From soundscape to species: identifying *Brotula multibarbata* as the source of a reef sound with conservation implications

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Abstract
Passive acoustic monitoring (PAM) is a powerful tool for collecting different kinds of data on species biology and ecol- ogy. A distinctive frequency-modulated sound, referred to as the "whoot", has been recurrently recorded in coral reef soundscapes of French Polynesia during the night. However, the identity of the emitter remained unknown. In this study, we combine tank and field acoustic recordings with morphological analyses to highlight that the whoot is produced bythe goatsbeard brotula, *Brotula multibarbata*, a cryptic, nocturnal ophidiiform fish. Some individuals were recorded in captivity, and their calls matched field recordings in structure, duration, frequency, and modulation pattern. The sound- producing apparatus consists of three main components: (1) a thin, flexible region of the anterior swimbladder (swimblad- der fenestra), (2) a bony dome formed by enlarged epineurals (swimbladder plates) located dorsally above the fenestra, and
(3) a pair of fast-contracting sonic muscles. Muscle contractions induce rapid movements of the fenestra and vibration of the overlying plates, producing sound. Literature indicates whoot calls have been recorded across the Indo-Pacific, from Mozambique to French Polynesia, confirming both the wide geographic distribution of *B. multibarbata* and the potential of PAM to provide key ecological insights, all information being valuable for conservation strategies.

Keywords Acoustic communication · Cryptic species · Brotula · Ophidiiform

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Introduction

In marine environments, studies aiming to assess fish bio- diversity through acoustic methods have been expanding rapidly worldwide (Desiderà et al. 2019; Di Iorio et al. 2021; Puebla-Aparicio et al. 2024; Ríos et al. 2025). The main approach employed is passive acoustic monitoring (PAM), which first detects and then catalogues the various sounds present in a given soundscape (Bolgan 2025). Fish sounds, once identified, are used as proxies to estimate bio-diversity levels (Mooney et al. 2021; Parsons et al. 2022).

Beyond biodiversity assessment, this technique also offers the opportunity to investigate specific behaviors, such as spawning periods in certain fish groups (Jublier et al. 2020;Parmentier et al. 2017a; Picciulin et al. 2013; Rowell etal. 2012), to characterize diel activity rhythms in different species, and to document the alternation of acoustic com- munities within a given habitat (Boyle et al. 2022; Lin and Kawagucci 2024; Ruppé et al. 2015). These studies have revealed that the organization of acoustic space is structuredaccording to a few key principles aimed at avoiding cacoph-ony. Two mechanisms have been particularly emphasized. Species produce stereotyped distinguishable sounds and/or produce them at specific times of the day only. Unlike diurnal fishes, individuals belonging to nocturnal acoustic communities have limited opportunities to rely on pheno- type or visual displays to stand out within the group. Their identification must therefore rely primarily on acoustic traits. Consequently nocturnal sounds preferentially employ distinct acoustic features that enhance individual or species identification (Bolgan et al. 2022; Ruppé et al. 2015; Wall et al. 2013).

Despite these various approaches, a certain degree of frustration must be acknowledged: not all of the distinct sound types recorded in the environment can be reli- ably assigned to a specific species (Ross et al. 2023). As a result, researchers often work with acoustic categories or numerical entities, which introduces a level of abstraction since studies report primarily on sound types rather thanon identified species (Puebla-Aparicio et al. 2024; Raicket al. 2025a). The main challenge, therefore, is to achieve species-level identification whenever possible. This task is further complicated by the fact that we do not always knowwhether a single species can produce multiple sound types.Through studies focusing on individual species, it is some- times possible to recognize specific species within broader soundscapes (Bertucci et al. 2021; Parmentier et al. 2017a).This identification is naturally facilitated when the species produces sounds with unique acoustic features, as is the casefor species such as toadfish (Fine and Thorson 2008; Jordãoet al. 2012) or cusk-eels (Mooney et al. 2016; Parmentieret al. 2022; Picciulin et al. 2019; Sprague and Luczkovich 2001). In other situations, identification may be limited to the genus or family level of the vocalizing fishes (Di Iorio etal. 2018; Raick et al. 2022).

Within reef environments, numerous sound-producing species have been documented (Parmentier et al. 2021;Tricas and Boyle 2014). In French Polynesia, a recent study estimated that approximately 60 fish species producesounds within the upper 20 m of the water column (Raicket al. 2025a, 2022), and that at least 16 vocal species are still present as deep as 300 m in the aphotic zone (Raick et al. 2025b). However, the fact that acoustic traits of several vocal reef species such as Pomacentridae (Mann and Lobel1995; Parmentier et al. 2009), Balistidae (Parmentier et al. 2017b), Ostraciidae (Lobel 1996; Parmentier et al. 2019), Serranidae (Nelson et al. 2011; Schärer et al. 2014), Carapi-dae (Kéver et al. 2014b; Parmentier et al. 2016a, 2003), and Holocentridae (Banse et al. 2024b, 2024a, 2023b) have beendescribed does not necessarily mean that they can easily beidentified within natural soundscapes.

