



The acoustic behavior of Southern King Weakfish (*Macrodon atricauda*-Sciaenidae)

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Abstract Many species of fishes use acoustic signals for a variety of purposes, and sciaenid are well-known producers of sound. The Southern King Weakfish (*Macrodon atricauda*- Sciaenidae) possesses sexually dimorphic bilateral sonic muscles used for sound production. The bilaterally paired muscles lie on the inner body wall of the male, surrounding the swimbladder. The Southern King Weakfish produces three different sounds: advertisement calls, disturbance calls and dual-knocks, these sounds were recorded from Rio de la Plata estuary, Uruguayan coastal waters and laboratory. The advertisement call, related to courtship, was recorded in the field and from spawning males in the laboratory. Disturbance calls were produced when captive *M. atricauda* were startled, chased with a net or grabbed by the tail. Disturbance calls consist of a burst of pulses produced at short intervals. In disturbance call interpulse interval increased and dominant frequency decreased linearly ($P < 0.05$), pulse duration did not change with fish size. *M. atricauda* start producing disturbance call at 14 cm LT (Total Length), but only individuals over than 25 cm LT were who produced the advertisement call. Dual-knocks, call compose of only two pulses together, was recorder only in captivity. Sounds are a valuable non-invasive tool for fisheries biologists can used to monitor on males in spawning populations.

Keywords Sound production · Rio de la Plata · Sonic muscle · *Macrodon atricauda*

Introduction

Fishes produce sounds to communicate with one another during feeding, mating, and aggression (Fine et al. 1977; Tavolga 1980; Amorim 2006; Parmentier et al. 2014). In a number of teleost families, such as Batrachoididae, Gadididae, Holocentridae, Sciaenidae, Pomacentridae, Gobiidae and Salmonidae, sound production is associated with agonistic and reproductive behaviour (Hawkins and Rasmussen 1978; Ladich 1997; Amorim et al. 2015; Fine and Parmentier 2015; Parmentier and Fine 2016; Bolgan et al. 2017). Sound plays an important role in species identification (Winn 1964; Fine et al. 1977; Ladich et al. 2006; Amorim 2008; Malavasi et al. 2008; Parmentier et al. 2009; Phillips and Johnston 2009; Bolgan et al. 2018). Passive acoustics has been used to record temporal and spatial patterns of fish reproduction by detecting sounds associated with spawning (Lobel and Mann 1995; Luczkovich et al. 2008). However, fish specific behavioral contexts of sound production during spawning are not known (Lobel 2002).

The family Sciaenidae is an important world fish resource (Nelson 2006), especially in the western Atlantic. With about 78 genera and 282 species this family is widely distributed in the tropical, subtropical and temperate seas, with some genera inhabiting freshwater

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habitats (Nelson 2006), and are fisheries species commonly found in shallow coastal waters (Shao 2005). Sciaenids (often called “croakers” or “drums”) produce sound by contracting specialized sonic swimbladder muscles (Schneider and Hasler 1960; Tavolga 1964; Ono and Poss 1981; Hill et al. 1987; Connaughton et al. 1997; Ladich and Fine 2006; Tellechea et al. 2010a, b; Locascio and Mann 2011), and most likely evolved the ability to produce acoustic signals in order to communicate in turbid estuaries where the water visibility is minimal (Holt et al. 1981; Holt 2008). Only a small fraction of the 282 sciaenid species have been recorded, and most of this research has been performed on species that inhabit the Eastern North American waters (Ramcharitar et al. 2006). Males form breeding aggregations and produce advertisement calls that exhibit species specific differences (Fish and Mowbray 1970; Myrberg 1981; Saucier and Baltz 1993; Luczkovich et al. 1999; Fine et al. 2004). Field-recorded sounds have been verified using voluntary sounds recorded in captivity from a small number of sciaenids including weakfish *Cynoscion regalis*, speckled trout *Cynoscion nebulosus*, Atlantic croaker *Micropogonias undulatus*, sand seatrout *Cynoscion arenarius*, whitemouth croaker *Micropogonias furnieri*, red drum *Sciaenops ocellatus* and *Pogonias cromis* (Fish and Mowbray 1970; Saucier and Baltz 1993; Luczkovich et al. 1999; Connaughton et al. 2000; Fine et al. 2004; Locascio and Mann 2008; Tellechea et al. 2010a, b; Parmentier et al. 2014; Montie et al. 2016), the orangemouth corvina *Cynoscion xanthurus* and white seabass *Atractoscion nobilis* from the Pacific coast (Fish and Cummings 1972; Aalbers and Drawbridge 2008), the brown meagre *Sciaena umbra* and the shi drum *Umbrina cirrosa* from Europe (Lagardère and Mariani 2006; Picculin et al. 2012, 2016), Japanese croaker *Argyrosomus japonicus* and blackspotted croaker *Protonibea diacanthus* from Taiwan (Ueng et al. 2007; Mok et al. 2009) are some examples. In most Sciaenids, males are the prominent sound producers; however, in the Atlantic croaker, black drum and whitemouth croaker, both male and female have sonic muscles and call (Hill et al. 1987; Tellechea et al. 2010a). In most cases, sound production is associated with defending territory and reproduction (Mok and Gilmore 1983).

