

Fish biophony in a Mediterranean submarine canyon^{a)}

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ABSTRACT:

Although several bioacoustics investigations have shed light on the acoustic communication of Mediterranean fish species, the occurrence of fish sounds has never been reported below -40 m depth. This study assessed the occurrence of fish sounds at greater depths by monitoring the soundscape of a Mediterranean submarine canyon (Calvi, France) thanks to a combination of Static Acoustic Monitoring (three stations, from -125 to -150 m depth, 3 km from coastline) and of hydrophone-integrated gliders (Mobile Acoustic Monitoring; from -60 to -900 m depth, 3–6 km from coastline). Biological sounds were detected in 38% of the audio files; ten sound types (for a total of more than 9,000 sounds) with characteristics corresponding to those emitted by vocal species, or known as produced by fish activities, were found. For one of these sound types, emitter identity was inferred at the genus level (*Ophidion* sp.). An increase of from 10 to 15 dB re $1 \mu\text{Pa}$ in sea ambient noise was observed during daytime hours due to boat traffic, potentially implying an important daytime masking effect. This study shows that monitoring the underwater soundscape of Mediterranean submarine canyons can provide holistic information needed to better understand the state and the dynamics of these heterogeneous, highly diverse environments.

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I. INTRODUCTION

A. Fish sounds as natural tags in deep-sea environments?

Fish calls are major contributors of coastal marine soundscapes (Rountree *et al.*, 2006; Mann *et al.*, 2016; Lindseth and Lobel, 2018; Desiderà *et al.*, 2019). Passive Acoustic Monitoring (PAM) has been used to investigate fish presence (e.g., Picciulin *et al.*, 2018), distribution (e.g., Picciulin *et al.*, 2013; Wall *et al.*, 2013), diversity (e.g., Wang *et al.*, 2017; Desiderà *et al.*, 2019), relative abundance (e.g., Rowell *et al.*, 2017), diel, lunar, and seasonal cycles of activity (e.g., Mann and Lobel, 1995; Locascio and Mann, 2008; Ruppé *et al.*, 2015; Wang *et al.*, 2017), for delimitating spawning areas (e.g., Luczkovich *et al.*, 2008) and for studying spawning behaviour (e.g., Fine and Thorson, 2008). However, most of these studies deal with coastal fish populations. Only a few studies have reported the occurrence of fish sounds emitted by populations inhabiting deeper waters (from -548 to -696 m, Mann and Jarvis, 2004; -682 m, Rountree *et al.*, 2012; max -200 m, Wall *et al.*, 2013; -430 to 490 m, Erbe *et al.*, 2015; -430 to 490 m, McCauley and Cato, 2016; max -273 m, Wall *et al.*,

2017). This research paucity is surprising since anatomical studies have shown that many deep-sea fish should be able to emit sounds as they possess the required anatomical structures, e.g., large drumming muscles, modified ribs, connection between the swimbladder and the muscle that move the upper pharyngeal teeth (Marshall, 1967, 1973; Fine *et al.*, 2007; Nguyen *et al.*, 2008; Ali *et al.*, 2016; Parmentier *et al.*, 2018). Different Mediterranean deep-living species including Brotulidae, Gadidae, Ophidiidae, Scorpaenidae, and Triglidae belong to families with known vocal abilities. In the Mediterranean Sea, the biodiversity between -200 and -4000 m include more than 100 fish species (Danovaro *et al.*, 2010; Priede, 2017). Among these, the grenadiers (Macrourinae, Gadiformes) possess large sound-producing muscles on either side of the forepart of their swimbladders (Marshall, 1967, 1973), similarly to several other shallow-waters Gadidae, which sound production has been characterized in details (Hawkins and Picciulin, 2019). Sound producing apparatus are also found in many deep-living cusk-eels (i.e., Ophidiiformes; e.g., Fine *et al.*, 2007; Nguyen *et al.*, 2008; Ali *et al.*, 2016; Parmentier *et al.*, 2018), but sounds were recorded in few shallow water species (i.e., *Ophidion marginatum*, Mann *et al.*, 1997; Rountree and Bowers-Altman, 2002, and *O. rochei*, Parmentier *et al.*, 2010; Kéver *et al.*, 2012; Kéver *et al.*, 2014) and in two deep living species (*Genypterus chilensis* and *G. maculatus*, Parmentier *et al.*, 2018). Finally, other important deep-sea

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fish are the rockfish (Sebastidae) (IUCN Centre for Mediterranean Cooperation, 2004) for which sound production has been documented in a dozen coastal species (Nichols, 2005; Širović and Demer, 2009; Širović *et al.*, 2009; Zhang *et al.*, 2015).