Among the approximately 60 distinct sound types recorded on French Polynesian reefs, one in particular stands out due to its highly specific and unique acoustic characteristics. First recorded in March and April 2015 on the north coast of Moorea Island (French Polynesia), this long-duration sound, referred to as the "whoot", is char- acterized by a frequency modulation around 200 Hz and a distinctive amplitude envelope that changes during its pro- duction (Bertucci et al. 2020). The acoustic properties of thissound suggest that it is produced through a so-called "forcedresponse" mechanism involving the action of fast-contract-ing muscles on the swimbladder (Fine and Parmentier 2015;Parmentier and Fine 2016). Since the initial recordings in Moorea, whoot sounds have also been detected on several other Polynesian islands offering insights into the emit- ter's biology (Raick et al. 2025a, 2022) and further dem- onstrating the method's reliability for diversity assessment.From these previous studies, the whoot is typically emitted between sunset and the first part of the night (7 pm – 12 am),with its occurrence decreasing during the second half of thenight, and a secondary activity peak occurring around 5:00 a.m. until sunrise. These sounds are rarely produced during daytime (Bertucci et al. 2020; Raick et al. 2023). In Poly- nesia, whoots have been detected from the surface down todepths of 120 m but were not recorded on the outer slope ofMoorea at 300 m depth (Raick et al. 2025b).

During nocturnal dives, divers encountered *Brotula multibarbata* (Ophidiidae) in the immediate vicinity of the hydrophones when whoot calls were detected. This obser- vation prompted to direct some investigations towards this species, aiming to test whether they could produce such sounds. Sounds produced by Ophidiiformes have been documented in only a few species, primarily within the Carapidae (Lagardère et al. 2005; Parmentier et al. 2016a, 2003) and Ophidiidae (Mann et al. 1997; Parmentier et al. 2022, 2018; Rountree and Bowers-Altman 2002) families. In Ophidiidae specifically, the organization of acoustic parameters is such that these fishes can be easily recognizedwithin the soundscape (Mooney et al. 2016; Picciulin et al. 2019; Sprague and Luczkovich 2001). The acoustic signalsof other taxa within the order remain undescribed, despite the presence of an internally well-developed sound-pro- ducing apparatus that strongly suggests acoustic commu- nication (Fine et al. 2018, 2007; Howes 1992; Parmentier et al. 2006a). Together with their observation in the field, the capacity of these taxa to produce unique sounds fur- ther supports the hypothesis that they could be the sourceof the distinctive "whoot" calls. Within Polynesian reef ecosystems, Ophidiiformes include at least Carapidae and Brotulidae species (Siu et al. 2017). No data are available on the sounds produced by Brotulidae. This family, which comprises a single genus with currently seven valid species(Wong and Chen 2024), is easily recognizable by the bar- bels on the snout and chin, and by pelvic fins featuring tworays inserted at approximately the level of the preopercle. Brotulids can reach up to 75 cm in length and are distrib- uted across tropical and subtropical seas worldwide, from shallow reefs to depths of around 650 m (Greenfield 2005; Nielsen et al. 1999). On coral reefs, *B. multibarbata* is a cryptic, exclusively nocturnal species.

The aim of this study is to determine whether *B. multi- barbata* could be responsible for the whoot calls detectedin Polynesian coral reef soundscapes, by identifying itsvocal capacities through sound recordings in different con- texts and analyzing its morphology. Successfully addressingthese objectives would not only resolve the question of the emitters identity but would also provide additional informa-tion through PAM regarding the species behavior, ecology,and distribution. Such information is of critical importance to the primary purpose of PAM: providing essential data tosupport conservation management.

Methods

Fish collection

Three *B. multibarbata* specimens (total length 25.5–27.5 cm) were collected at night during the full moonperiod (10–12 May 2025) on the fringing reef of Moorea island (17°29′48 S; 149°51′7 W), at depths ranging from 2 to 5 m. After capture, the fish were transported in coolers filled with seawater and housed at the Centre de Recherches Insulaires et Observatoire de l'Environnement (CRIOBE). This study complies with the rules defined by the Directionde l'Environnement de la Polynesie Fran-çaise (DIREN) regarding experiments on coral reef fish in aquaria. The fishwere maintained together in a 1500 L tank (172 cm diam- eter, 60 cm water height) supplied with a continuous flow ofseawater directly from the environment. Rocks were placedin the tank to provide shelter.

Previous work demonstrated that large plastic tanks minimize acoustic distortions com- pared to smaller glass aquaria (Banse et al. 2023a).