The southern king weakfish *Macrodon atricauda* (Günther, 1880) is a sciaenid fish that inhabits shallow

coastal waters in soft bottom areas near estuaries from Espírito Santo state (Brazil) to northern Argentina. This species was recently discriminated from *Macrodon ancylodon* (Bloch and Schneider, 1801), which can be found from northeastern Brazil to Venezuela (Santos et al. 2006; Carvalho-Filho et al. 2010; Cardoso et al. 2012). Five population groups of *M. atricauda* have been genetically identified (Rodrigues et al. 2014). The largest one occurs between Rio de la Plata estuary (Lat. 36°) and Santa Marta Grande Cape in southern Brazil (Lat. 28°). It is commercially important and caught mainly in southern Brazil, Uruguay and Argentina by coastal trawl fisheries (Haimovici and Vieira 1986; Militelli and Macchi 2004; Jaureguizar and Milessi 2008).

In the Río de la Plata estuary and adjacent marine waters, the Sciaenidae family is the most important with respect to abundance and landings (Cousseau 1985) and *M. atricauda* is one of those species (Jaureguizar and Milessi 2008). *M. atricauda* is a coastal demersal species, euryhaline with a salinity range between 15.5 and 32.9‰ (Vizziano and Berois 1990). Adult specimens prefer the coastal zones of mixing between the Río de la Plata and the Atlantic Ocean, and spawns in the Río de la Plata estuary from spring to late summer (October to March) (Vizziano and Berois 1990). Bimodal spawning is indicated by two mean GSI peaks, one during November followed by another in March (Militelli and Macchi 2004).

The aims of the present study were to describe for the first time the sounds produced by *M. atricauda* and the associated acoustic behavior, determine if there is a relationship between sizes and call characteristics and to examine the gross structure of the swimbladder muscle.

Material and methods

Field and captivity sound recordings

Recordings of *M. atricauda* were carried out during the spawning season (Militelli and Macchi 2004) between October 2017 and March 2018. Recordings were taken at the artisanal fishing ground in the Río de la Plata estuary (34°79 S, 55°86 W) (Fig. 1) and at the adjacent coast on board a small boat in the town of Pinar in the second spawning peak (March 2018). First were

recorded sounds in a known spawning area for *M. atricauda* (Advertisement call) adjacent to the coast. Water temperature was between 22 and 23 °C, and salinity was 20‰. The hydrophone was placed at depths between 2 and 3 m. during daylight.

Captivity recordings were carry out with captured fishes ($N=47$; 26 males and 21 females) with a fishing rod and trawls. These fishes were kept alive on board in a plastic tank with estuarine water. For recording, individual fish were transferred to the laboratory polystyrene tanks ($1.50 \times 1 \times 1$ m) and the hydrophone was placed 50 cm from the fish. *M. atricauda* emit disturbance calls when held in the hand as do other sciaenids, i.e., weakfish *C. regalis* (Connaughton et al. 2000), Atlantic croaker *Micropogonius undulatus* (Fine et al. 2004) and whitemouth croaker *Micropogonias furnieri* (Tellechea et al. 2010a, b). The water temperature and salinity in the tanks were the same as in the estuary, 23 °C, and 20‰. Once the specimens died naturally were determine the sex, and the sonic muscles were also examined.

To witness sound production during courtship behavior were carried out additional captivity recordings of 10 marked fishes by small cuts in the tail fin (free-swimming individuals (five males and five females) polystyrene tanks ($2 \times 1.5 \times 0.50$ m) in the laboratory. These five males and five females were part of the fishes obtained previously ($N=47$). The fishes in laboratory were monitored very close from 9 to 25 March 2018, started its voluntary calls (advertisement call) in 13 March and died one by one from day 25 naturally. For prolonged and continuous recording of sound, the same recording equipment was used and connected to an external battery.

