth, 50 cm depth) 12 h before the recording of sounds and behaviour in order to avoid any stress to the fish. The characteristics of the water in the experimental tank (physicochemical composition, temperature and oxygen level) were similar to those in the rearing tank. A hydrophone (HTI-96-Min Series; High Tech, MS, USA) was positioned in the middle of the tank and coupled to a camera (Canon Legria FS19) in order to record sounds and behaviours simultaneously. Each recording lasted 2 h. A mussel was placed in the experimental tank, 90 min after the start of recording, in order to analyse fish sound production and behaviour during food competition.

Each sound was analysed using Avisoft-SASLab pro software (Avisoft Bioacoustics, Berlin, Germany) and associated with fish behaviour by video observation. Only sounds with a good signal-to-noise ratio were analysed. Temporal features were measured from oscillograms, and frequency parameters were obtained from power spectra transformed with a fast Fourier transformation (Hamming window). The following temporal and spectral characteristics of the sound waves were measured: (1) pulse and call duration (ms): time between the onset of one pulse or call and its end; (2) pulse period (ms): time between the main peaks of two successive pulses; (3) number of pulses within a sound; (4) dominant frequency (Hz) with the highest energy in the whole sound.

The types of behaviour observed were classified as: (1) frontal display: two individuals moving rapidly towards each other and staying face to face. This action can be followed by direct contact between the two protagonists but is rarely associated with biting. (2) Circling and fighting: two or more individuals presenting aggressive behaviour with direct contact between fish and biting. This behaviour was generally preceded by the 'Karrusel' (head-to-tail rounds), as described by Markl (Markl, 1971). Fighting was often observed during food competition. (3) Chasing: one piranha pursuing another individual rapidly.

### Morphofunctional study

The experiment was performed on 12 fish (86±16 g; 14±1 cm SL). Measurements of swimbladder vibration were made with a Polytec laser Doppler vibrometer (LDV), including a vibrometer controller (OFV 5000) and a vibrometer sensor head (OFV 505; Polytec GmbH, Waldbronn, Germany). Piranhas were anaesthetised by immersion in a 200 mg l$^{-1}$ tricaine methanesulfonate salt (MS-222) solution. Water containing 100 mg l$^{-1}$ of the anaesthetic was recirculated into the mouth and across the gills. The sonic muscles and swimbladder were completely exposed on one side by incision of the body musculature. The laser beam was focused on reflective discs placed on the cranial or caudal sac of the swimbladder. The sonic muscles were stimulated using hook electrodes (stimulation voltage: 6 V; stimuli duration: 1 ms) at different frequencies – for example, 1, 20, 50, 100, 150, 200 and 300 Hz.

The following variables were analysed: (1) twitch duration (ms): interval between the onset of one swimbladder wall displacement and its end; (2) twitch period (ms): time interval between the main peaks of two consecutive twitches; (3) dominant frequency (Hz) with the highest energy in the entire swimbladder wall movement.

Each twitch was arbitrarily divided into different parts (Fig. 1) in which duration (ms) and velocity (mm s$^{-1}$) were analysed: A–B: velocity increase of swimbladder displacement (with a focus on variability of peak amplitude); B–C: velocity decrease of swimbladder displacement; C–D: return of the swimbladder to its initial position (recovery phase).