Recordings and analysis

Sounds were obtained using two different methods. 1) The fish were hand-held in open seawater at a depth of 15 cm and at a distance of 5 cm from the hydrophone (Banse etal. 2023a). Recordings were made using an HTI-96-MIN hydrophone (High Tech Inc., Long Beach, USA; sensitiv- ity: − 164.4 dB re 1 V μPa^{-1}) connected to a TASCAM DR-05X recorder (Milton Keynes, UK).

Sounds were digitized at 44.1 kHz (16-bit resolution), low-pass filtered at 1.5 kHz, and analyzed using Avisoft- SASLab Pro 4.33 software. Only sounds with a good signal-to-noise ratio were retained for analysis. Temporal featureswere measured from oscillograms, while frequency parame-ters were obtained from power spectra. The following soundparameters were measured: peak period calculated as the average peak-to-peak interval between consecutive ampli- tude peaks (in milliseconds) and sound duration (ms). Sincewhoot calls are frequency-modulated, dominant frequencies(Hz) were measured across different segments of the soundsusing power spectra and spectrograms, with the aim of pro-viding data useful for future species identification. These sounds were then compared with previously recorded data from various islands in French Polynesia. Eleven sounds were selected from the dataset of Raick et al. (Raick et al. 2025a) and fifteen sounds from Bertucci et al. (Bertucci et al. 2020).

Anatomy

After recording, all specimens were euthanized with MS222(Sigma-Aldrich), fixed in a 5% formalin solution for 2 days.After formalin fixation, a specimen has been used for optical histology. The left muscle associated with the swimbladder,white epaxial fibers, swimbladder and gonads were sampledand dehydrated in butanol, embedded in paraffin, sectionedserially at 10 µm (Reichert microtome) and stained using Gill III haematoxylin. Histological sections were observed with a Digital microscope VHX—7000 (Keyence, Osaka, Japan) that allowed measurements of muscle cells areas anddiameters on the cross sections. The two other specimens were transferred to 70% ethyl alcohol.

Micro CT scannings of these two specimens were com- pleted using a FleXCT system consisting of a customized UniTOMXL scanner from Tescan XRE (Samber et al. 2021).Images of *B. multibarbata* were generated at a voltage of60 kV and a current of 760 µA. This generated 2200 imageswith a voxel size of 40 µm. The image reconstruction was performed using the Panthera software from Tescan XRE. Segmentation, visualization, and analysis were performed using the Aquila TM software. Three-dimensional (3D) images were produced in 16-bit and subsequently converted into 8-bit voxels using ImageJ (Abramoff et al., 2014). Direct volume renderings (iso-surface reconstruction) wereused to visualize the subset of selected voxels of skeleton and swim bladder in AMIRA 2019.2. After scanning, speci-mens were dissected and examined with a Wild M10 bin- ocular microscope coupled with a camera lucida.

Statistical analyses

As sonic muscle fibre measurements (diameter and cross- sectional area) and white epaxial fibre measurements did not follow a normal distribution (Shapiro–Wilk test), non- parametric Mann–Whitney U tests were used to compare thetwo muscle types. All statistical analyses were performed using GraphPad Prism version 8.4.2 (GraphPad Software, San Diego, USA).

Results

Hand – held sounds

Sounds recorded from hand-held fish consisted of short pulse trains containing 7 to 14 pulses (mean ± SD: 8.6 ± 1.6,n = 29), emitted with an average period of 5.7 ± 1.1 ms(n = 226). This corresponds to an average sound durationof 50.7 ± 8 ms (n = 30) and a stable dominant frequencyof 187 ± 4 Hz (n = 30). The correspondence between pulse period and dominant frequency supports the hypothesisthat these sounds are produced by fast-contracting muscles (Fig. 1**, SP1**).

Whoots

When a pair of fish was left undisturbed in the tank over- night, three long-duration sounds were recorded (**SP2**). As a rough

description, these sounds lasted 1500–2000 ms anddisplayed a biphasic structure: Part 1 (1600–1700 ms) withgradually increasing amplitude, followed by a short silent gap, then Part 2 (80–120 ms) with higher energy (Fig. 2A).The pulse period varied from 4 to 5.5 ms, with a dominant frequency around 200 Hz accompanied by harmonics. Audi-bly, the call resembles a biphasic "whoot"-like sound com-posed of a prolonged first component followed by a shortersecond component, consistent with its temporal and spectralstructure.

Although the number of tank recordings may appearlimited, their specific acoustic features closely match those previously recorded in the field (Fig. 2B,C). However, the signal-to-noise ratio in field recordings was not always suf-ficient to clearly distinguish the sound contours on oscil- lograms, as they were often masked by background noise (Fig. 2C). Visual inspection of oscillograms is thereforenot the most reliable method for identifying these calls. In contrast, whoot calls recorded in the field are easily distin- guishable on spectrograms, thanks to their characteristic fre-quency modulation and harmonics.

