



First highlight of sound production in the glassy sweeper *Pempheris schomburgkii* (Pempheridae)

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Abstract

Many sounds produced by fishes remain to be described. Understanding sound production for vocal species would permit the development of passive acoustic monitoring of fish diversity. The present study investigated sound production in the glassy sweeper *Pempheris schomburgkii* in Guadeloupe reefs, French West Indies. Two recording approaches were used: passive acoustic monitoring in the wild and active recordings with hand-held individuals in captivity. Calls consisted of series of harmonic pop sounds with a dominant frequency of 360 Hz. On coral reefs, they were produced in chorus, starting after sunset and lasting up to 3 h. Sounds recorded in situ were longer with more pulses than sounds recorded from captive specimens. These differences in temporal features suggest two types of sounds: acoustic signals that act as distress calls and those that might be involved in group-level activities such as group cohesion and reproduction. A morphological study was also performed to describe the anatomy of the sound production apparatus which consisted of a pair of large sonic muscles which inserted dorsally on a contractible anterior part of the swim bladder. Contractions of these muscles extend rostrally this part of the swim bladder while an inner sheet of elastic connective tissue acts as a recoiling system to help the swim bladder recover its initial position during relaxation of the sonic muscles. The present results, therefore, contribute to the description of sound production by fishes found in an underexplored region and further illustrate how passive acoustics may be used to monitor fish populations in the future.

Introduction

More than 800 fish species from over 100 families have been documented to produce sounds (Ladich and Fine 2006; Bass and Ladich 2008), but this number is most probably an underestimate (Fine and Parmentier 2015). Contrarily to

Jacques-Yves Cousteau's statement in 1956, the ocean has never been a silent world as acoustic cues can be involved in spatial orientation, intra- and inter-specific communication, predation, predator avoidance and navigating obstacles (Popper et al. 2001; Parmentier et al. 2015). Thus, the calling behaviour of marine animals, together with abiotic sounds, provide natural tags for the identification, tracking and estimation of stocks (Mann and Lobel 1995), as well as for the description of marine soundscapes (Bertucci et al. 2015). In recent years, a lot of progress has been made in the field of underwater acoustics, notably enhancing our understanding of the diversity of acoustic signals in marine and freshwater environments (Fine and Parmentier 2015; Ruppé et al. 2015) and the impact of anthropogenic sounds on fish populations (Vasconcelos et al. 2007; Slabbekoorn et al. 2010; Picciulin et al. 2012). Passive acoustic monitoring (PAM), i.e. the use of automatic audio recorders in the wild, can now help uncover both broad and fine-scale ecological patterns (Sueur and Farina 2015). Furthermore, it can provide information on ecosystem functioning by documenting the activities and dynamics of soniferous (i.e. sound-producing) species over

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a wide range of temporal and spatial scales (Rountree et al. 2006; Gannon 2008; Parmentier et al. 2017). Sounds are produced in different behavioural contexts, including territorial defence, food competition or predatory attacks (Myrberg et al. 1986; Hawkins and Amorim 2000; Lagardère et al. 2005). Sounds associated with reproductive behaviours have been the most studied types of signals in fish bioacoustics (Amorim 2006). These sounds are generally produced by males to attract potential mates (Parmentier et al. 2010; Longrie et al. 2013), during courtship and to synchronise spawning activities at aggregation sites (Lobel 1992; Rowell et al. 2015; Erisman and Rowell 2017; Jublier et al. 2020), especially the synchronisation of gamete release by conspecifics (Lobel 2002). Using these signals as natural tags, acoustic recordings have been used to locate spawning sites (Lowerre-Barbieri et al. 2008; Walters et al. 2009), define spawning seasons (Luczkovich et al. 2008; Picciulin et al. 2013; Rowell et al. 2015), highlight the presence of cryptic species (Kéver et al. 2016; Picciulin et al. 2019), investigate changes in community richness and diversity (Bertucci et al. 2016; Desiderà et al. 2019), and reveal aspects of the phenology of fish communities (Ruppé et al. 2015; Bertucci et al. 2020) for example.