### Data analysis

Data were checked for normality with the Shapiro–Wilk test and for homogeneity of variances with the Bartlett test; the data all complied with the parametric tests to be used. A factorial ANOVA was used to compare the average differences in swimbladder displacement (A–B) between stimulation frequencies and the swimbladder sac. Homogeneous groups were determined with an *a posteriori* Newman and Keuls test (Dagnélie, 1975). For all tests, the threshold for significance was $P<0.05$, and analyses were performed using Statistica software (Statsoft, Tulsa, OK, USA).
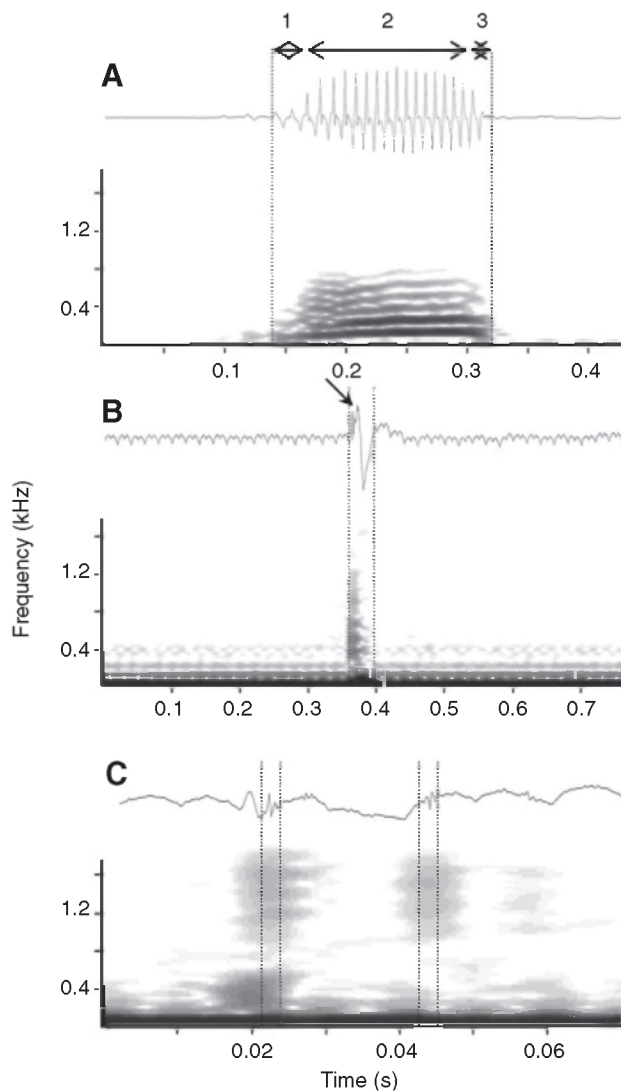
A

B

Frequency (kHz)

C

Time (s)

Fig. 2. Oscillograms and sonograms of recorded sounds in *Pygocentrus nattereri*. (A) Sound type 1, or bark (1, initial; 2, main; 3, terminative sequence of sound); (B) sound type 2 (black arrow indicates the first part of the sound); (C) sound type 3. The dotted lines indicate the beginning and the end of each sound.
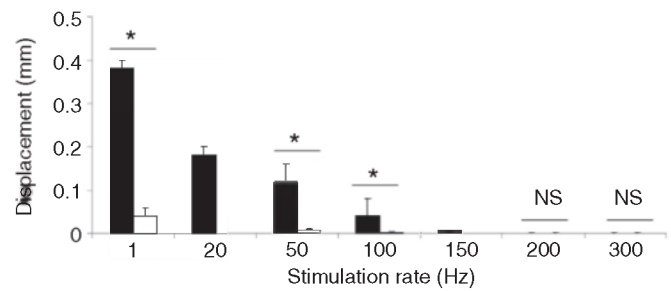


Fig. 3. Maximum displacement (A–B; see Fig. 1) amplitude of cranial (black) and caudal (white) swimbladder sac at different sonic muscle stimulation rates. NS, not significant difference; *, significant differences (P<0.05) between swimbladder sacs (factorial ANOVA, Newman and Keuls test).

## RESULTS
### Sounds emitted and associated behaviour
Three types of sounds were recorded in piranhas living in the aquarium. In each case, the dominant frequency corresponded to the fundamental frequency. The first call was a harmonic sound (type 1), which lasted approximately 140 ms, and the main energies were found in the fundamental frequency of approximately 120 Hz (Fig. 2A, Table 1). This sound comprised 12 to 21 pulses, each lasting

4±1 ms and with a pulse period of 8±1 ms. During the first part of the call (1), sound pressure increased gradually from pulse to pulse, and the pulse period decreased from 12 ms to 7 ms. During the main sequence (2), amplitude and pulse period were relatively constant. At the end of the call (3), signal amplitude returned to its initial level in 10–30 ms. This sound was produced in 80% of cases during frontal display between two fish, but the remaining 20% of cases could not be associated with a given behaviour.