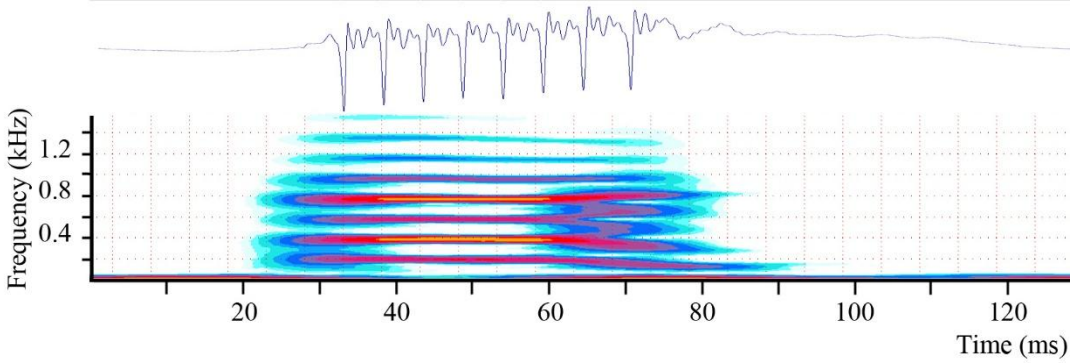

Fig. I Oscillogram (**A**) and spectrogram (**B**) of an example of a hand-held sound composed of a train of nine pulses

The following description applies to whoot calls recordedboth in captivity and in the field. In Part 1, the acous-tic structure is characterized by a stepped frequency band arrangement resembling a staircase pattern. Three main fre-quency bands are consistently observed, all of which can exhibit harmonics (Fig. 2). The first fundamental frequency(F_1), carrying the most energy, is located between 210 and 260 Hz (237 ± 12 Hz, n = 26) and corresponds to the first part of the sound. The second frequency band (F_2), also energy-rich, ranges from 160 to 240 Hz (206 ± 19 Hz, n = 26) and corresponds to the second step. The third frequency band (F_3) occurs between 160 and 195 Hz (177 ± 11 Hz, n = 18).Additional frequency bands may occasionally be pres- ent, but establishing consistent correspondence betweentank and field recordings for these secondary frequencies is uncertain due to inherent variability among sounds. At least, these additional bands are not necessary for identi- fying whoot calls. In Part 2, two dominant frequencies are observed: a fundamental frequency ranging from 210 to260 Hz (235 ± 12 Hz, n = 26) and its first harmonic, with the harmonic generally carrying more energy than the funda- mental (Fig. 2).

Anatomy

Histological examination of the gonads confirmed that the specimens recorded in captivity were males. The first five vertebrae of the vertebral column all possess epineurals (Fig. 3A). While the first two vertebrae and the fifth pos- sess rod-like epineurals, those of the third and fourth ver- tebrae are plate-like, forming two swimbladder plates that surround the anterior part of the swim bladder.

Brotula multibarbata possesses a thick swim bladder extending from the first to the fifteenth vertebra, its pos- terior end being limited by the ventral fusion of the par- apophyses of the fifteenth vertebra. The swim bladder is