B. Combining different PAM techniques for holistic monitoring: Static acoustic monitoring (SAM) and mobile acoustic monitoring (MAM)

Recently, Picciulin *et al.* (2018) have demonstrated that PAM is an irreplaceable method for monitoring cryptic fish species in coastal areas. This necessity becomes even more stringent at depths where light penetration is reduced or absent and which are difficult to access. Previous PAM studies attempting to monitor deep-sea fish sounds suffered from self-generated noise from the inboard instrumentation, which compromised the possibility of recording fish calls (Rountree and Juanes, 2010; Wall *et al.*, 2014). Nevertheless, these studies provide valuable lessons for maximizing further attempts. A fundamental requirement for a successful PAM of deep-sea fish is a type of deployment, which minimizes self-noise (Rountree and Juanes, 2010; Wall *et al.*, 2014). This is the case of SAM (Mann and Jarvis, 2004; Carriço *et al.*, 2019) and of hydrophone-integrated gliders (MAM; Wall *et al.*, 2013; Wall *et al.*, 2017). SAM is a static and silent PAM technique (e.g., hydrophone arrays deployed on the sea bottom) already used to record deep-sea fish sounds in the Bahamas (Mann and Jarvis, 2004), in the Welkers Canyon (USA) (Rountree *et al.*, 2012), in the Perth canyon (Australia) (Erbe *et al.*, 2015; McCauley and Cato, 2016) and in Azores seamounts (Portugal) (Carriço *et al.*, 2019).

Gliders are Automated Underwater Vehicles (AUV) which allow for the collection of ocean parameters over large temporal and spatial scales. The absence of a drive motor and propellers minimizes glider mechanical noise supporting this device as an excellent candidate to board hydrophones (Wall *et al.*, 2013; Wall *et al.*, 2017; Lembke, *et al.*, 2018; Beguery *et al.*, 2018). The combination of SAM and of MAM can provide complementary information (Wall *et al.*, 2013) that is essential to increasing our understanding of fish population dynamics. SAM can provide long-term acoustic data which can inform on diel and seasonal patterns of activity, while MAM can inform on large scale, stratigraphic distribution of vocal fish populations.

C. Mediterranean submarine canyons

Submarine canyons are steep-walled sinuous valleys with V-shaped cross sections and represent key structures for ecosystem functioning in the Mediterranean Sea, where they play a fundamental role in the connectivity between coastal and deep-sea environments (Würtz, 2012). Canyons are characterized by higher mixing rates, upwelling dynamics and sediment transportation than surrounding areas; this results in increased primary production in the upper layers, which effects extend to the entire food web and stratigraphy

(Würtz, 2012; Priede, 2017). At the head of submarine canyons, fish population density and biodiversity can be from 2 to 15 times higher than in surrounding areas (Würtz, 2012).

To date, in the Mediterranean Sea, no study has attempted to monitor vocal fish populations at depths greater than -40 m, and no study has ever been conducted in submarine canyons. Our study aimed to evaluate the potential of PAM to provide novel information about the distribution of vocal fish species in these pivotal Mediterranean environments. In particular, our specific aims were to: (i) investigate whether fish biophony exists in a Mediterranean submarine canyon and (ii) assess the potential of different PAM configurations for providing complementary information on fish vocal activities occurring in the canyon.

II. MATERIAL AND METHODS

A. Study area

The study area was located off the coast of Calvi, on the North-West coast of Corsica ($42^{\circ}34'48''$ N, $8^{\circ}43'43''$ E, France), adjacent to the research station STARESO. The Calvi coastal area is characterized by a small-scale, very narrow (ca. 3 km mean width), deep (ca. 600 m mean depth), and steep-sided (up to 40° bottom slope) canyon, which intrudes approximately 6 km onto an irregular and narrow shelf. The canyon head, located in front of the Calvi Bay, bisects the shelf into two parts (Skiriris *et al.*, 2001).

The sites and depths were chosen according to different logistic and scientific considerations. Both grenadiers (*Coelorhynchus coelorhynchus* and *Nezumia aequalis*) and rockfish (*Helicolenus dactylopterus*) were potential targets of our investigation since they possess sound producing mechanisms and they show a marked preference for canyons (Marshall, 1967; Hallacher, 1974; Stefanescu *et al.*, 1994; Würtz, 2012). SAM deployment depths were chosen because the heads of Mediterranean canyons host more complex fish communities than surrounding areas (Würtz, 2012). The canyon itself was studied with hydrophone-integrated glider (MAM).