Animal care protocols were approved by the Comisión Honoraria de Experimentación Animal (CHEA), Universidad de la República, Montevideo, Uruguay.

Acoustics analyses

A calibrated omnidirectional Aquarian hydrophone H1a (Useful range: <1 Hz to >100 KHz, 100 KHz = -220 dB re: 1 V/ μ Pa), connected to an amplifier with antialiasing filter and a TASCAM DR-HP-d2 digital recorder (sampling frequency of 44.1 kHz) was used for recordings. The recordings were analyzed using Audacity 1.2.3 free software, (Mazzoni 2006) power spectra were

calculated using a 1024 point Fast Fourier Transform (FFT) with a Hanning window. Pulse duration, interval between pulses (interpulse interval), and dominant frequency were measured for each sound recorded.

Statistical analyses

The relationship between mean pulse duration, pulse interval and dominant frequency with LT (Total Length) were analyzed using segmented linear regression (Sokal and Rohlf 1995), nonparametric tests including the Kruskal-Wallis test and Mann-Whitney test were used. The critical α level for these analyses was 0.05. Past (version 1.95), using a free statistical software package (Hammer et al. 2001).

Results

Sound production

Advertisement choruses were recorded at sites that match the known distribution for the artisanal fishermen of *M. atricauda* in the Rio de la Plata, Uruguay. Calls were recorded at depths of 2–4 m from October to March over the coast. Individual sound pulses, consisting of multiple cycles, often overlapped and were difficult to distinguish in field recordings (Fig. 4D). Trawls indicated that *M. atricauda* was the dominant species at recording sites although occasional *M. furnieri* was also caught along with other demersal species. Dissection of the 20 specimen (10 males recorded and 10 females) indicated that only males possessed sonic muscles and produced sound.

Disturbance calls were recorded from 26 captive males obtained from the field and advertisements call from the five males recorded during the spawning time in the lab belonging to the 26 males.

Disturbance call

Disturbance calls, were evoked when the male fishes were handled or under disturbance condition as try to grab them with a hand net. They were recorded in 26 individuals that were not yet ripe (size range: 14 to 28 cm LT) and from five (size range: 26 to 28.9 cm LT) males in spawning condition as determined by sound production or sperm release upon gentle



Fig. 1 (A) Regional distribution of *Macrodon atricauda* in the south-west Atlantic Ocean from Cardoso et al. (2012). (B) Station on the Uruguayan coast with recorded *M. atricauda*

abdominal pressure. Were analyzed a total of 111 calls, with a total of 973 pulses. The disturbance call is a train of pulses, and the number of pulses per burst varied from 6 to 32, with each specimen emitting 1–4 bursts per call (Fig. 2). Pulses consisted of about five cycles, and most energy occurred in the second and third cycle, with the fourth cycle often greatly attenuated (Fig. 2B). The average pulse duration was 19 ± 2.95 ms, the interval was 18 ± 1.05 ms, and the dominant frequency was 466 ± 36.6 Hz for fish recorded in captivity (Table 1). Interpulse interval increased and dominant frequency decreased linearly ($P < 0.05$), but pulse duration did not change with LT (Fig. 3).