Although a multitude of coral reef species produce sound, many of these sounds have not yet been described (Fine and Parmentier 2015). The glassy sweeper *Pempheris schomburgkii* (Müller and Troschel 1848) is a nocturnal coral reef fish living from 3 to 30 m depth, distributed within the western Atlantic tropical ocean, off Bermuda island and from Florida to southern Brazil (Collette et al. 2015). The distribution of another member of the family Pempheridae, the curved sweeper *Pempheris poeyi* (Bean 1885), can overlap with that of *P. schomburgkii*. Individuals can reach a maximum size of 15 cm (Humann and Deloach 2004). They feed on zooplankton as larvae and invertebrates and small fish as adults. Individuals hide in caves and crevices during the day and forage in groups at dusk and during the night before returning at dawn (Gladfelter 1979). Sounds characteristics and some elements of the sonic apparatus have been described in other members of the family Pempheridae present in the Indo-Pacific region, i.e. the New Zealand bigeye *Pempheris adspersa* (Griffin 1927) in New Zealand (Radford et al. 2015), the silver sweeper *Pempheris schwenkii* (Bleeker 1855) in Japan (Takayama et al. 2003) and the blackspot sweeper *Pempheris oualensis* (Cuvier 1831) in Taiwan (Mok et al. 1997; Parmentier et al. 2016). In this family, sounds consist of harmonic pop sounds produced individually or in series with frequencies ranging from 107 to 121 Hz in *P. oualensis* to 405 Hz in *P. adspersa*, and all species show up to three harmonic frequencies. Sounds are produced in chorus (i.e. the concurrent acoustic signalling of a large number of individuals) predominantly at night when the calling rate increases. For example, it can increase

from around 73 vocalisations per hour during the day to 127 vocalisations per hour at dusk and 117 vocalisations per hour at night in *P. adspersa* (Radford et al. 2015).

Although there are many differences between species in terms of the swim bladder and its attachments to the vertebral column, muscle origins, and morphology of the recoiling apparatus, the underlying sonic mechanisms are all constructed in a similar way. The rostral part of the swim bladder is connected to a pair of large sonic muscles originating in the head whereas the caudal part is fused with ventral bony expansions of vertebral bodies. Two bladder regions are separated by a stretchable fenestra that allows forward extension of the anterior bladder during fast contraction of sonic muscles, i.e. 100–250 Hz. The mechanism is reset by a recoiling apparatus that runs between the inner face of the anterior swim bladder and a vertebral body expansion. The elasticity of this recoiling apparatus allows the swim bladder to return quickly to its initial position during sonic muscle relaxation (Parmentier et al. 2016).

Contrary to the Indo-Pacific species, little is known about the vocal behaviour and sound production mechanism of the Caribbean species. Using passive acoustics in the wild and captive acoustic recordings, the present study aims to investigate sound production in *P. schomburgkii*, primarily to describe the acoustic characteristics of the signals produced by this species and its phenology. In addition, a morphological study was performed to describe the anatomy of the sound production mechanism. The results of the present study will contribute to the description of acoustic diversity in the Caribbean reefs and also illustrate that passive acoustics can be used to monitor fish populations.

Materials and methods

Acoustic recordings

Four individuals (95–127 mm Total Length) were captured using large landing nets (40 × 40 × 40 cm) during snorkelling sessions performed in May 2019 during the day in the “Grand Cul-de-Sac Marin” in the North of the Guadeloupe archipelago (16°21'N; 61°34'W) at a depth of 5–10 m. The gender of individuals is unknown. They were placed in a cooler filled with sea water at 28 °C for approximately 10 min before being recorded individually. Fish were gently hand-held and maintained within a submerged landing net in the centre of which a hydrophone HTI-96-Min (sensitivity: -163.9 dB re 1 V μPa^{-1} ; flat frequency response range 2 Hz–30 kHz; High Tech, Inc. Long Beach, MS, USA) was placed and connected to a TASCAM DR-05 portable audio recorder (sampling frequency: 44 kHz, 16-bit resolution; TEAC, Wiesbaden, Germany). These recordings were made at sea (within 1.2 m depth) to avoid any issues with

sound deformation that can occur due to reverberation in an aquarium setting (Akamatsu et al. 2002; Parmentier et al. 2014). Fish were positioned at about 3 cm from the hydrophone until sounds were obtained. This methodology aimed to elicit the type of sounds produced by the fish when captured by a predator or during distressing events (Parmentier et al. 2011a, 2011b). Recordings were conducted for a maximum of 3 min and were ceased when a sufficient number of sounds were recorded.

Passive acoustic recordings were performed in the area where individuals were captured (Site 1), and in a coral patch close to the slope of Cochon islet in the southern part of the island (16°12'N; 61°32'W; Site 2). Recordings were made with an autonomous SNAP acoustic recorder (Loggerhead Instruments, Sarasota, FL, USA) connected to a HTI-96-Min hydrophone (sensitivity: -170 dB re 1 V μPa^{-1} ; flat frequency response range: 2 Hz–30 kHz; High Tech Inc, Long Beach, MS, USA) positioned on the bottom at a depth of 10 m by professional divers of the Marine Biology laboratory at the University of the French West Indies. The system was programmed to record for 1 min every 10 min (sampling frequency of 44 kHz, 16-bit resolution). On site 1, recordings were made from July 8 to 10, 2019. On site 2, three recording sessions were made, the first one from May 6 to 9, 2019, another from November 20 to 22, 2019 and finally from January 15 to 17, 2020.