B. Acoustic data collection

Acoustic data were collected using a combination of SAM (three campaigns, from -125 to -150 m depth, 3 km from coastline) and MAM (SeaExplorer, Alseamar, from -900 to -60 m depth, from 6 to 3 km from coastline). A total of 11 160 min of continuous recordings were collected and manually analyzed.

1. SAM

Three SAM deployments were conducted at the head of the Calvi submarine canyon (Fig. 1, Table I) by using underwater acoustic dataloggers deployed on a vertical mooring line [Fig. 1(b), Table I]:

- (1) STATION A: A continuous 24-h sampling was conducted in October 2016 at *ca* -157 m (hydrophone depth, i.e., 6 m from the bottom) using an autonomous recorder SDA 14 (RTSYS) connected to a HTI-92-WB

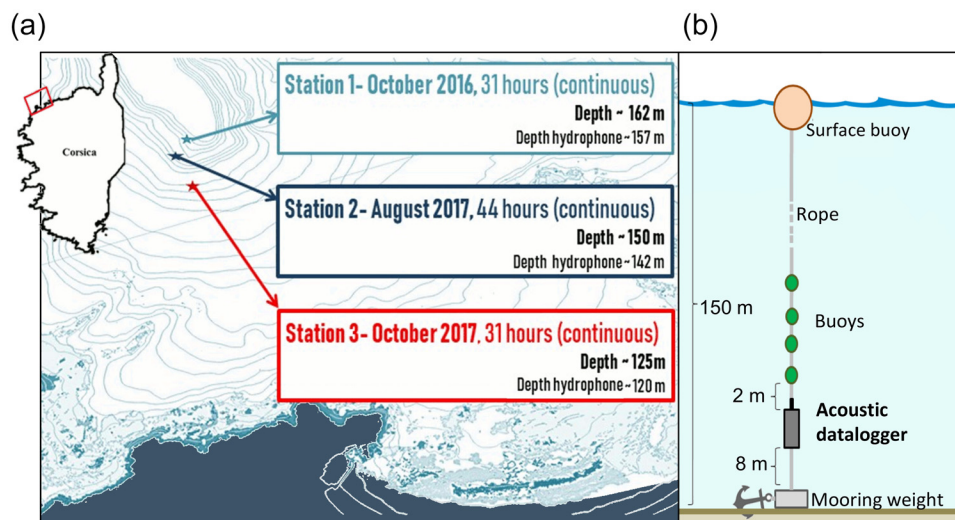
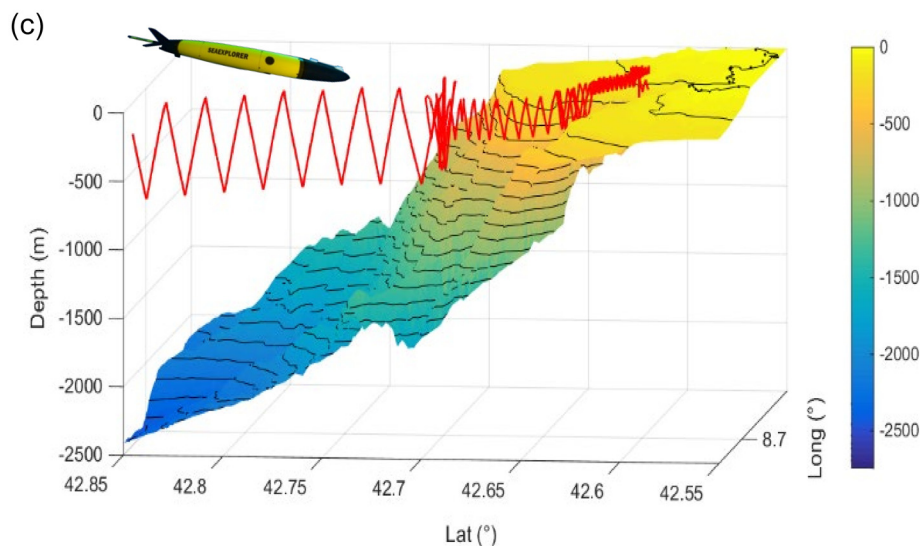


FIG. 1. (Color online) (a) Bathymetric map of Calvi Bay, Corsica (France) showing the head of the canyon and the three SAM recording sites; (b) SAM deployment configuration; (c) glider trajectory (red line) in the Calvi canyon from which acoustic data have been analyzed as part of this study.



hydrophone (High Tech Inc., flat sensitivity = -155 dB re $1\text{ V } \mu\text{Pa}^{-1}$ between 5 Hz and 50 kHz). Acoustic recordings were sampled at a rate of 156 kHz and with a 24 -bit resolution.