The second sound (type 2) lasted 36±8 ms and had a fundamental frequency of approximately 40 Hz (Fig. 2B, Table 1). It was characterised by a single pulse that seemed to comprise two parts. On the first part of the cycle, the positive peak possessed smaller peaks that lasted 11±2 ms (black arrow on Fig. 2B). The second part was more regular. This sound was produced in 70% of cases during circling and fighting behaviour, mostly associated with food competition. Fish producing this sound were usually among the largest in the group.

The third sound (type 3) was characterised by a single pulse lasting 3 ms, with a fundamental frequency of approximately 1740 Hz (Fig. 2C, Table 1). These sounds generally comprised three to four pulses, but the unpredictability of the pulse period meant that they could not be considered to be part of a single call. This sound was associated in 90% of cases with a chasing behaviour towards a conspecific. Video analysis revealed that this sound was produced when a fish snapped its jaws in order to bite a conspecific.

### Swimbladder vibrations
A comparison of the swimbladder wall displacement (A–B) for the cranial and caudal sac (Fig. 3) showed that the vibrations of the cranial part were significantly higher than those of the caudal part, except at 200 Hz and 300 Hz ($F_{4,171}$=421.89, $P<0.001$). The displacement amplitude of the cranial sac of the swimbladder decreased significantly for a muscle stimulation from 1 Hz to 150 Hz. Thereafter, the swimbladder displacement amplitude remained stable until 300 Hz ($F_{6,121}$=457.41, $P<0.001$). According to Kastberger (Kastberger, 1981a; Kastberger, 1981b), temporal

Table 1. Characteristics of three types of sounds made by red-bellied piranha

|  | Sound type 1 (N=30) | Sound type 2 (N=23) | Sound type 3 (N=30) |
|---|---|---|---|
| Sound duration (ms) | 140±17 |  |  |
| Pulse duration (ms) | 4±1 | 36±8 | 3±1 |
| Number of pulses | 12–21 | 1 | 1 |
| Pulse period (ms) | 8±1 |  |  |
| Peak frequency (Hz) | 120±4 | 43±10 | 1739±18 |

Values are means ± s.e.m.
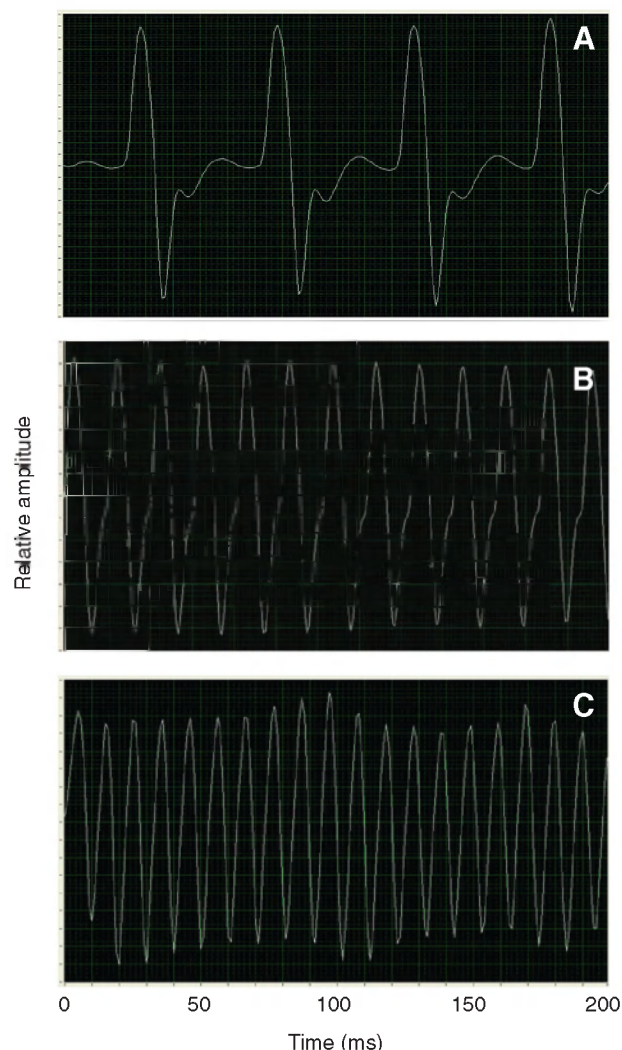
Fig. 4. Oscillograms of cranial swimbladder movement for a sonic muscle stimulation at 20 Hz (A), 100 Hz (B) and 150 Hz (C).