Acoustic data processing

All recordings were digitised at 44.1 kHz (16-bit resolution) and analysed with Avisoft SASLab Pro version 5.2.13 software (Avisoft Bioacoustics, Glienicke, Germany). The

sounds analysed included all those collected when individuals were hand-held as well as 20 sounds from passive acoustic recordings with a good signal-to-noise ratio (identified as originating from *P. schomburgkii* based on aural features characterised during the analysis of hand-held sounds). A band-pass filter between 50 Hz and 2 kHz was applied (Lobel et al. 2010; Tavalga et al. 2012). Sounds were produced in series and the following acoustic features were measured: the series duration (from the beginning of the first sound to the end of the last sound), the number of sounds in a series, the sound duration, the sound period (from the start of a sound to the start of the subsequent one), the dominant frequency and harmonics of the sound, the number of pulses detected within a sound and the pulse period (peak-to-peak interval between two consecutive pulses in a sound) (Fig. 1). Temporal features were measured from oscillograms whereas frequencies were obtained from logarithmic power spectra (Fast Fourier Transform FFT, 128 points, Hamming window, 75% overlap). Passive acoustic recordings were aurally and visually inspected to detect sounds of *P. schomburgkii*. Each detected sound was tagged using the “insert label” function of Avisoft software.

Morphology

After individual recordings, all four specimens were euthanized with an overdose of tricaine methanesulfonate (MS-222) and fixed in 7% formalin for approximately 2 weeks before transferring into 70% ethanol. Three fish specimens were dissected and examined with a Wild M10 (Leica) binocular microscope equipped with a camera lucida to study the swim bladder anatomy and muscle organisation. One of

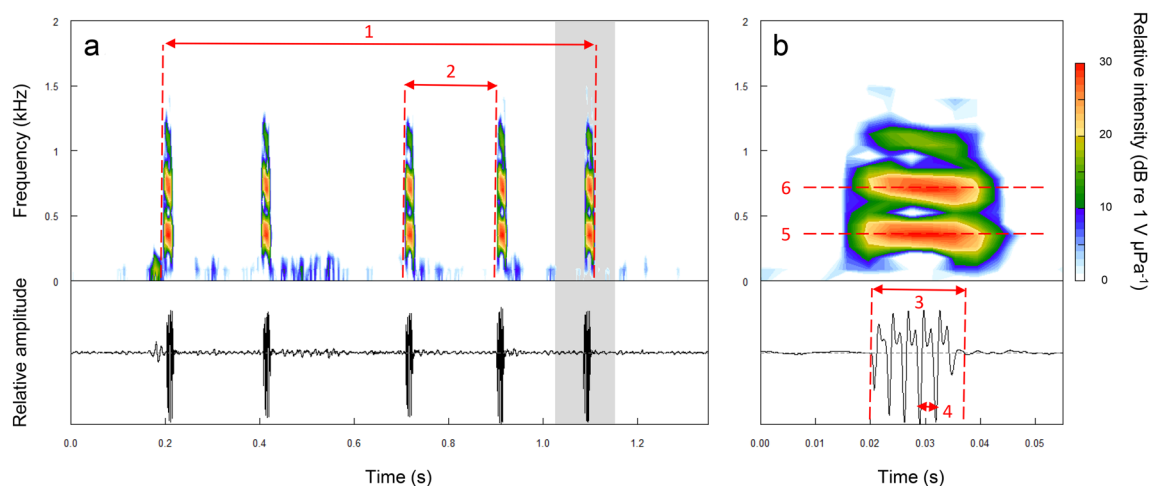


Fig. 1 Spectrograms (top) and oscillograms (bottom) of a series of five sounds (a) and of the last sound of the series (b) produced by the glassy sweeper *Pempheris schomburgkii* (made with R-studio using the Seewave package). Measured variables represented: duration of

the series (1), period of sounds (2), sound duration (3), pulse period (4), fundamental frequency (5) and first harmonic (6). Grey area in (a) indicates the sound illustrated in (b)

these specimens was then used to study the fish skeleton at the level of the sound-producing apparatus. Scanning was completed using a RX EasyTom (RX Solutions, Chavanod, France; <http://www.rxsolutions.fr>), with an aluminium filter. Images were generated at a voltage of 90 kV and a current of 333 μ A, with a set frame rate of 12.5 and 5 average frames per image. This generated 2370 images and a voxel size of 34.9 μ m. Reconstruction was performed using X-Act software from RX Solutions. Segmentation, visualisation, and analysis were performed using Dragonfly software (Object Research Systems (ORS) Inc, Montreal, Canada, 2019; software available at <http://www.theobjects.com/dragonfly>). Three-dimensional (3D) images were produced in 16-bit and subsequently converted into 8-bit voxels using ImageJ (Abràmoff et al. 2014). Three-dimensional processing and rendering, performed according to the protocols described by Zanette et al. (2014), were obtained after semi-automatic segmentation of the body, brain and inner ear using a 'generated surface'. Direct volume renderings (iso-surface reconstructions) were used to visualise a subset of selected voxels of body, brain and inner ear in AMIRA 2019.2.