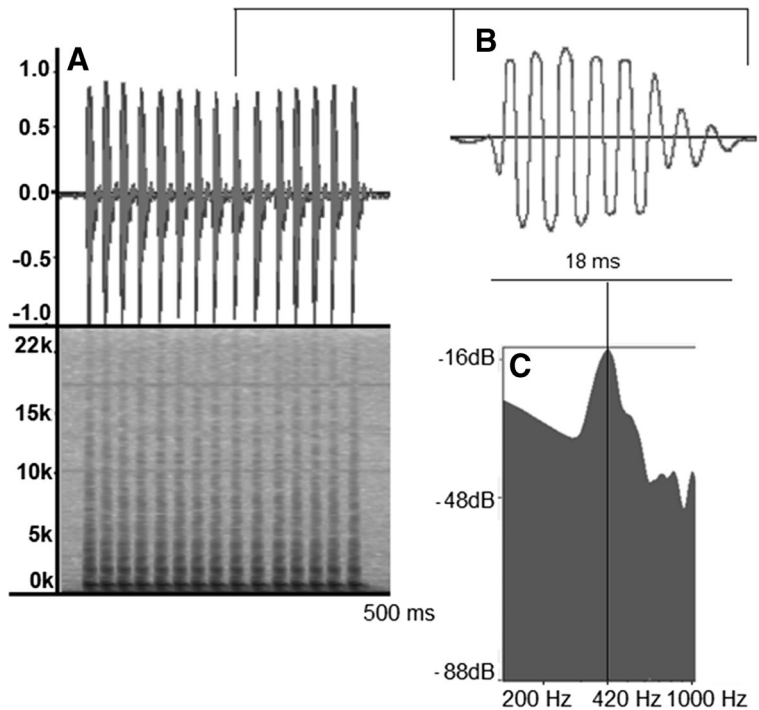
Advertisement call

During March (spawning season) a voluntary train of pulses was recorded only for mature spawning individuals ($n = 5$) in laboratory tanks. Was verified that individuals of ≥ 21 cm LT were mature spawning (running-ripe) (Militelli and Macchi 2004; Militelli et al. 2013) by the release of sperm when stripped. These fishes (five males and five females; the females was added for a possible stimulation) were acclimatized on the tanks for four days, after which was began recording sounds. The fishes were in the tanks three weeks. The water temperature and salinity in the tanks were the same as those at the site of field recordings. After day five the captive fishes, the two sexes were in spawning condition (running-ripe, i.e., males release sperm and females release hydrated oocytes when stripped). At the moment, the

males started to emit the advertising calls that consisted of a series of individual pulses that occurred at an average of 230 ± 92.4 ms (Fig. 4A). The average pulse duration was 25.8 ± 6.18 ms, the dominant frequency was 403 ± 1.66 Hz, and the number of pulses was 13 ± 2.38 in a period of recording of 3 h (Fig. 4). Advertising calls were heard when fish swam freely, alone or in groups, the males continued producing advertisement calls when females were near.

Field and captivity studies indicated a close link between male voluntary drumming behavior (Advertisement call) and reproductive activity. In the Río de la Plata coastal estuary (Pinar), at 23°C and 20‰ salinity) *M. atricauda* were recorded during part of their spawning season (from Oct. to Mar.) in shallow inshore waters (at depths of <5 m; Fig. 4D). Outside of the spawning season, this species was not fished, probably only approaches the coast in the reproductive season in the two spawning periods in November and March (Militelli and Macchi 2004), therefore was not detect this call in the field. In captivity after spawning the fishes stopped emit advertisement call. The choruses of advertisement calls were heard and recorded in the night (18:00–21:00) in captivity and in the field. After each recording session was verified the presence of *M. atricauda* by netting. No significant differences in pulse duration (pulses $n = 29$ $p = 0.23$) and dominant frequency ($p = 0.12$) occurred between advertisement calls in captivity and in the field (Table 1). The pulse interval and number of pulses could not be distinguished in field recordings due to overlapping sounds (Fig. 4).

Fig. 2 Disturbance call of a 26 cm total length (LT) *Macrodon atricauda* recorded in the laboratory tank. (A) Oscillogram (uncalibrated relative amplitude on the y-axis) of a disturbance burst, below sonogram of pulses (Hann window function and fast Fourier transformation size of 1024 points), (B) single pulse further expanded to illustrate the multicycle waveform and (C) typical power spectrum of a single pulse indicating dominant frequency (Hann window function and fast Fourier transformation size of 1024 points)



The number of pulses produced by disturbance calls ($n = 26$ fishes) were significantly greater (Mann-Whitney test, $p < 0.0001$) than those produced by advertisement calls ($n = 5$ fishes) (Table 2).

Dual-knocks

Dual-knocks was recorder only in captivity, was composed of only two pulses, with an interpulse dual-knock to dual-knocks of 109 ± 39.5 s. The average duration of pulse was 24 ± 1.8 ms, the interval between two pulses was 81 ± 14.21 s, and the dominant frequency was 601 ± 23.51 Hz for the fishes recorded. The dual-knocks were emitted in periods of 2 to 3 h in the course of the day. One day after spawning the five specimens began to issue dual-knocks (Fig. 5).

Sonic muscles

The *M. atricauda* possesses sexually dimorphic extrinsic sonic muscles. Bilaterally paired muscles were observed on the inner body wall of males, surrounding the swimbladder. They extended nearly the entire length of the body cavity and attached to the lateral body wall musculature by connective tissue (Fig. 6). The muscle changed seasonally, increasing in vascularization and deepening to a dark red during the spawning season as others sciaenids.

