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# SOUND PRODUCTION BY THE LUSITANIAN TOADFISH, *HALOBATRACHUS DIDACTYLUS*

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## ABSTRACT

Several batrachoidids have been known to produce sounds associated with courtship and agonistic interactions, and their repertoires have been studied acoustically and behaviourally. In contrast, sound production of the Lusitanian toadfish *Halobatrachus didactylus*, although often noted, has not been acoustically studied.

This sedentary predator of Northeastern Atlantic coastal waters is usually found in sandy and muddy substrates, under rocks or crevices. Sound recordings were made in Ria Formosa, a lagoon complex in southern Portugal. The sound producing apparatus was studied in adult individuals of both sexes captured by local fishermen.

It is shown that this species produces acoustic emissions similar to other batrachoidids. It produces a long, rhythmical, tonal sound, often in choruses, which is comparable to the boatwhistle or hum signals of *Opsanus* and *Porichthys*, and a complex of signals that were classified as grunts, croaks, double croaks and mixed calls ('grunt-croak'). As in other toadfishes, *H. didactylus* presents sonic muscles connected to a bi-lobed swimbladder. Asynchronous contractions of the sonic muscles were detected when massaging the ventral surface of the fish.

Keywords: toadfish, *Halobatrachus didactylus*, Batrachoididae, acoustic repertoire, sonic muscles.

## INTRODUCTION

Sound communication in fishes has been the subject of a growing number of studies, covering over 50 families of teleosts (Hawkins and Myrberg 1983, Hawkins 1993). Since the early 1900's batrachoidids have been known to produce sounds (Gill 1907, Tower 1908). Some species have been studied acoustically since the 1950's, mainly from

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the genus *Opsanus* (Fish et al. 1952, Fish 1954, Tavolga 1958, Fish and Mowbray 1959).

Within the batrachoidids, both toadfishes and midshipman produce sounds associated with courtship and agonistic interactions. During the breeding season, nest-holding male toadfish produce a mating call resembling an intermittent boatwhistle (for *Opsanus tau* see Gray and Winn 1961, and Fine et al. 1977; for *O. beta* see Breder 1968; and for *O. phobetron* see Fish and Mowbray 1970). In the midshipman, *Porichthys notatus*, breeding males emit a continuous humming (Ibara et al. 1983, Brantley and Bass 1994). In both genera, only nesting males produce these mating calls. It has also been demonstrated that they facilitate the calling of adjacent males and that females are attracted to the sound sources (Gray and Winn 1961, Winn 1967, 1972). Males increase calling rates as females approach their nests (Gray and Winn 1961, Fish 1972). Agonistic grunts have also been recorded from toadfish and midshipman, both male and female (Tavolga 1958, Brantley and Bass 1994).

Sound production results from the contraction of paired sonic muscles that surround the tense walls of the swimbladder, causing a rapid variation in bladder volume (Tower 1908, Skoglund 1961). The muscle contraction rate, not bladder resonance, determines the fundamental frequency of the produced sounds (Skoglund 1961, Cohen and Winn 1967). There is a marked sexual dimorphism in swimbladder and sonic muscle size, which grow larger in males (Fine 1975, Fine et al. 1990). This appears to be related to the fact that only males produce boatwhistles. Also, the swimbladder and sonic muscle function was shown to be androgen sensitive (Fine et al. 1986, Fine and Pennypacker 1988, Brantley and Bass 1991, Brantley et al. 1993a, Brantley et al. 1993b).

Male sexual polymorphism has been described in the midshipman, *P. notatus*. In this species a nestholding (Type I) and a sneaking male (Type II) morphotypes occur which differ in body size and gonadosomatic indices (Bass 1992, 1996). Only Type I males produce the mating call and show a more developed sonic apparatus (Brantley et al., 1993, Brantley and Bass, 1994).

The Lusitanian or Northeastern Atlantic toadfish *Halobatrachus didactylus* occurs from the Gulf of Biscay to the Ghana coast, including the Mediterranean Sea and Madeira archipelago (Roux 1986, Debelius 1997). This sedentary, solitary, benthic fish lives in sand and mud substrates and among rocks (Roux 1986). It is a generalist predator reaching about 30-cm standard length (Roux 1971, Cárdenas 1977). The breeding season in the South of Portugal lasts from May to August and the males nest under rocks or on crevices defending the clutch until the fry is free-swimming (pers. observations).