The last specimen was deposited at the Royal Belgian Institute of Natural Science and received the catalogue number IRSNB 25679.

Statistical analysis

The number of sounds identified from passive acoustic recordings were grouped in 8 periods of 3 h starting from 1200 h (period 1: 1200–1450 h, period 2: 1500–1750 h, ..., period 8: 0900 h–1150 h). The normality of the data was checked by Shapiro–Wilk tests ($W = 0.344–0.754$, all $p < 10^{-3}$) and non-parametric Kruskal–Wallis tests were performed to compare the number of sounds detected between the 3-h periods for each recording session. Post hoc Dunn's multiple pairwise comparisons tests were subsequently used to identify significant differences. All statistical analysis were performed with R-studio (1.0.143) with a significance threshold of $\alpha = 0.05$.

Results

Acoustic activity

Sounds recorded in captivity were produced in series of 6 ± 5 sounds (mean \pm SD; min–max = 2–26) which lasted 1060 ± 1120 ms (72–4940 ms) with a sound period of 197 ± 136 ms (38–1094 ms). Sounds lasted 16 ± 2 ms (10–23 ms), consisted of 5 ± 1 pulses (3–8) with a period of 3 ± 1 ms (3–4) ($N = 237$ sounds from 38 series) (Online Resource 1). The sound's fundamental frequency (H_0) was 359 ± 11 Hz (344–409) (Fig. 1). Up to 4 harmonics could be identified in the recordings. The first harmonic (H_1) was 720 ± 22 Hz (689–795) and the second harmonic (H_2) = 1074 ± 27 Hz. The last two harmonics were often weak or absent and could not be measured for all sounds (Table 1, Fig. 1).

Sounds recorded in May 2019 at Site 2 were significantly longer, 39 ± 7 ms (29–52 ms), than sounds recorded in captivity (Kruskal–Wallis, $\chi^2_4 = 148.98$, $p < 10^{-3}$) with significantly more pulses, 13 ± 2 pulses (9–17) (Kruskal–Wallis, $\chi^2_4 = 123.46$, $p < 10^{-3}$). No significant differences were found in the pulse period (Kruskal–Wallis, $\chi^2_4 = 2.774$, $p = 0.428$), fundamental frequency (Kruskal–Wallis, $\chi^2_4 = 2.024$, $p = 0.57$) or first harmonic (Kruskal–Wallis, $\chi^2_4 = 2.774$, $p = 0.428$) of the sounds (Table 1).

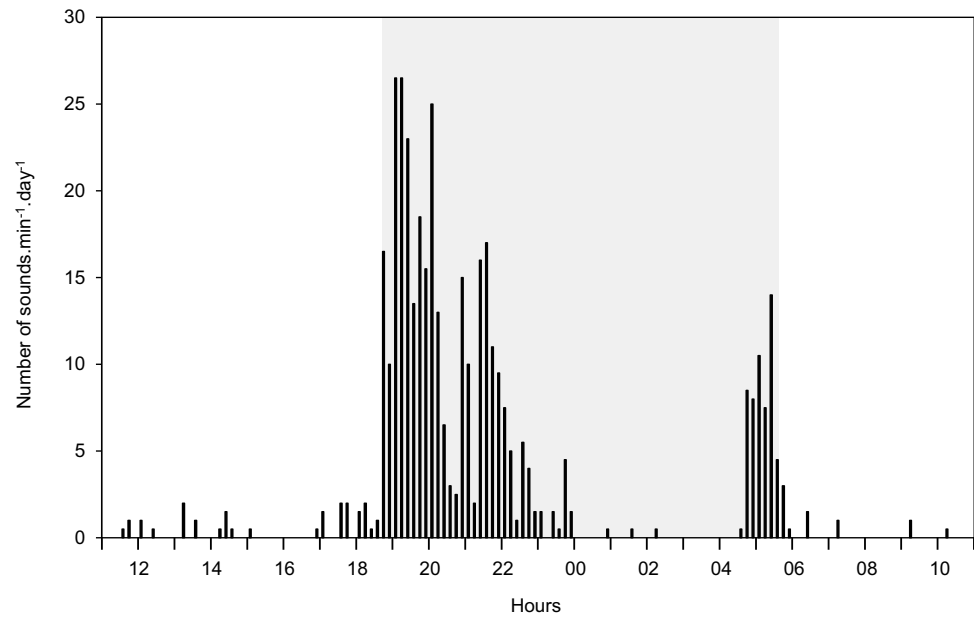
Recordings made at Site 1 (July 8–10 2019, where the individuals were captured) over 48 h revealed a drastic increase in the number of sounds at dusk (1800 h) with a maximum average number of 42 sounds min^{-1} detected. The chorusing nature of this activity prevented clear detection of series and sounds could only be detected as single units. This sustained acoustic activity then gradually decreased until 0000 h. Very few sounds could be detected until 1 h before dawn (0500 h). The latter period of sonic activity was less intense with 21 sounds min^{-1} and shorter, ending at 0600 h. During day, only a few sounds could occasionally be detected, never exceeding 4 sounds min^{-1} (Fig. 2).