Fig. 5. Oscillogram of cranial swimbladder movement at 100 Hz. The arrow corresponds to the end of sonic muscle stimulation.

summation begins at 150 Hz, and the muscle exhibits an unfused tetanus at 300 Hz. In line with Kastberger's findings, the weak displacement of the swimbladder from 150 to 300 Hz found here was obviously due to the tetanised condition, meaning that the rest of the data analysis was best focused only on the cranial sac vibrations at 1, 20, 50 and 100 Hz.

Sonic muscle stimulation of 1 Hz led to a single swimbladder twitch, which lasted 76±1 ms and had a peak frequency ranging from 20 to 40 Hz. Muscle stimulation at 20 Hz led to a succession of twitches lasting 43±1 ms, with a period of 50±1 ms (Fig. 4A). At 50 Hz, the twitches lasted 14±1 ms, with a period of 20±1 ms (Fig. 4B). Finally, at 100 Hz, the twitches lasted 8±1 ms, with a period of 10±1 ms (Fig. 4C). At this frequency, the swimbladder vibration was uninterrupted during the entire sonic muscle contraction period. When the muscle stimulation was stopped, the swimbladder vibration ceased immediately (Fig. 5).

The swimbladder recovery time (C–D) decreased as simulation frequency increased ($F_{3,85}$=3430.6, $P$<0.001; Fig. 6). The peak amplitude of the swimbladder movement showed a variability of between 2% and 7% for muscle stimulation between 1 Hz and 100 Hz and a high variability (21–25%) for stimulation between 150 Hz and 300 Hz (Fig. 6).
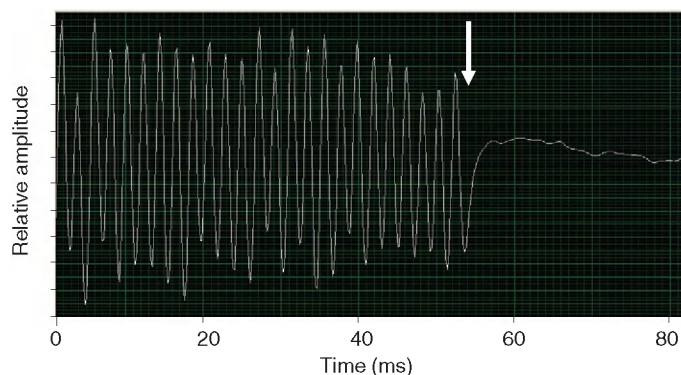
## DISCUSSION
### Behaviour and sounds

To date, only sounds produced by hand-held fish have been described for various piranha species (Markl, 1971; Kastberger, 1981a; Kastberger, 1981b). Under those conditions, piranhas were found to produce low-frequency, harmonic sounds of approximately 100–150 ms in duration, with a fundamental frequency varying between 100 Hz and 150 Hz (Kastberger, 1981a; Kastberger, 1981b). The temporal and spectral characteristics of the first kind of drumming sound observed in the present study (Fig. 2A) corresponded to the 'barks' emitted when a piranha was hand-held in previous studies (Markl, 1971; Kastberger, 1981a). From these previous studies focusing on the sound-producing mechanism, we can conclude that the type 1 sounds recorded here were emitted through movement of the swimbladder. This could also be the case for sound type 2 (Fig. 2B) because, first, the fish did not make any movement during sound production, meaning that there must have been an internal mechanism causing the sound to be produced and, second, the spectral frequency (40 Hz) and sound duration (36 ms) recorded are more typical of swimbladder sounds than of stridulatory sounds. Finally, sound type 3 (Fig. 2C) had a high frequency (1700 Hz) and consisted of short pulses (3 ms). Here, the piranha visibly snapped its jaws during sound production, highlighting the fact that the sound-producing mechanism relies on the jaws.