To our knowledge, sound production of *H. didactylus* has not been studied before. The aims of this study are to describe its acoustic repertoire and the structures involved in sound production.

## METHODS

### Sound recordings

The study areas were located at Ria Formosa (see geographical location below) and the Guadiana estuary (37° 10' N, 7° 24' W), on the southern coast of Portugal, where *H. didactylus* is an abundant species. At Ria Formosa, a sea water lagoon complex, two sites were chosen: one near the docks of Olhão (37° 01' N, 7° 49' W) and the other near the islet of Faro (37° 00' N, 1° 59' W). Maximum depth at all three sites was 3 m, and the substrate was mud and fine sand, with loose rock barriers. Toadfish find shelter in these rock aggregations.

The recordings were made between 17 and 24 July 1996. Each site was sampled twice, in sessions of 15 to 60 minutes duration; once in daytime, and once at night, from the same shore-based location. In these areas, average temperatures during this period ranged approximately from 20.0° to 24.0°C, and salinity was 3.61%. Six TDK DA-R60EB tapes were used during these field sessions, recording a total of 219 minutes of signals. In order to verify that toadfish were the source of the sounds recorded, observation dives were made simultaneously with preliminary recording sessions. Altogether, we estimate that at least 12 different animals of undetermined sex were recorded in the field. A Brüel and Kjær 8101 hydrophone with a Sony TCD-D10 Pro DAT recorder were used. The system had a flat frequency response (± 1 dB) between at least 20 Hz and 22 kHz.

Previous work (Gray and Winn 1961) on other species, and our own observations indicated that toadfish produce grunts when handled. For this reason, some further recordings were made at the University of Algarve, in tanks with isolated toadfish of known sex and length, captured at Ria Formosa. Nineteen males and nineteen females were studied, with body lengths ranging from 17.0 to 22.8 cm (males, $\bar{x}$ = 20.1 cm, females, $\bar{x}$ =18.7 cm). The hydrophone was placed inside the 1 $m^3$ fibre-glass tanks, with a sand bottom and half flowerpots as shelters. Water temperature in the tanks was 25.0°C, and salinity 3.8%. Aeration was stopped at the beginning of each recording session. Also, several individuals of both sexes were carefully held, with the thumbs of the observer over the ventral surface, on each side of the body. They were then softly massaged to stimulate sound emissions. The bilateral location of the experimenter's thumbs gave us a rough idea of the relative timing of contraction on each side when sounds were produced.

### Sound classification and description

All tapes were first aurally indexed according to the different types of sounds that the listeners could distinguish, and the background noise level of the recordings was noted. From each of the tapes only the signals with higher signal-to-noise ratio and with no overlapping of other sounds (e.g. boats or a different type of call) were selected for analysis. The sounds were analysed using the Canary v. 1.2 software (Cornell University) on a PowerMacintosh 7100 computer, using a sampling frequency of 11.1 kHz (Nyquist frequency, 5550 Hz). In order to perform the measurements the signals were first graphically depicted in time (waveform) and frequency (spectrogram or sonogram) domain representations. To describe each type of acoustic emissions the following features were measured: sound duration, number of pulses, pulse duration, pulse peak-to-peak interval, peak frequency, and fundamental frequency. For composite sounds, bout duration and number of signal elements were also measured. Statistical procedures included the non-parametric Friedman two-way analysis of variance test and the Wilcoxon signed ranks test (Siegel and Castellan 1988). The software package Statistica 5.0 for Windows (StatSoft, Inc.) was used for most tests.

## RESULTS

### Sound classification and description

The sounds recorded in the field were aurally and visually classified into 5 categories: boatwhistles, grunts, croaks, double croaks and mixed calls ('grunt/croak').

The boatwhistle call (Figure 1) is a pulsed, low-pitched, vocal sound. The duration of each boatwhistle ranged from 434 to 790 ms ($\bar{x}$ ± s.e.= 674.6 ± 24.9 ms, N = 21), with number of pulses between 31 and 54 ($\bar{x}$ ± s.e.= 44.7 ± 1.5, N=21). The dominant frequency is usually below 200 Hz ($\bar{x}$ ± s.e.= 183.9 ± 19.2 Hz, N = 21). The production of this type of call was observed with the fish at the entrance of a shelter. These signals may be emitted by the same individual in a regular fashion. Choruses of several animals can be heard for several hours, making boatwhistles the most conspicuous acoustic element around toadfish aggregations.