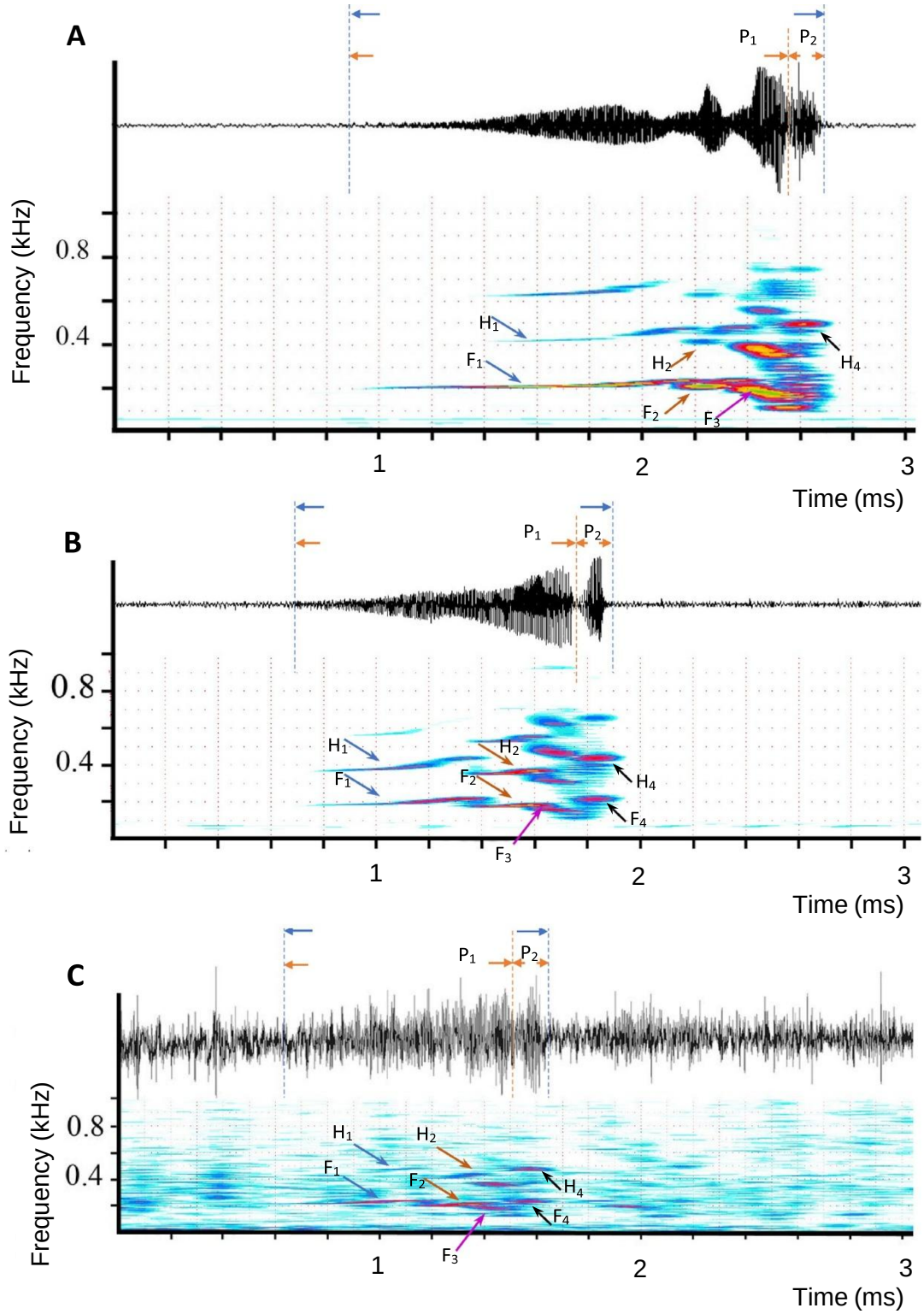

Fig. 2 Oscillograms and spectrograms of *Brotula multibarbata* sounds recorded in the tank (**A**) and in the field (**B** and **C**). Panel B showsa sound from Raick et al. (2025), and panel C from Bertucci et al. (2020). In all three cases, the main acoustic features allow for easy identification of the sounds. The oscillogram highlights the biphasic structure of the call, while the spectrogram reveals its characteristic frequency modulation. P: part of the sound; F: fundamental frequency;H: corresponding harmonics. F_1 to F_3 are observed during Part 1 (P_1), and F_4 corresponds to Part 2 (P_2). Space between blue arrows corresponds to the sound duration.