Discussion

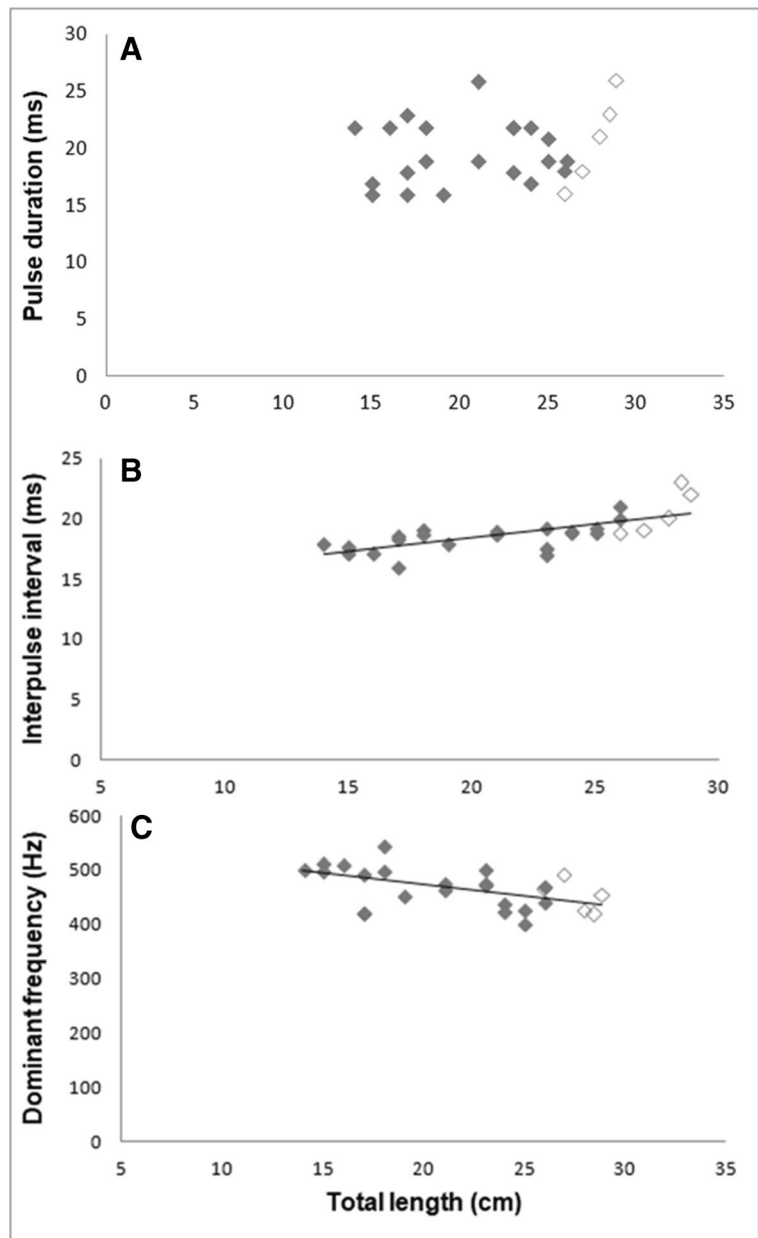
The male of southern king weakfish (*M. atricauda*) possess sonic muscles that are absent in females as in

Table 1 Average, standard deviation and range of call characteristics for the disturbance call

Pulses ($n = 1350$)	Average	S.D.	Minimum	Maximum
Pulse duration (ms)	19.2	2.95	16	26
Interpulse interval (ms)	18.4	1.51	16	23
Dominant frequency (Hz)	466	36.6	403	544
Number of pulses	18	8.6	6	32

Fig. 3 Relationship of (A) pulse duration, (B) interpulse interval, and (C) dominant frequency to total length (LT) in *Macrodon atricauda* disturbance call.