In a more detailed analysis of this type of call, three different stages could be discriminated: beginning, middle and end of the signal. Each one of these stages is characterised by differences in pulse duration, pulse peak-to-peak interval and peak frequency (Table 1). Pulse duration and pulse peak-to-peak interval decrease from the beginning of the signal towards the end (Friedman two-way analysis

TABLE 1

Measurements of acoustic parameters in three different stages of boatwhistles (Mean ± s.e.)

| | Beginning | Middle | End |
|---|---|---|---|
| Pulse duration (ms) (N=11) | 12.7 ± 2.0 | 12.0 ± 1.7 | 8.9 ± 1.6 |
| Pulse peak-to-peak interval (ms) (N=11) | 16.6 ± 0.8 | 13.8 ± 0.8 | 10.2 ± 1.2 |
| Peak frequency (Hz) (N=16) | 157.7 ± 52.3 | 218.0 ± 98.3 | 180.4 ± 97.1 |

of variance, N = 11, d.f. = 2, $p < 0.01$, $p < 0.001$, respectively), while peak frequency is higher in the middle of the signal than in the other stages ($p < 0.05$).

Grunts (Figure 2) are short pulsed signals, in most instances emitted in bouts of 3 to 21, with a drumming appearance. Each grunt signal ranged in duration from 18.4 to 34.2 ms ($\bar{x}$ ± s.e.= 22.5 ± 0.5 ms, N = 211), with 1 to 5 pulses. Each pulse had an average duration of 4.2 ± 0.1 ms. The signal peak frequency is higher than in boatwhistles ($\bar{x}$ ± s.e.= 376.4 ± 17.8 Hz, N = 167) and mean pulse peak-to-peak interval is 7.5 ± 0.2 ms.

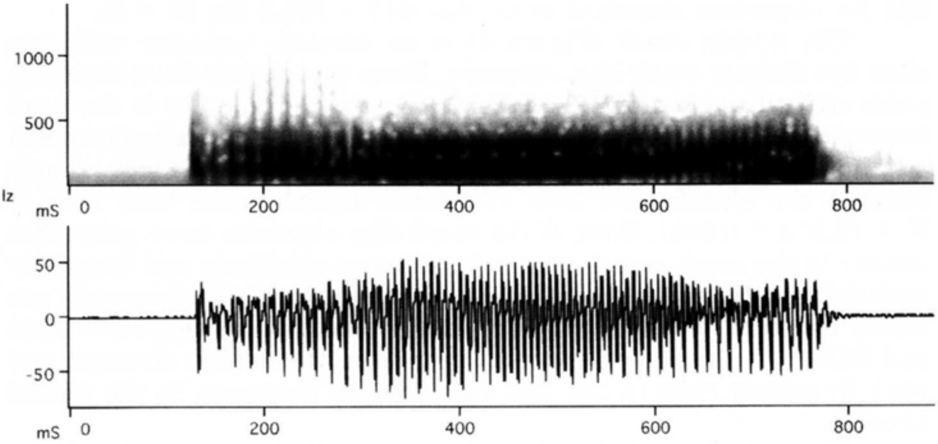

Figure 1. A representative sample of a boatwhistle call. Top: Sonogram, with time on the X-axis and frequency on the Y-axis; Filter bandwidth: 352.9 Hz; grid resolution: 5.8 ms. Bottom: Waveform or oscillogram, with time on the X-axis and uncalibrated relative amplitude on the Y-axis.