The same pattern was observed at Site 2 for the recordings performed in May and November 2019 and in January 2020 (Fig. 3). The duration of the dusk chorus, however, was shorter, occurring mostly between 1800 and 2100 h, and the dawn activity scarcely detectable. Up to 492 sounds min^{-1}

Table 1 Acoustic characteristics of the sounds attributed to *Pempheris schomburgkii*

	Total duration (ms)	Number of pulses	Pulse period (ms)	Fundamental frequency (Hz)	First harmonic (Hz)	Second harmonic (Hz)
Captivity $N = 236$	16.03 ± 2.46 (10.4–22.9)	5.04 ± 0.83 (3–8)	2.84 ± 0.18 (2.3–4.1)	358.67 ± 7.83 (344–409)	720.56 ± 21.76 (689–795)	1074.56 ± 26.35 (1017–1157)
May 2019 $N = 20$	39.15 ± 6.31 (29–52)	12.85 ± 2.06 (9–17)	2.74 ± 0.62 (1–5.7)	344.26 ± 10.76 (323–356)	696.89 ± 23.02 (667–728)	1036.5 ± 33.23 (1013–1060)

Fig. 2 Average number of sounds attributed to *Pempheris schomburgkii*, as detected every 10 min on a 24 h basis on Site 1, from July 8, 2019 to July 10, 2019. Grey area represents night time



and 426 sounds min^{-1} were detected, respectively, in May 2019 and January 2020. The vocal activity detected between 1800 and 2100 h was significantly decreased in November 2019 (Kruskal–Wallis, $\chi^2_2 = 10.55$, $p = 0.0051$) with only 180 sounds. min^{-1} detected.

Morphology

P. schomburgkii has a two-chambered swim bladder connected by a short duct, and the anterior chamber is shorter than the posterior one (Fig. 4). The anterior chamber of the swim bladder extends from the 1st to the 8th vertebra, and the posterior chamber to the 9th–11th vertebra (Fig. 4). This second chamber is kidney shaped, its posterior part lying against the first haemal spine. The anterior chamber possesses two bands of fibrous connective tissue (originating from the tunica externa) that extends from the dorsal surface of the swim bladder to the 3rd vertebral centra, just beyond the insertion of the 3rd epineural. This pair of bands is also the posterior margin of a narrow slit that corresponds to the swim bladder fenestra and runs perpendicular to the swim bladder from the right to the left band. In front of the slit, the anterior part of the first chamber can undergo antero-posterior movement. The posterior part is firmly attached to the margins of the ventral bony expansions of the central vertebrae (4th, 5th and 6th vertebrae). Moreover, a sheet of elastic connective tissue extends from the bony expansion of the 4th vertebrae and inserts on the posterior margin of the anterior part of the swim bladder. A pair of large sonic muscles originates on the postero-lateral part of the skull (on the prootic) and inserts dorsally on the movable anterior part of the first chamber, between the swim bladder bands. Contractions of these muscles pull the anterior part of the