The great majority of sounds emitted by fish are produced within a social context and involve interactions between individuals (Amorim et al., 2003; Malavasi et al., 2009). Previous studies have failed to determine the biological context of sound emission in piranhas (Markl, 1971). In this study, the sound made by each piranha was emitted in conjunction with a specific behaviour. The bark sound was mostly produced during frontal display between two fish. This sound could therefore be interpreted as a warning signal during an intimidation phase between two individuals. According to this interpretation, sounds made by hand-held fish cannot definitively be considered as alarm sounds. Sound type 2 was principally produced during circling and fighting behaviour, generally associated with food competition. This sound could thus be interpreted as a signal of threat and of strong aggression between fish. Sound type 3 was emitted only during chasing behaviour during a bite attempt on a conspecific or a prey. These behaviours are analogous to those observed in juvenile schooling tigerfish *Therapon jarbua*, where 'drumming sounds' are usually produced during moderate attacks, whereas 'threatened sounds' are produced mainly during vigorous attacks (Schneider, 1964). Furthermore, sound type 2 was often emitted when fish were competing for food in the tank, confirming that aggression is often
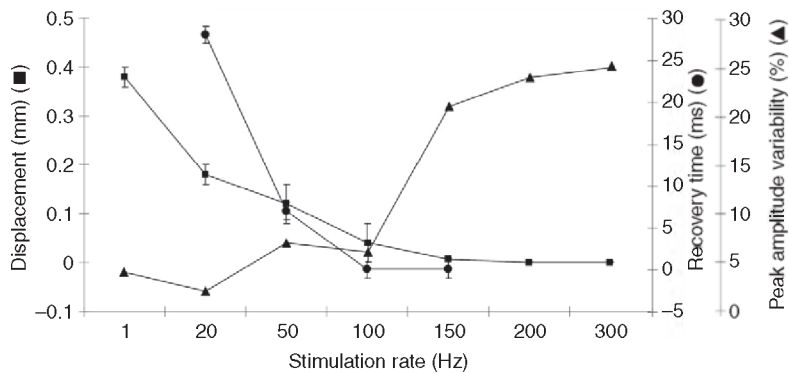
Fig. 6. Amplitude of cranial swimbladder displacement (squares), peak amplitude variability (triangles) and recovery time (circles) for each sonic muscle stimulation rate.

associated with competition for limited and unevenly distributed resources such as food (Archer, 1988). If food is presented in a way that enables one or a few animals in a group to monopolise the resource (contest competition), feeding success will be proportional to the fighting ability of an individual (McCarthy et al., 1992; Grant, 1993). This observation was confirmed here in *P. nattereri* as the fish producing the sound was also the most aggressive and the largest and consequently could be characterised by the best fighting ability and the greatest feeding success.

### Swimbladder vibrations

This study revealed that only the cranial part of the piranha swimbladder plays a role in sound production, as previously hypothesised by Markl (Markl, 1971). Fine and colleagues found that, for toadfish, the swimbladder wall displacement was maximal in time and amplitude at low frequency, but with no clear peak frequency (Fine et al., 2001). They found also that the peak sound energy occurs in the middle of displacement (muscle contraction) when swimbladder velocity is maximal and acceleration is zero. In the present study, the characteristics of swimbladder displacements were the same. This shows an interesting case of evolutionary convergence in which the same kinds of problems are solved in an analogous way. In these two phylogenetically distant fishes, muscle insertions, swimbladder shape and muscle orientations are completely different. However, in both cases, rapid muscle evolved to generate sound from an inefficient highly damped system. The perfect correspondence between the stimulation rate and the movements of the swimbladder indicates that the dominant frequency was determined by the velocity of the swimbladder, as driven by the sonic muscle rather than by its natural frequency. In *P. nattereri*, stopping the electrical stimulation of the sonic muscle corresponded with a rapid decrease in the swimbladder vibrations (Fig. 5), indicative of the highly damped nature of the swimbladder. As in toadfish (Fine et al., 2001; Fine et al., 2009), in weakfish (Connaughton et al., 2002), in searobin (Connaughton, 2004) and in ariid catfishes *Galeichthys* and *Bagre* (Tavolga, 1962), the piranha bladder is a low-Q resonator; damping is an intrinsic property of the swimbladder and not of the fish tissue surrounding it.