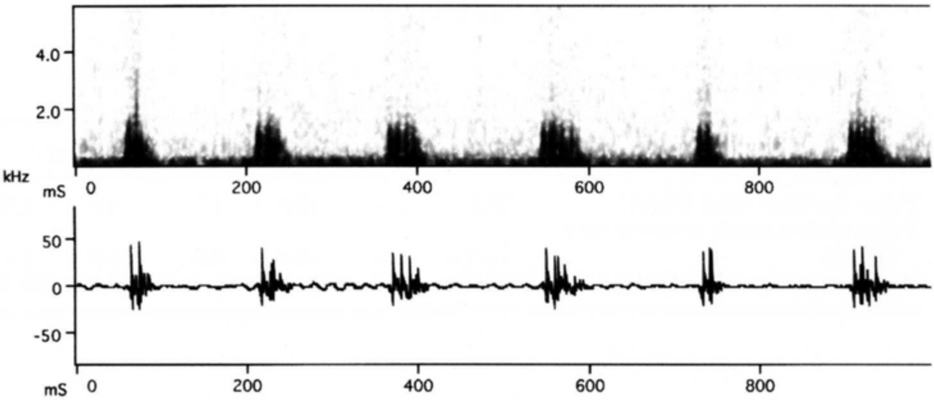

Figure 2. A representative sample of a grunt bout. Top: Sonogram, with time on the X-axis and frequency on the Y-axis; Filter bandwidth: 705.9 Hz; grid resolution: 2.9 ms. Bottom: Waveform, as in Figure 1.

Compared to grunts, croaks (Figure 3) are also composed of a rapid but longer pulse series, with a vocal appearance. The number of pulses ranged from 11 to 30 ($\bar{x}$ ± s.e.= 17.5 ± 2.1, N = 8) and the duration from 72.1 to 196.9 ms ($\bar{x}$ ± s.e.= 110.1 ± 14.0 ms, N = 8). Mean pulse duration and mean pulse peak-to-peak frequency were 3.8 ± 0.2 ms and 6.0 ± 0.1 ms, respectively. Average peak frequency and its respective standard error was 647 ± 158.5 Hz (N = 8).

The double croak (Figure 4) is an acoustic emission with two close but distinct croak-like elements. These two signals have the same pulse structure and similar duration. There is a difference in the peak frequency values between the two elements, which is aurally perceived as a pitch difference. In our small sample, that difference almost reached the significance level (Wilcoxon signed ranks test: N = 5, W = 15.0, p = 0.062). Each of the croak-like elements have properties similar to the croak sound, except for distinct amplitude and frequency modulations. In croaks, pulse amplitude and sound peak frequency are nearly constant, while in a typical double croak, pulse amplitude rises and falls in the first element, rising again in the second element; and peak frequency rises in the first element and decreases in the second element.

The mixed grunt/croak call (Figure 5) is composed of two different types of signals: a bout of grunt signals preceded or followed by one or two croaks. Each of the different parts of this call has acoustical properties similar to its signal type.

Fundamental frequency was difficult to measure due to the relatively high ambient noise. In our more reliable measurements

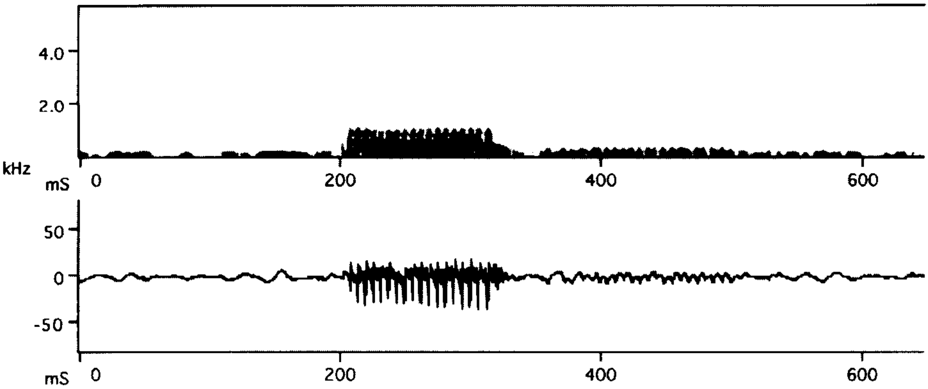

Figure 3. A representative sample of a croak call. Top: Sonogram, with time on the X-axis and frequency on the Y-axis; Filter bandwidth: 705.9 Hz; grid resolution: 1.4 ms. Bottom: Waveform, as in Figure 1.