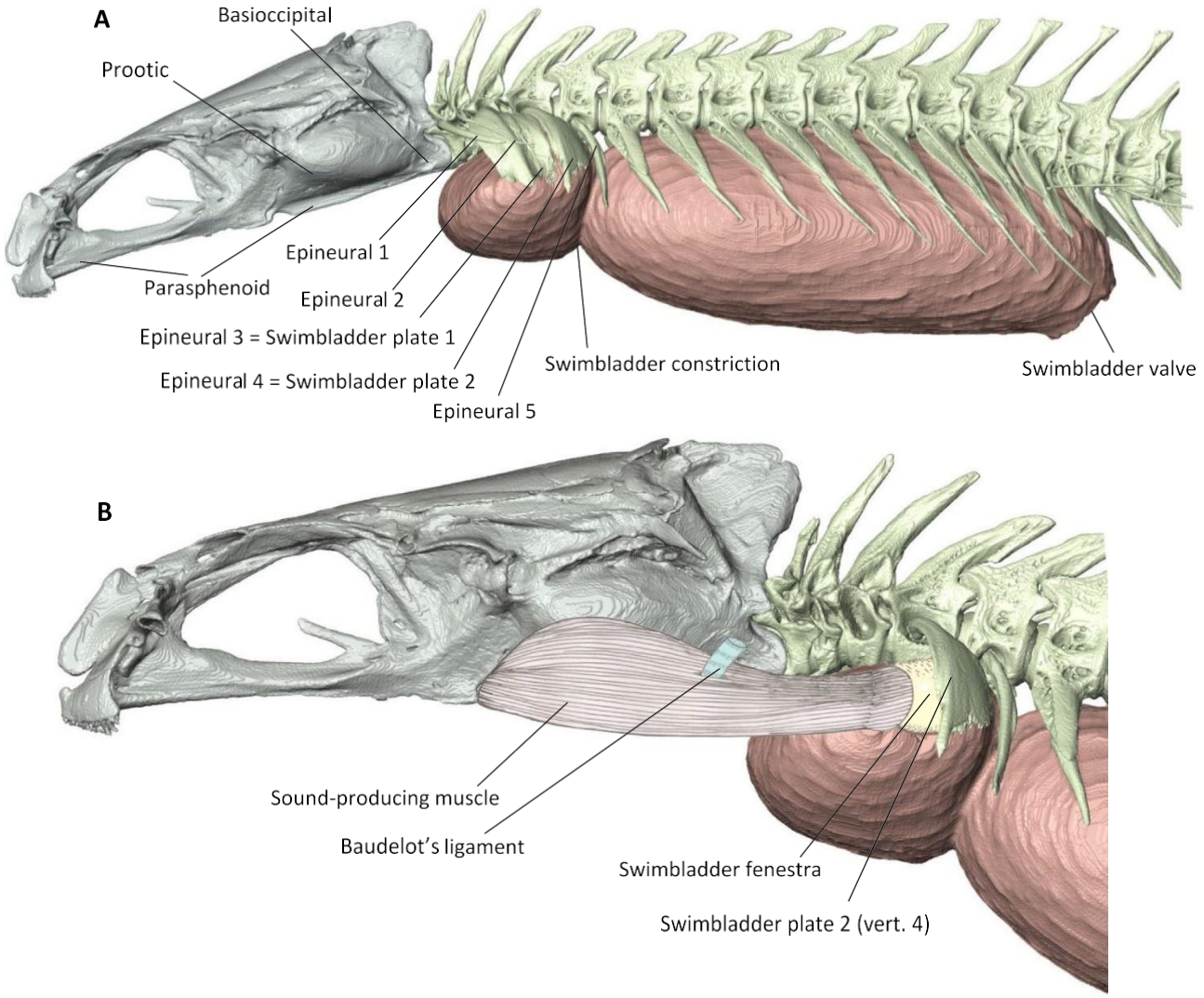

Fig. 3 Left lateral view of the anterior part of vertebral column and skull in male (**a**) of *Brotula multibarbata*. In B, epineurals 1 to 3 have been removed to show the location of the swimbladder fenestra and sound-producing muscle has been added

divided into two inequal parts separated by a bottleneck area(constriction). The small anterior part is spherical, extend- ing from the first to the fifth vertebra, while the posterior part is longer and tubular (Fig. 3A). The white swimbladderwalls are relatively thick (350–650 µm), rigid, and resistantto deformation. These properties are primarily due to the tunica externa, composed of three layers of elastic and col- lagen fibres: two outer layers oriented perpendicularly and an inner longitudinal layer. Dorsally, at the level of the ante- rior part, the swim bladder possesses a thin swimbladder fenestra (Fig. 3B), corresponding to a zone lacking tunica externa (Howes 1992; Parmentier et al. 2008), measuring approximately 10 µm in thickness. This fenestra covers an area extending from the third to the fourth vertebrae, posi- tioned below the swimbladder plates. The fenestra is defined by a thinner, more elastic area of the swim bladder wall that allows displacement of the anterior part of the swim blad- der with minimal or no movement of its posterior section. Manual handling confirmed this functional assumption. A large, rounded flexible zone, approximately 1 mm thick,the swimbladder valve, is also found in the caudal region ofthe posterior part of the swim bladder (Fig. 3A). This areais similarly devoid of the thick tunica externa and appearsto consist mainly of mucosa (Fig. 4), suggesting that this region may allow local pressure release or deformation.

The sound-producing muscle is particularly well devel- oped relative to the neurocranium. It originates on the skullat the level of the prootic, extends horizontally towards the swim bladder, passes through the Baudelot's ligament, and inserts onto the swim bladder anterior to the swimblad-der fenestra (Fig. 3B). In *B. multibarbata*, sonic muscle fibres are significantly narrower than white epaxial fibres (Mann–Whitney $U = 0$, $p < 0.0001$). Their mean diam- eter and cross-sectional area are 20.5 ± 6 µm ($n = 3834$)and 359 ± 237 µm^2 ($n = 318$), respectively, compared to 171 ± 24 µm ($n = 3834$) and 23429 ± 6436 µm^2 ($n = 318$) for the white epaxial fibres.