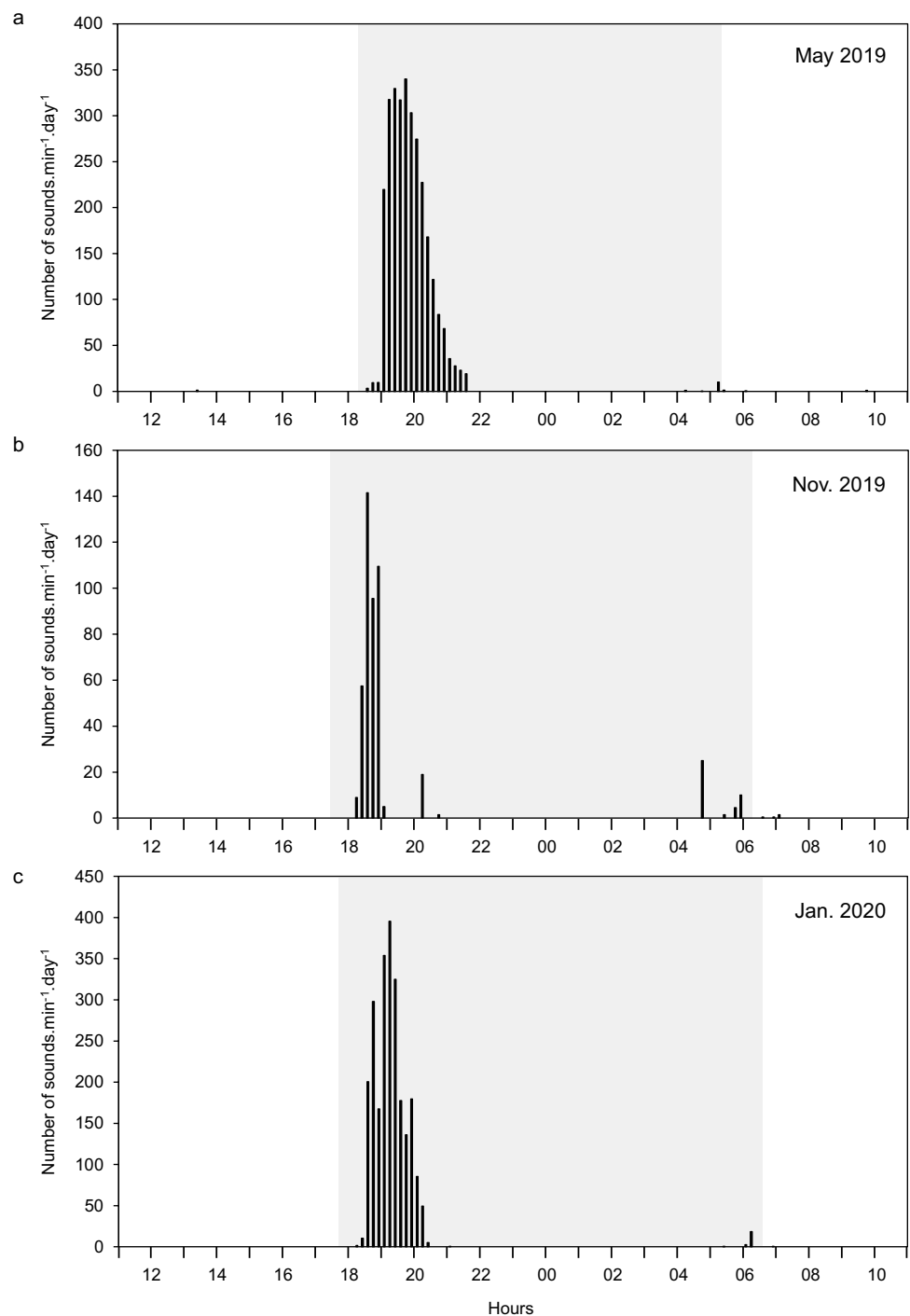
swim bladder rostrally but the inner sheet of connective tissue should function as a recoiling system that antagonises the action of the sonic muscles. Indeed, the elastic nature of the recoiling apparatus supports its role in helping the swim bladder to recover its initial position during relaxation of the sonic muscles.

Discussion

Passive acoustic surveys and recordings performed in captivity were employed to characterise the sound produced by the glassy sweeper *P. schomburgkii* together with its phenology. Sounds consisted of a series of harmonic pops with a dominant frequency of approximately 360 Hz. They were produced in chorus, commencing after sunset and lasting up to 3 h. A few sounds could also be detected before sunrise. In addition, an anatomical study permitted the description of the specialised morphology of the swim bladder and the associated structures that could be involved in the sound production mechanism of the family Pempheridae.

The discrepancy between sounds recorded on the reef and captive animals suggest that there are different types of sounds with different biological functions. This is supported by the significantly longer sounds with more pulses recorded at sea than when individuals were hand-held. Short sounds (with few pulses) would be intended for heterospecifics whereas longer sounds (with more pulses) would be addressed to conspecifics. Similar results were found in the yellowtail damselfish *Dascyllus flavicaudus* (Randall and Allen 1977) (Parmentier et al. 2010) and in the Hawaiian dascyllus *Dascyllus albisella* (Gill 1862) (Mann and Lobel 1998). The shortest sounds were

Fig. 3 Average number of sounds attributed to *Pempheris schomburgkii*, as detected every 10 min on a 24 h basis on Site 2. **a** From May 6, 2019 to May 9, 2019, **b** from November 20, 2019 to November 22, 2019 and **c** from January 15, 2020 to January 17, 2020. Note the difference in the y-axis between **a–c** and **b**. Grey areas represent night time



produced by males during encounters with heterospecifics or fights with conspecifics, while longer sounds were produced towards conspecifics during courtship displays and signal jumps, a behaviour initiated by males when female(s) entered their territory or in response to signal jumps made by other males.