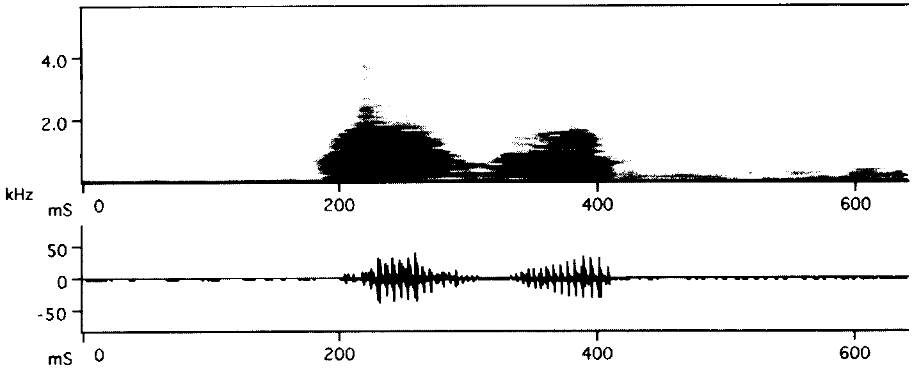

Figure 4. A representative sample of a double croak call. Top: Sonogram, with time on the X-axis and frequency on the Y-axis; Filter bandwidth: 176.5 Hz; grid resolution: 11.5 ms. Bottom: Waveform, as in Figure 1.

fundamental frequency values ranged in all signal types between 76 Hz (measured in a boatwhistle) and 240 Hz (measured in a croak). Averages were 133 Hz for boatwhistles and 175 Hz for croaks, with intermediate values for the other sounds.

It should be noted that grunts, croaks, double croaks and mixed calls (but so far not boatwhistles) may easily be heard from tanks with more than one specimen.

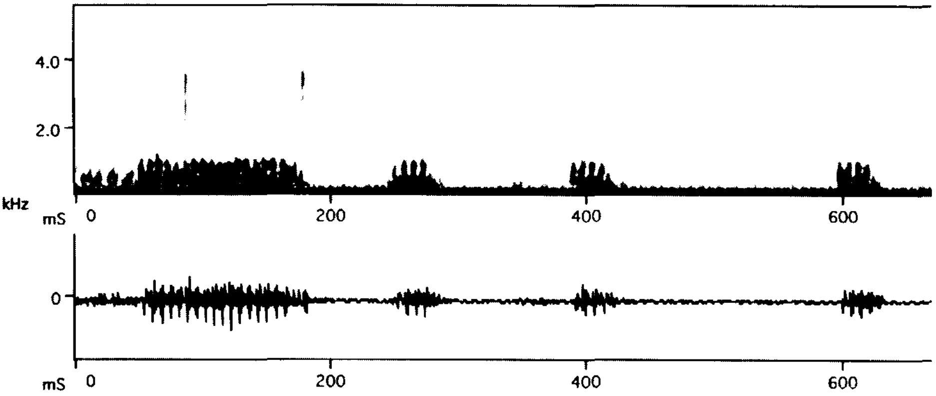

Figure 5. A representative sample of a mixed grunt/croak call. Top: Sonogram, with time on the X-axis and frequency on the Y-axis; Filter bandwidth: 705.9 Hz; grid resolution: 1.4 ms. Bottom: Waveform, as in Figure 1.

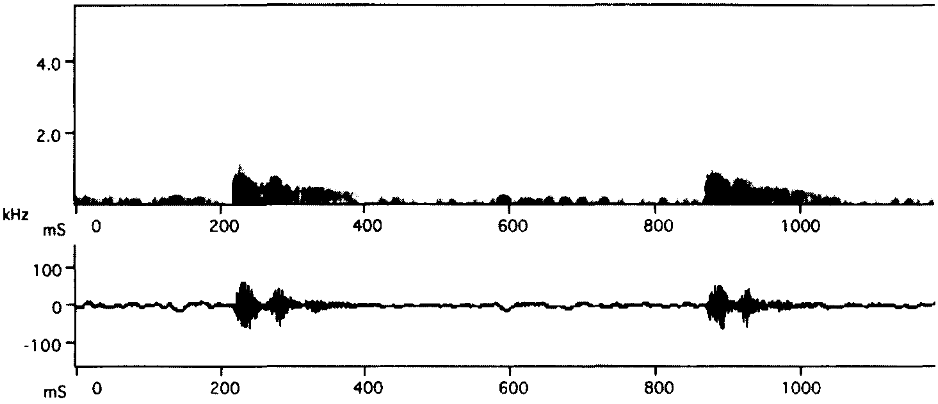

Figure 6. A representative sample of two knocks. Top: Sonogram, with time on the X-axis and frequency on the Y-axis; Filter bandwidth: 699.4 Hz; grid resolution: 2.9 ms. Note that each call is composed of a pair of unequal sounds. Bottom: Waveform, as in Figure 1.