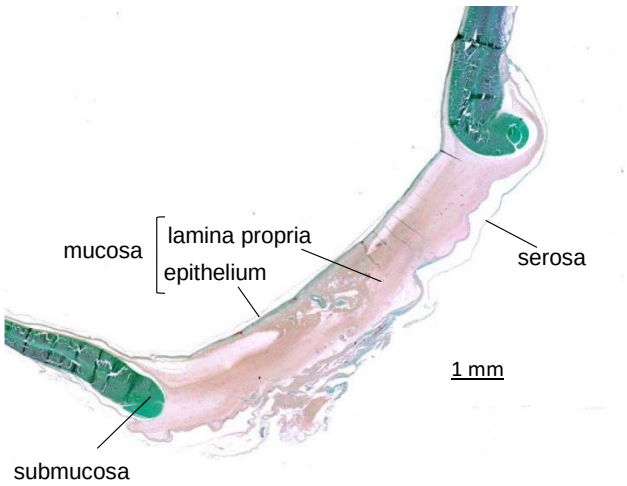

Fig. 4 Longitudinal section at the level of the swimbladder valve

Discussion

The similarity between the oscillograms and spectrograms of whoot calls recorded from *B. multibarbata* both in captiv-ity and in the field in French Polynesia leaves no doubt thatthese sounds are produced by this species. This comparisonis further facilitated by the fact that few fish taxa are capableof producing sounds with frequency modulation (Amorim and Vasconcelos 2008; Lobel 1992; Rice and Bass 2009). Additionally, these calls are produced primarily during the first part of the night after sunset, and again before sunrise,with little or no activity during daytime (Raick et al. 2023).This pattern is consistent with the acoustic behavior gener- ally observed in shallow-water Ophidiiformes, which showa marked aversion to daylight (Kéver et al. 2014b; Parmen-tier et al. 2022, 2018, 2010). When not inhabiting aphotic zones (Nielsen et al. 1999; Wong and Chen 2024), many species in this order remain hidden during the day buried insand, as in *Ophidion rochei* or *O. marginatum* (Kéver et al.2016; Mann et al. 1997; Matallanas and Riba 1980), or shel-tered inside hosts, as Carapidae (Parmentier et al. 2016b; Parmentier and Eeckhaut 2024; Parmentier and Vandewalle2005), resulting in predominantly nocturnal activity pat- terns. In the Mediterranean Sea, for instance, *O. rochei* washistorically classified as data deficient by the IUCN due to its elusive nocturnal habits and infrequent visual observa- tions (Bolgan et al. 2023). Its presence was primarily docu-mented through fisheries records. However, a recent study demonstrated, through the species unique acoustic signa- ture, that *O. rochei* is in fact widely distributed throughout the Mediterranean basin, from Spain to Cyprus (Bolgan et al. 2023; Picciulin et al. 2019).

Similarly, whoot calls produced by *B. multibarbata* now offer the opportunity to identify this species on amuch larger scale, spanning the entire Indo-Pacific. While whoots were first reported in French Polynesia (Bertucciet al. 2020; Raick et al. 2022), recent literature indicates that identical calls have been recorded on coral reefs in Mozambique (Puebla-Aparicio et al. 2024), approximately 16,000 km from Polynesia. This assertion is further sup- ported by recordings we received from Mayotte, where the spectrograms show the typical frequency arrangement of *B.multibarbata* whoots, fully consistent with the parameters described here (Simon Elise, pers. comm.). The whoot of *B. multibarbata* has also been identified in a dataset from Fiji (Ceraulo et al. 2024), which the authors kindly shared with us. The reliability of these identifications is reinforcedby the remarkable consistency in whoot characteristics. Outof a total of 2,318 calls recorded between 60 and 120 m depth across six Polynesian islands, covering millions of square kilometres, 99.6% exhibited the same acoustic pat- tern described here (Raick et al. 2023). This low variabil- ity makes *B. multibarbata* whoots an ideal acoustic marker for future species identification and large-scale monitoring efforts. Moreover, the identification of whoot calls across multiple Indo-Pacific locations is fully consistent with the broad distribution range attributed to the goatsbeard brot- ula, from South Africa and the Red Sea to Japan, Australia,Micronesia, the Hawaiian Islands, and the Society Islands (Greenfield 2005; Hubbs 1944). As *B. multibarbata* is a cryptic species, passive acoustic monitoring (PAM) could provide key insights into its biology and ecology.

While the number of recorded calls does not allow for a direct estimation of the number of individuals present, the vocal behaviour of this species offers a valuable proxy for monitoring population trends on coral reefs. In French Poly-nesia, despite unexplained differences observed among six studied islands, a total of 2,318 whoot calls were recorded over 682 h of

monitoring at 60 and 120 m depth. Notably, over 96% of these calls were recorded between 5 p.m. and5 a.m., with an estimated rate of 600 calls per hour at 120 mdepth between 7 p.m. and midnight (Raick et al. 2023). Based on these data, *B. multibarbata* appears to be a noc- turnal species, with activity concentrated in the first part of the night. Its vertical distribution between 60 and 120 m varies depending on the island (Raick et al. 2025a). These findings provide only preliminary insights into the species ecology and could serve as a basis for further studies onits habitat preferences and the broader community in whichit occurs. The behavioral context of whoot production nevertheless remains unknown. However, the stereotyped and repetitive nocturnal production of these calls suggests a potential role in social communication, possibly linked toreproductive or spacing interactions. Such a calling pattern is unlikely to correspond to simple aggressive or defensive signals, which are typically produced more sporadically andin direct association with specific interactions. The highly unusual acoustic structure of the whoot call, including its stepped frequency organization and pronounced frequency modulation, strongly facilitates its identification within reefsoundscapes. More broadly, recent work emphasized that although acoustic species specificity cannot be considereda universal rule across teleosts, some taxa nevertheless pos-sess sufficiently distinctive acoustic signatures to allowreliable identification in natural soundscapes (Parmentier and Banse 2026). The whoot call of *Brotula multibarbata* appears to represent such a case.