A clear conclusion on the function of the distress calls produced by hand-held individuals could not be drawn. The signals suggest that stress can motivate sound production,

and calls can serve as a warning signal to conspecifics or an aposematic signal for predators (Kaatz 2002; Boshier et al. 2006). In *P. schwenkii*, sounds were observed during the approach of a school suggesting they may indeed possibly function as a distress call or as an alert signal indicating the threat of heterospecific intruders (Takayama et al. 2003). Furthermore, acoustic signals produced in choruses are also thought to be important for territory defence and mate attraction (Rehberg-Besler et al. 2017). The recordings

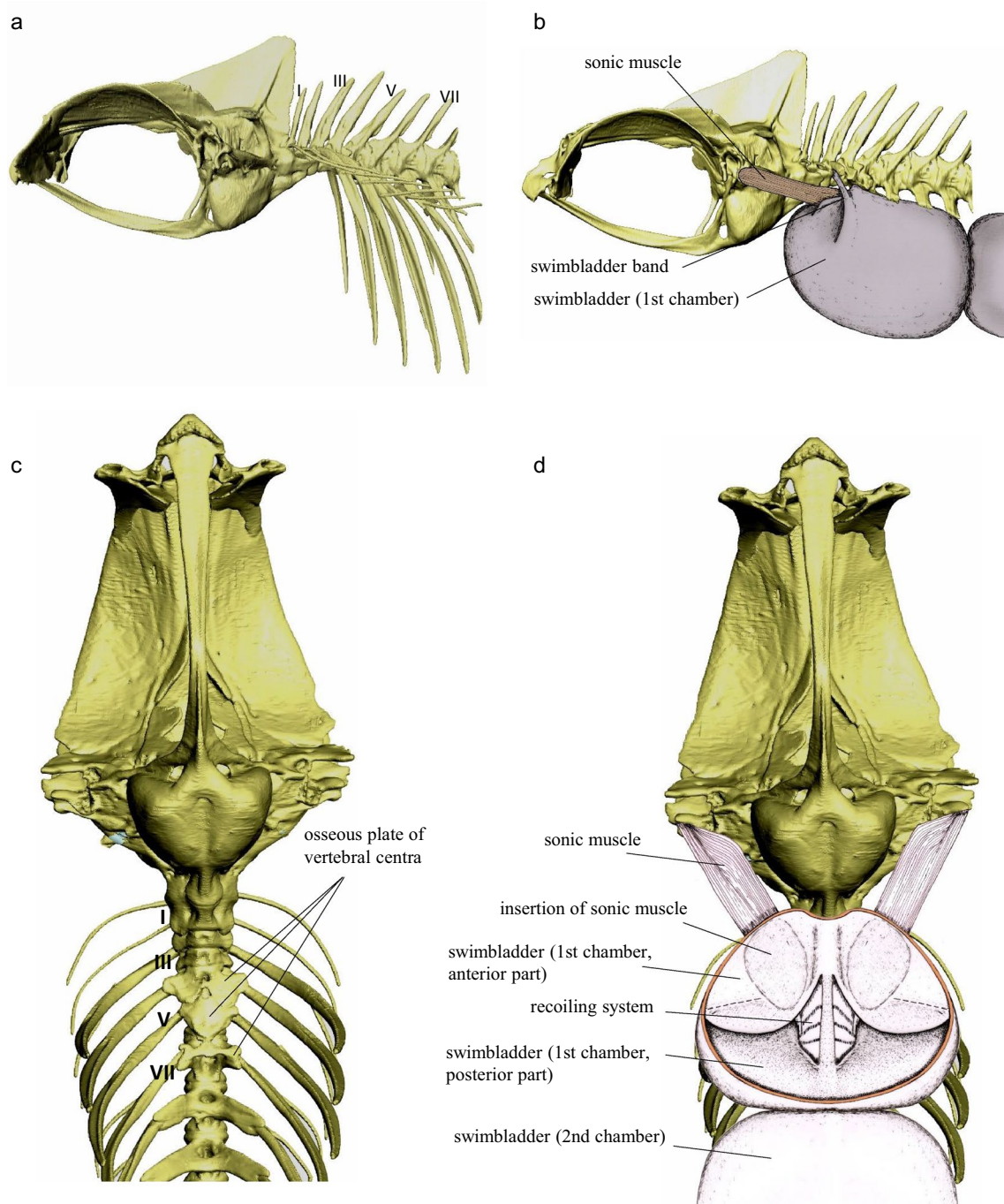


Fig. 4 Left lateral (a, b) and ventral views (c, d) of the sound-producing apparatus in *Pempheris schomburgkii* showing the anterior part of the skeleton, the swim bladder and associated muscles. The ventral view allows for the discrimination of the bony expansions at the level

of the vertebra (c). The ventral wall of the swim bladder has been removed for viewing of the inner organisation of the swim bladder and the recoiling system organisation (drawn by E. P)

suggest that sounds produced at sea could perform a different function and may be involved in other social contexts. For example, Pempheridae may use chorusing sounds as contact calls to rapidly locate conspecific aggregations in dark environments. The potential role of sound production in contact calls is supported by both the study of Gladfelter

(1979), indicating that *P. schomburgkii* becomes more active after dusk and before dawn, and by the temporal pattern of sound production, observed in the present study and in other members of the genus. Therefore, the diel pattern of sound production found in the present study would indicate that acoustic signals are particularly important for the

synchronisation of schooling and other behaviours when individuals leave their shelter at night (Larsson and Abbott 2018). Radford et al. (2015) estimated that the active space of *P. adspersa* signals, ranging from a minimum distance of 0.6 m to a maximum distance of 31.6 m, allows fish to reliably swim toward their conspecifics and maintain school cohesion. This could potentially be a way to optimise food foraging (Helfman 1986) or as a strategy to reduce predation risk (Krause and Ruxton 2002) which becomes more important when predators such as Serranidae (groupers and hamlets), Lutjanidae (porgies and snappers) and Aulostomidae (trumpetfish) are present (Gladfelter 1979).