### Relationship between sound and swimbladder vibrations

Drumming sounds are naturally produced with a frequency of approximately 100 Hz. As previously shown by Kastberger, the unfused response during twitch trains exhibits an optimum tension at a stimulus rate of approximately 100 Hz (Kastberger, 1981a). The superimposition of different characteristics relating to the behaviour of the swimbladder during stimulation at different frequencies, shown in Fig. 6, provided a better understanding of the required

conditions for the production of this type of sound. Around the frequency of 100 Hz, three factors were observed and seemed required to make sounds: (1) no recovery time, meaning that the swimbladder is continuously in movement; (2) small peak amplitude variability (6%); and (3) short but sufficient displacement amplitude. Thus, the muscle contraction rate at approximately 100 Hz forced a steady and constant displacement of the swimbladder.

In *Opsanus tau*, Fine and colleagues showed the relationships between the sound waveform, swimbladder displacement and muscle action potential of a single twitch (Fine et al., 2001). The oscillogram of sound type 2 and the response of the swimbladder evoked by a muscle stimulation of 1 Hz in the piranha are strikingly similar to the results of Fine and colleagues. Consequently, sound type 2 could be due to only one contraction of the sonic muscles and reflect the complete recovery time of the swimbladder when it is being driven at one single twitch.

### Conclusions

This study has shown that: (1) each kind of sound emitted by piranhas is associated with a specific behaviour; (2) the caudal swimbladder does not play a role in sound production; (3) the vibration frequency of the cranial swimbladder corresponds exactly to the sonic muscle contraction rate; (4) bark (sound type 1) is produced by sonic muscle contraction at 100 Hz because this frequency brings together the conditions necessary to produce this type of sound; (5) sound type 2 might be produced by only one sonic muscle contraction; and (6) sound type 3 is the result of the jaws snapping.

### REFERENCES

Amorim, M. C. P., Fonseca, P. J. and Almada, V. C. (2003). Sound production during courtship and spawning of *Oreochromis mossambicus*: male-female and male-male interactions. *J. Fish Biol.* **62**, 658-672.

Archer, J. (1988). *The Behavioural Biology of Aggression*. Cambridge: Cambridge University Press.

Bergeijk, W. A. V. (1964). Directional and nondirectional hearing in fish. In *Marine Bioacoustics* (ed. W. N. Tavolga), pp. 281-299. New York: Pergamon Press.

Connaughton, M. A. (2004). Sound generation in the searobin (*Prionotus carolinus*), a fish with alternate sonic muscle contraction. *J. Exp. Biol.* **207**, 1643-1654.

Connaughton, M. A., Fine, M. L. and Taylor, M. H. (2002). Weakfish sonic muscle: influence of size, temperature and season. *J. Exp. Biol.* **205**, 2183-2188.

**Dagnélie, P.** (1975). Théorie et méthodes statistiques. In *Applications Agronomiques*, Vol. 2, pp. 463. Gembloux: Presses Agronomiques de Gembloux.

**Demski, L. S., Gerald, J. W. and Popper, A. N.** (1973). Central and peripheral mechanisms of teleost sound production. *Am. Zool.* **13**, 1141-1167.

**Fine, M. L., Malloy, K. L., King, C. B., Mitchell, S. L. and Cameron, T. M.** (2001). Movement and sound generation by the toadfish swimbladder. *J. Comp. Physiol. A* **187**, 371-379.

**Fine, M. L., King, C. B. and Cameron, T. M.** (2009). Acoustical properties of the swimbladder in the oyster *Opsanus tau. J. Exp. Biol.* **212**, 3542-3552.