However, it remains necessary to record the sounds of other *Brotula* species to confirm these findings and avoid potential misattributions. The genus *Brotula* currently includes seven valid species, six of which are present inthe Indo-Pacific (Wong and Chen 2024). Two species, *B. clarkae* and B. *ordwayi*, are restricted to the Eastern Pacific,from the Mexican coast to Peru (Hildebrand and Barton 1949; Hubbs 1944), and therefore do not overlap geographi-cally with *B. multibarbata*. One species, *B. townsendi*, is reported from New Caledonia to Hawaii (Fowler 1900), while two more recently described species, *B. flaviviridis* and *B. phenax*, have only been recorded in restricted areas, namely Fiji and Vietnam, respectively (Greenfield 2005; Prokofiev 2004).

Morphological differences in the sound-producing appa-ratus should help determine whether the calls of these spe- cies are identical or not, as significant variation is knownin the anatomy of sound-producing apparatus among Ophi-diiformes, even between phylogenetically close species (Howes 1992), or even also between sexes within a single species (Kéver et al. 2012). We hypothesize that the calls ofother *Brotula* species are also based on frequency modula- tion. Since several of these species are targeted by fisher- ies (Fall and Niass 2014; Herrera et al. 2017; Herrón et al. 2018), gaining a deeper understanding of their behavioural ecology is critical for developing effective managementstrategies. For instance, *B. clarkae* is reported to have a spawning period extending from May to October, with frac-tional spawning events centred around specific peak periods such as June and September (Acevedo et al. 2007). Passiveacoustic monitoring should make it possible to identify the timing of these spawning events with greater precision.

The morphological features observed in *B. multibarbata*are fully consistent with its identification as the emitter of the whoot calls. The presence of powerful sonic muscles with exceptionally small-diameter fibres, characteristic of high-speed muscles, supports a mechanism where muscle contraction frequency directly determines the sound's fun- damental frequency. While the mean fibre diameter in B. *multibarbata* is 20.5 ± 6 µm, it measures 28.8 ± 2.5 µm in *Parophidion vassali* and 29 ± 6 µm in *Ophidion rochei*,two other Ophidiiform species in which the fundamental frequency of the sound matches the contraction rate of the sonic muscle (Kéver et al. 2014a; Parmentier et al. 2022). Such muscle architecture suggests that potential variations in emission frequency are likely influenced more by ambi- ent temperature than by the size of individual emitters, as previously observed in similar species (Connaughton etal. 2002; Fine and Parmentier 2015; Kéver et al. 2015). In parallel with Carapidae (Parmentier et al. 2006b), which exhibit a roughly comparable morphological organization (dorsal swimbladder fenestra with sonic muscle insertion onthe anterior part and swimbladder plates), we hypothesize that muscle contraction is related to the forward displace- ment of the anterior part of the swimbladder, stretching the swimbladder fenestra. Muscle relaxation induces a rapid backward displacement of the swimbladder's anterior part. This sudden recoil would set the swimbladder plates into vibration, producing sound. At the posterior end, the swim-bladder valve likely acts as a pressure-release mechanism, preventing tissue damage from pressure fluctuations. In addition to whoot calls, *B. multibarbata* was observed to produce shorter pulse trains when hand-held. These soundsconsist of a limited number of pulses with a lower dominantfrequency, producing a distinctly pulsed acoustic pattern. This secondary sound type suggests, as in other ophidi- iform species (Parmentier et al. 2022, 2018, 2016a), that *B.multibarbata* is capable of producing different sound types in different behavioural contexts. The ability to modulate acoustic signals using the same underlying mechanism may serve multiple communicative functions. Whether these hand-held-like sounds also occur in the natural soundscape remains to be determined.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00227-0 26-04897-4.

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Author contributions The study was conceived and supervised by EP. Data collection was performed by EP, FB, GS and DL. Morphologi- cal analyses, 3D reconstructions, figure preparation and data analyseswere performed by EP. Funding was acquired by EP. The first draftof the manuscript was written by EP and all authors commented on previous versions of the manuscript. All authors read and approved thefinal manuscript.

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Data availability All necessary data is included in the article. Further inquiries can be directed to the corresponding author.

Declarations

Conflict of interest The authors declare that they have no known com-peting financial interests or personal relationships that could have ap-peared to influence the work reported in this paper.

Ethics approval This study complies with the rules defined by the Direction de l'Environnement de la Polynésie Française (DIREN) re- garding experiments on coral reef fishes in aquaria.

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