In situ recordings also yielded insights into the seasonality of sound production in the species and sounds may be related to reproductive behaviour. The most active periods were recorded in May and January. Recordings performed in November showed a lower number of sounds as well as a shorter chorus. Reproduction occurs in *P. schomburgkii* in June and from September to October (Pastor Gutiérrez and Báez Hidalgo 2003). The sustained vocal activity observed in May could, therefore, be associated with the imminence of the first reproductive period while the reduced choruses recorded in November could indicate the end of the second one. Thus, acoustic signals could serve the function of facilitating aggregation and attraction of individuals during critical mating periods, as observed in other families, such as Serranidae (Bertucci et al. 2015; Jublier et al. 2020) or Sciaenidae (Connaughton and Taylor 1995; Parmentier et al. 2017).

The level of acoustic activity detected in January was similar to the level detected in May. This may indicate that the reproductive period is longer than previously described for this species or alternatively, it may indicate that sounds are also associated with another social activity. In either case, this result further emphasises that passive acoustics can identify previously unknown sounds produced by fish species and can also help to understand the phenology of its biological activities (Jublier et al. 2020). These findings call for additional long-term passive acoustic monitoring and visual observations to learn more about the social role of vocal communication in the glassy sweeper. Future studies may reveal that the second Caribbean species, the curved sweeper *P. poeyi*, also produces sound in the same areas with potential species-specific features. Sounds of *P. poeyi* may then possibly be present in the passive recordings performed in the present study, further illustrating the need to describe acoustic diversity across different species of fish.

Aside from the previously mentioned temporal features, sounds presented no differences in their pulse period and spectral composition, strongly suggesting that they were produced by the same mechanism. A similar mechanism is currently known only in Glaucosomatidae and Pempheridae (Parmentier et al. 2016). The dominant frequency of

the sounds resulting from this mechanism and the presence of multiple harmonics indicate that the sounds are most probably elicited by superfast muscles, as already suggested for *Terapon jarbua*, *Pempheris oualensis* and *Pelates quadrilineatus* (Parmentier et al. 2016). Therefore, despite other species-specific variations in acoustic features, the shared acoustic features support a common sonic mechanism across these species, which suggests that the sound production mechanism is a synapomorphy within Pempheriforms (Betancur-R et al. 2013). It is worth noting that certain acoustic characteristics, particularly the dominant frequency, can provide information on the individual producing the sound for some species, such as its size, sex or age (Lobel and Mann 1995; Colley et al. 2009). In species producing sounds with fast contracting muscles, the relationship between the dominant frequency and the fish size is weak, as further supported by the low variability in frequencies recorded in this study (Parmentier and Fine 2016). Thus, it may not be possible to resolve information on individuals using passive acoustic recordings from this species, however, recordings may still confirm the potential group-level functions of sound production in Pempheridae.

In conclusion, passive acoustic recordings made during this study have permitted the description of the sounds produced by a common Caribbean fish and have also offered insights into the pattern of calling at different times of the day and year. While further studies are required to complement the present results, this study contributes to continuing efforts to describe the diversity of sound production in fishes, the role it may play in their ecologies. Furthermore, the recoiling apparatus described in this study further highlights the diversity of sound production mechanisms found in teleost fishes. These data may be of particular interest to surveys of ichthyological diversity based on sound recordings. Since biotic sounds are the first to change in response to environmental degradation (Sueur and Farina 2015), their monitoring appears to be a good proxy for environmental change, allowing fluctuations to be identified as early as possible, thereby permitting rapid action to reduce their impact (Risch and Parks 2017).

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Author contributions FB, EP, DL and MR-T designed the study. FB, EP, SC and DL collected the data. FB, EP and AH analysed the data. FB wrote the manuscript. All the authors contributed to substantial revisions.

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Availability of data and material Data will be made fully available upon reasonable request to FB.

Compliance with ethical standards

Conflict of interest The authors declare no conflicts of interest and no competing interests.

Ethical approval The research required no permits and morphology investigations followed rules approved by the ethical commission of the University of Liège.

Consent for publication All listed authors agreed on the publication of the present research and accepted responsibility for the work presented here.

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