Curves of significant regressions are shown: (B) $y = 0.0408x + 18.951$ ($r^2 = 0.0312$, $P = 4.45E-05$) and (C) $y = -4.1873x + 557.18$ ($r^2 = 0.2727$, $P = 0.00036$). □ ripe *U. canosai*; ■ *U. canosai* not in spawning condition



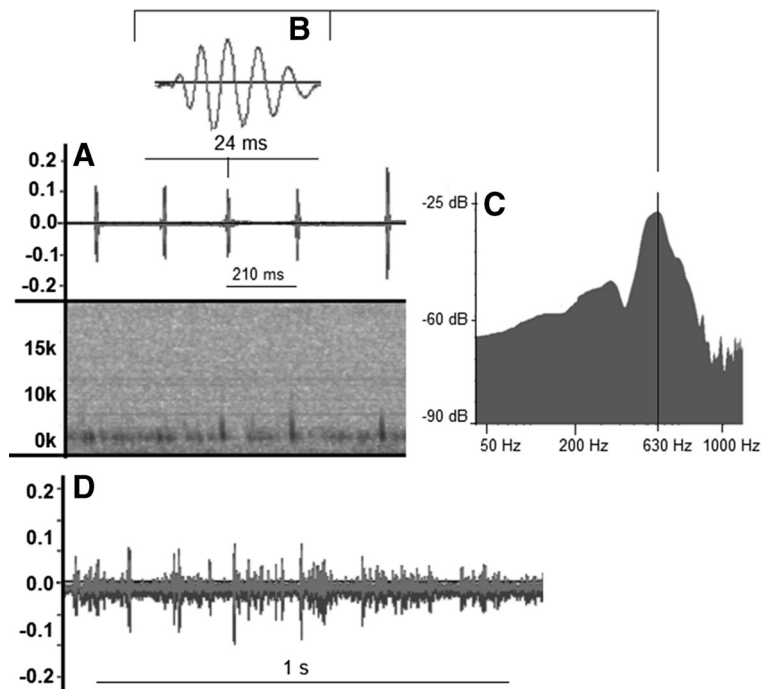
other sciaenid (Smith 1905; Chao 1978; Hill et al. 1987; Connaughton et al. 2000; Tellechea et al. 2010a, b; Tellechea and Norbis 2012; Borie et al. 2014). The sounds emitted by *M. atricauda* are related to spawning and disturbance behaviors.

Disturbance calls start producing at 14 cm LT, similar to *C. regalis* (Connaughton et al. 2000), *C. guatucupa* (Tellechea and Norbis 2012) and *U. canosai* (Tellechea et al. 2017). However the advertisement call is emitted by only in spawning condition,

this suggest a correlation of sonic-muscle development (color change and increment mass) with puberty, the length at first maturity for *M. atricauda* is 21 cm LT for both sexes (Militelli and Macchi 2004; Militelli et al. 2013).

In *M. atricauda*, as in other weakfish (e.g., *C. regalis* and *C. guatucupa*), drumming behavior (advertisement calls) was correlated with spawning in the field (Connaughton and Taylor 1994; Tellechea and Norbis 2012; Tellechea et al. 2017) and in captivity

Fig. 4 Advertisement call of a 26 cm total length (*LT*) male *Macrodon atricauda* courting females in a laboratory tank. (A) Oscillogram of pulse call with an interpulse interval of 210 ms, (B) expanded oscillogram of a pulse indicating multicycle waveform, (C) typical power spectrum of a single pulse indicating dominant frequency (Hann window function and fast Fourier transformation size of 1024 points and (D) sonogram of courtship chorus recorded in the Pinar town, Rio de la Plata coast



(Connaughton and Taylor 1996; Tellechea and Norbis 2012; Montie et al. 2017). Herein, was confirmed that the *M. atricauda* advertisement call recorded in the field was similar to voluntary calls recorded by fish in tanks during the spawning season. The pulses produced during advertisement calls have longer inter-pulse intervals, suggesting that disturbances cause a more-rapid pacing of pattern generators in the central nervous system than courtship vocalizations (Tellechea et al. 2010a,