Our attempts to elicit sound emissions from the animals kept in the laboratory resulted in the production by both sexes of peculiar grunt-like sounds that we called knocks (Figure 6). In most cases, these calls consisted of pairs of pulses, with the pair lasting from 65 to 88 ms ($\bar{x}$ ± s.e.= 72.8 ± 8.5 ms, N = 19), and with dominant frequencies of about 260 Hz ($\bar{x}$ ± s.e.= 256 ± 13 Hz, N = 19). While recording these double-pulse knocks that were elicited by handling the fish, it could be perceived tactically that the muscles on either side of the swim bladder were contracting asymmetrically.

## Sound producing apparatus

As in other toadfish, *H. didactylus* presents sonic muscles connected to the swimbladder. The swimbladder has two well-separated unequal lobes, the left one being somewhat larger. The lobes communicate via a narrow duct located in the posterior half of the bladder (Figure 7). The sonic muscles, with a brownish coloration, are attached to the outside portions of each lobe, running along the complete lobe. The muscles are conspicuous, especially in the dorsal region of the bladder. The muscle fibres run along the short axis of the swimbladder. Internally, the left lobe is divided in two chambers of different sizes, separated by a perforated diaphragm located posteriorly to the duct between the lobes. The right lobe is not divided. Gas-secreting glands can be found in the inner ventral region of each lobe, near the duct opening. These gas glands are easily detected due to the red capillary rose-shaped bundles that irrigate them. In this species there is no sexual dimorphism in the bladder's internal structure.

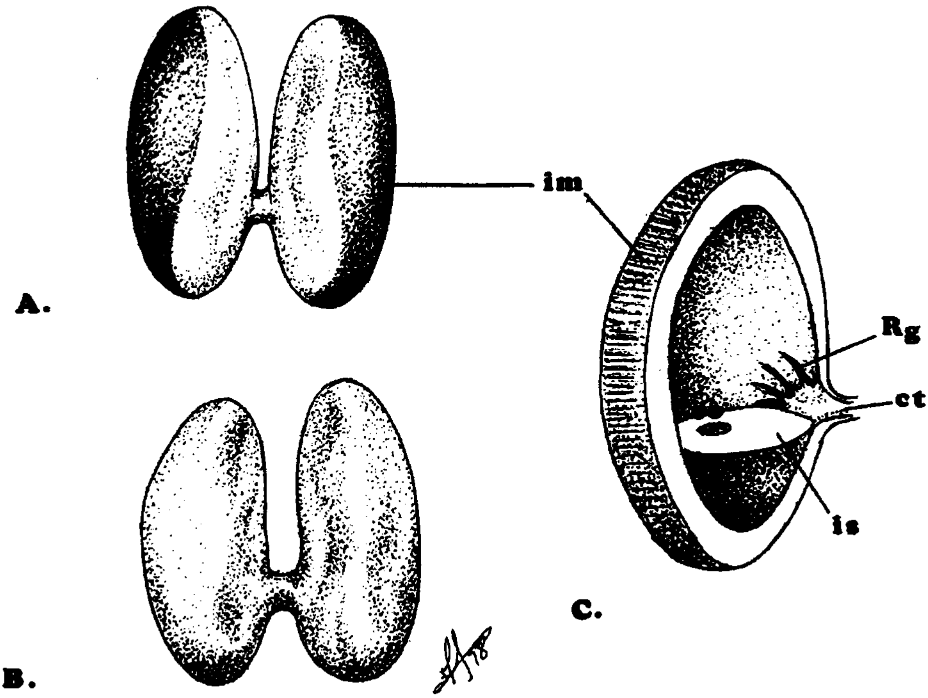

Figure 7. **A.** Dorsal view of the swimbladder: **im** intrinsic muscles. **B.** Ventral view of the swimbladder. **C.** Internal view of the left lobe of the swimbladder: **im** intrinsic muscles; **is** internal septum; **co** central opening of the septum; **ct** connecting tube; **Rg** red gland (gas gland).