**Fowler, H. W.** (1950). Peixes de agua doce do Brasil. *Arq. Zool. Sao Paulo* **6**, 205-404.

**Foxx, R. M.** (1972). Attack preferences of the red-bellied piranha (*Serrasalmus nattereri*). *Anim. Behav.* **20**, 280-283.

**Goulding, M.** (1980). *The Fishes and the Forest: Explorations in Amazonian Natural History*, 280 pp. Berkeley: University of California Press.

**Grant, J. W. A.** (1993). Whether or not to defend? The influence of resource distribution. *Mar. Behav. Physiol.* **23**, 137-153.

**Harris, G. G.** (1964). Considerations on the physics of sound production by fishes. In *Marine Bioacoustics* (ed. W. N. Tavolga), pp. 233-247. New York: Pergamon Press.

**Kastberger, G.** (1981a). Economy of sound production in piranhas (Serrasalminae, Characidae): I. Functional properties of sonic muscles. *Zool. Jb. Physiol.* **85**, 113-125.

**Kastberger, G.** (1981b). Economy of sound production in piranhas (Serrasalminae, Characidae): II. Functional properties of sound emitter. *Zool. Jb. Physiol.* **85**, 393-411.

**Ladich, F. and Bass, A. H.** (2005). Sonic motor pathways in piranhas with a reassessment of phylogenetic patterns of sonic mechanisms among teleosts. *Brain Behav. Evol.* **66**, 167-176.

**Magurran, A. E. and Queiroz, H. L.** (2003). Partner choice in piranha shoals. *Behaviour* **140**, 289-299.

**Malavasi, S., Valerio, C. and Torricelli, P.** (2009). Courtship sounds and associated behaviours in the Canestrini's goby *Pomatoschistus canestrinii. J. Fish Biol.* **75**, 1883-1887.

**Markl, H.** (1971). Sound production in Piranhas (Serrasalminae, Characidae). *Z. Vgl. Physiol.* **74**, 39-56.

**McCarthy, I. D., Carter, C. G. and Houlihan, D. F.** (1992). The effetct of feeding hierarchy on individual variability in daily feeding of rainbow trout, *Oncorhynchus mykiss. J. Fish Biol.* **41**, 257-263.

**Meschkat, A.** (1957). Von den stimmen der fische im Amazonas. *Fischwirt* **7**, 67-68.

**Onuki, A., Ohmori, Y. and Somiya, H.** (2006). Spinal nerve innervation to the sonic muscle and sonic motor nucleus in red piranha, *Pygocentrus nattereri* (Characiformes, Ostariophysi). *Brain Behav. Evol.* **67**, 111-122.

**Pauly, D.** (1994). Quantitative analysis of published data on the growth, metabolism, food consumption, and related features of the red-bellied piranha, *Serrasalmus nattereri* (Characidae). *Environ. Biol. Fishes* **41**, 423-437.

**Sazima, I. and Machado, F. A.** (1990). Underwater observations of piranhas in western Brazil. *Environ. Biol. Fishes* **28**, 17-31.

**Schneider, H.** (1964). Physiologische und morphologische Untersuchungen zur bioakustik der tigerfische (Pisces, Theraponidae). *Z. Vgl. Physiol.* **47**, 493-558.

**Tavolga, W. N.** (1962). Mechanisms of sound production in the ariid catfishes, Galeichtkys and Bagre. *Bull. Am. Mus. Nat. Hist.* **124**, 1-30.

**Tavolga, W. N.** (1971). Sound production and detection. In *Fish Physiology*, Vol. 5 (ed. W. S. Hoar and D. J. Randall), pp. 135-205. New York: Academic Press.

**Tower, R. W.** (1908). The production of sound in the drumfishes, the searobin and the toadfish. *Ann. N. Y. Acad. Sci.* **18**, 149-180.

**Uetanabaro, M., Wang, T. and Abe, A. S.** (1993). Breeding behaviour of the red-bellied piranha, *Pygocentrus nattereri*, in nature. *Environ. Biol. Fishes* **38**, 369-371.