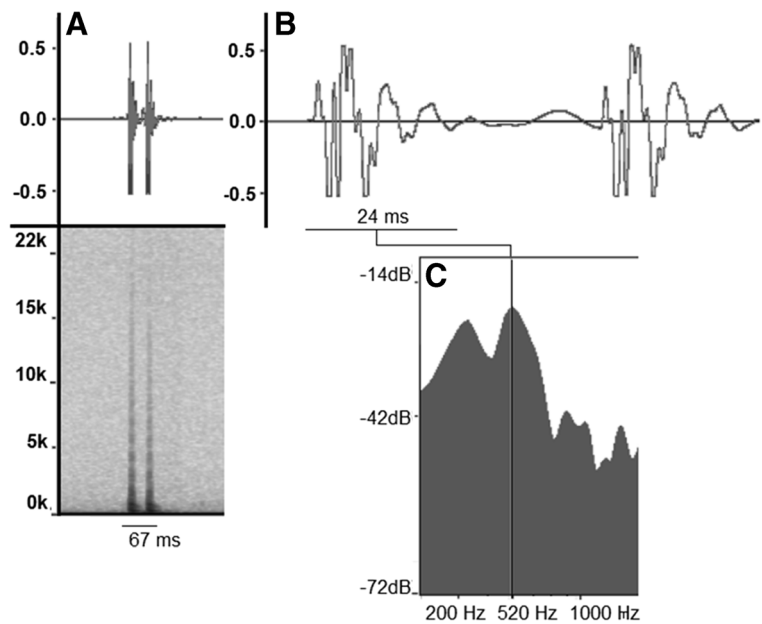
2017; Tellechea and Norbis 2012). Which implicates control of contraction timing to a pattern generator in the central nervous system (Bass et al. 2015) as in toadfish *Opsanus tau* and piranha *Pygocentrus nattereri* (Kner, 1858) (Fine et al. 2001; Millot et al. 2011).

The sounds of sciaenids exhibit ontogenetic changes that correlate with development of the sonic muscles, the swimbladder, and gonads (Hill et al. 1987). Larger *C. regalis* produce sounds with lower dominant

Table 2 Average, standard deviation and range of call characteristics for the advertisement call (*: impossible to obtain data by the overlap of the pulses in the field)

Male captive recordings (<i>n</i> = 5)				
	Average	S.D.	Minimum	Maximum
Pulses (<i>n</i> = 58)				
Pulse duration (ms)	25.8	6.18	23	27
Interpulse interval (ms)	230	92.4	88	300
Dominant frequency (Hz)	403	1.66	392	630
Number of pulses	13	2.38	8	17
Field recordings				
	Average	S.D.	Minimum	Maximum
Pulses (<i>n</i> = 20)				
Pulse duration (ms)	26	1.8	24	27
Interpulse interval (ms)	*	*	*	*
Dominant frequency (Hz)	411	3.26	402	417
Number of pulses	*	*	*	*

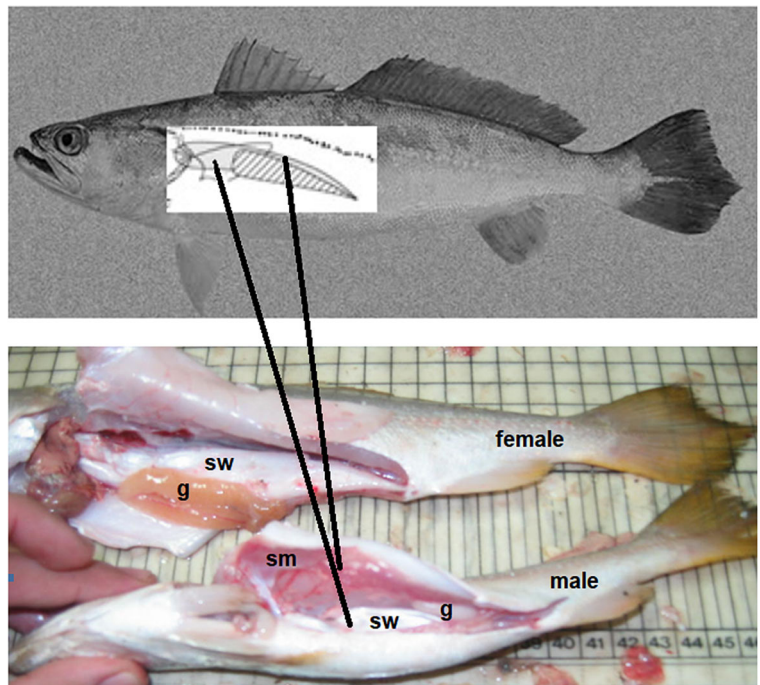
Fig. 5 Dual knock of a 26 cm total length (LT) male *Macrodon atricauda* in a laboratory tank. (A) Oscillogram of a double pulse with a duration of 67 ms, (B) double pulsed expanded oscillogram indicating multicycle waveform, (C) typical power spectrum of a single pulse indicating dominant frequency (Hann window function and fast Fourier transformation size of 1024 points)



frequencies (Connaughton et al. 2000) and it has been argued that decreasing frequency reflects a forced rather than a resonant response because larger sonic muscles require more time to complete a twitch (Hill 1950; Wainwright and Barton 1995; Fine et al. 2001) such that

slower movement of the bladder decreases the dominant pulse frequency among larger fish, as found in *M. furnieri* (Tellechea et al. 2010a). In the same way, the disturbance call characteristics of *M. atricauda* varied with size, interpulse interval increased and dominant