## DISCUSSION

The natural repertoire of the Lusitanian toadfish is composed of four basic vocalisations, and is similar to that of other batrachoidids. The conspicuous boatwhistle call is comparable to that of *Opsanus* sp. and to the hum signals of *P. notatus*. Interestingly, the final section of the boatwhistles often shows frequency modulation, with a slight increase of the dominant frequencies. In the double croak sound, the rapid changes in pulse repetition rate also produce an ascending and descending frequency pattern so characteristic in spectrograms. Grunts are also common in other toadfishes and this call type may be characteristic of the family Batrachoididae. Boatwhistles are apparently only produced during the breeding season and, contrary to the other sounds, we have not been able to record them in aquaria. It might, as in other species, be a male sexual advertisement call.

It appears that grunts, croaks and mixed calls are all based on stereotyped pulses. By changing temporal patterns (i.e. varying the frequency of pulse production), toadfishes are able to produce these different calls. For instance, croaks result from an increase in the pulse repetition rate typical of grunts. Other toadfish species have variable intergrunt intervals suggesting the potential for generating alternative grunt-like sounds. Signals similar to grunts and croaks can be heard when toadfish are joined by other individuals, or when handled. Hence, these calls are likely related to agonistic and spacing functions. *H. didactylus* also expands its repertoire size by combining two signal types to produce a mixed grunt-croak signal. There is as yet no information concerning the possible specific effects or proximal causes of these signal variations.

When manually handled, the fish in this study showed a noticeable asymmetry in sonic muscle contraction, concomitant to the production of knock sounds. This apparent mode of contraction, and the differences between the pulses in the knocks may be related to the unequal size of the lobes. We confidently suggest that each pulse is generated by an independent contraction of a single sonic muscle. It would be of course necessary to examine interpulse amplitude asymmetry and sonic muscle asymmetry in the same animals, with electrophysiological measurements to verify the timing of contractions.

Other authors (e.g., Gray and Winn 1961) observed that toadfish *Opsanus tau* grunt when handled, but they did not note whether these grunts involved asynchronous muscular contraction. Fish and Mowbray (1959) observed the isolated occurrence of double sounds and suggested that asynchronous contraction of the sonic muscles could be a mechanism for the production of these double sounds. Fine (1982) also suggested that the sonic muscles may contract asynchronously, based on his analysis of three “anomalous cases” involving the production of double sounds in oyster toadfish. These limited suggestions of asynchronous contraction are in contrast to the majority of past studies of toadfish, which present sound producing systems leading to the generation of synchronous contraction of the two sonic muscles. This would include the general "wiring" of the sonic motor nucleus for synchronicity (Fine and Mosca, 1995) and the well established electrical coupling of the bilateral sonic motor nuclei (e.g., Pappas and Bennet 1966, Bass and Baker 1990 and 1991, Bass and Marchaterre 1989). Moreover, Skoglund (1961) observed that the sonic nerve has an unimodal compound action potential and he observed the two sonic muscles contract in phase. It should be noted, though, that there are remarkable similarities in swimbladder structure between the Lusitanian toadfish and the more distantly related sea robin *Prionotus carolinus* (Triglidae), which interestingly has been demonstrated to contract asynchronously (Bass and Baker 1991).

Other details of the vocal behaviour of this quite soniferous fish remain to be understood, namely signal function, possible sexual dimorphism in production and the circadian and seasonal patterns. Another aspect of interest for future research on the vocalisations of toadfish is their potential for eavesdropping by possible predators. For example, the idea that vocalising batrachoidids may be detected, tracked and captured by bottlenose dolphins *Tursiops truncatus* using their sophisticated audition has received growing support. In fact, the species *O. tau and O. beta,* in Florida, and the species *P. notatus* and *P. myriaster*, in California, have been found in the stomach contents of bottlenose dolphins in numbers disproportionate to their abundance (Barros and Odell 1990, Hanson and Defran 1993). It is possible that acoustic detection of toadfish also occurs in the Sado estuary, on the western coast of Portugal, where bottlenose dolphins are often observed foraging while vocalisations of *H. didactylus*, namely boatwhistles and grunts, are conspicuously audible in the background (dos Santos 1998).

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