Fig. 6 Upper: illustration of the location and sexual dimorphism of sonic muscles in the *M. atricauda*. Lower: photograph of the body cavity of a sperm-producing male, showing the dark red sonic muscle during the spawning season; also photograph of the right body wall of a pre-spawning female without sonic muscle. sw, swimbladder; sm, sonic muscle; g, gonad



frequency decreased linearly, but pulse duration did not change with *LT*, similar sound characteristic of others sciaenids reported (Connaughton and Taylor 1994; Connaughton et al. 1997; Tellechea et al. 2010a, b, 2017; Tellechea and Norbis 2012). The development of sonic muscles, together with a fish's size and water temperature, determines characteristics of the sound parameters (Connaughton et al. 1997).

Sonic muscles of the *M. atricauda* undergo a yearly hypertrophy cycle whereby muscles increase in thickness and mass during the spawning season (Connaughton and Taylor 1994; Connaughton et al. 1997). Sound production by male *M. atricauda* is also seasonal and correlated with spawning activities in natural conditions and with courtship behavior observed prior to spawning in captivity as in other sciaenids (Connaughton and Taylor 1995, 1996; Tellechea and Norbis 2012; Tellechea et al. 2017). The coloration of the sonic muscles of the male *M. atricauda* was darker in the spawning season. This darkening occurs simultaneously with dramatic seasonal variations in the sonic muscle size, when the sonic muscle triples in mass during the spring spawning season and decreases to its pre-spawning mass by the end of the summer in response to changing androgen titers (Merriner 1976; Connaughton and Taylor 1994, 1995, 1996; Tellechea and Norbis 2012; Tellechea et al. 2017). The observations of the reproductive status, including male and female gonad conditions (females with hydrated oocytes and males producing milt when handled and stripped), suggest that spawning activities for this species coincide with peak drumming activity.

Number of pulses was lower in advertisement than in disturbance calls in *M. atricauda* as in *C. regalis*, *M. furnieri* and *U. canosai* (Connaughton et al. 2002; Tellechea et al. 2010a, 2017). Overlap of advertisement choruses with population locations from different places along the Rio de la Plata estuary suggests that *M. atricauda* is reproductively active in multiple sites on the shallow continental shelf throughout the species range in Uruguay. It has been suggested that time between pulses could be used for species-specific recognition in sciaenids (Locascio and Mann 2008) and in other species (Winn 1972; Spanier 1979; Mann and Lobel 1997). Their suggestion agrees with the separation of disturbance and advertisement calls in *M. atricauda*.

There is not much information about the dual knock call. As was described by Mok and Gilmore (1983) in

spotted seatrout (*Cynoscion nebulosus*- Sciaenidae) and Lin et al. (2007) in the big-snout croaker (*Johnius macrorhynus*- Sciaenidae) the dual-knocks seem not to be a fright-response sound. In *C. nebulosus* this call was produced in spawning aggregation (Mok and Gilmore 1983). The big-snout croaker dual-knocks often being placed in the initial phase of a series of call and the purrs (disturbance call) often being chained together suggest the communication signal of this species is actually not very diverse. However in the case of *M. atricauda*, this call was issued in a state of calm and free swimming in the laboratory tanks without any stimulus of threat. This sound was recorded solo without being part of disturbance call as is described by Lin et al. (2007). It would seem that double knocks is a common call in some sciaenid species sound producers, in personal observation in later acoustic studies of whitemouth croaker *M. furnieri* (Tellechea et al. 2010a) were recorded dual knocks. Perhaps this call could be more related to spawning or courtship, since the specimens in captivity in this study were spawning conditions, in addition to this Mok and Gilmore (1983) recorded this sound in spawning groups in *C. nebulosus*. In this way it would be necessary to make a deeper study about sciaenid sound emissions in captivity or in the wild to know if this call is common and what would be its roll.

Sounds produced by sciaenid have been associated with the mating season since the early twentieth century (Smith 1905), and are now routinely used to monitor spawning populations in the field (Mok and Gilmore 1983; Saucier and Baltz 1993; Connaughton and Taylor 1995; Rountree et al. 2006).

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