(2) STATION B: A continuous 48 -h sampling was conducted in August 2017 at ca. -142 m (hydrophone depth) using an autonomous recorder Cyclops (Loggerhead instruments,

Florida, USA) connected to a HTI 96-min hydrophone (High Tech Inc., flat sensitivity = -170 dB re $1\text{ V } \mu\text{Pa}^{-1}$ between 2 Hz and 30 kHz). Acoustic recordings were sampled at a rate of 44.1 kHz and with a 16 -bit resolution.

(3) STATION C: A continuous 24 -h sampling was conducted in October 2017 at ca. -120 m (hydrophone depth, i.e., 6 m from the bottom) using a SM2M

TABLE I. SAM recording stations code and details; geographical coordinates, depth, recording period, schedule and total recording time.

| | | Station code | | |
|----------------------------|------------|------------------------|------------------------|------------------------|
| | | A | B | C |
| Coordinates | Lat. | $42^{\circ}35.7959'$ N | $42^{\circ}35.7310'$ N | $42^{\circ}35.5744'$ N |
| | Long. | $8^{\circ}44.7727'$ E | $8^{\circ}44.7255'$ E | $8^{\circ}44.7736'$ E |
| Depth (m) | Bottom | Ca. -162 | Ca. -150 | Ca. -125 |
| | Hydrophone | Ca. -157 | Ca. -142 | Ca. -120 |
| Recording period | From | 04/10/2016 | 29/08/2017 | 02/10/2017 |
| | To | 05/10/2016 | 31/08/2017 | 04/10/2017 |
| Schedule | | Continuous | Continuous | Continuous |
| Total recording time (min) | | 1860 | 2640 | 1860 |

autonomous recorder (Wildlife acoustics) provided with a HTI-96 hydrophone (High Tech Inc., flat sensitivity = -164 dB re 1 V μPa^{-1} between 2 Hz and 30 kHz). Acoustic recordings were sampled at a rate of 96 kHz and with a 16-bit resolution.

2. MAM

In European waters, within the frame of the CALME network (CHORUS Research Institute and French Water Agency), SeaExplorer gliders (Alseamar) have been integrated with hydrophones (HTI92-WB, High Tech Inc., flat sensitivity = -155 dB re 1 V μPa^{-1} between 5 Hz and 50 kHz) for the main goal of collecting ambient noise data for the Descriptor 11-criterion 2 of the Marine Strategy Framework Directive (Gervaise *et al.*, 2019). During September–October 2017, a 30 days glider run was successfully carried out over 700 kilometers in the Ligurian Sea. Acoustic recordings were sampled at a rate of 32 kHz and with a 24-bit resolution. For the purpose of this study, five days of continuous acoustic recordings collected when the glider was running from the open-sea into the Calvi canyon and its head (i.e., where the SAM deployments were carried out) were selected and manually analyzed [Fig. 1(c)].

C. Acoustic analysis

1. Fish sounds

All collected files were analyzed by hearing and by visual assessment using Raven Pro 64 1.5 (Bioacoustic Research Program, Cornell Laboratory of Ornithology, Ithaca, NY; sound files down-sampled at 4 kHz, fast Fourier transform (FFT) size 256 points, 50% overlap, Hanning window). All sounds with characteristics similar to those emitted by vocal species, or known as produced by fish activities, were recognized, selected, and counted. The Raven selection table identifies each selection made by the operator (i.e., each sound) thanks to its start and end time and to its lowest and highest frequency. The time stamps of the Raven selection tables used in MATLAB R2014b (custom-built script) to identify the selected sounds and measure their received (RL) sound pressure levels (SPLs) [$\text{SPL}_{\text{p-p}}$ and sound pressure level root-mean-square (SPL_{rms}), in dB re 1 μPa] from the original.wav files. Median power spectral density (PSD) received levels (dB re 1 $\mu\text{Pa}^2\text{Hz}^{-1}$) over the frequency band of the different sound types were also estimated for comparison with ambient noise levels. The time stamps were also used to relate each sound recorded by the hydrophone-integrated glider with the glider's position, its depth and bottom depth.

Sound types were categorized on the basis of a dichotomous framework proposed by Desiderà *et al.* (2019) for Mediterranean coastal rocky reefs and adapted for this study (Fig. 2). For each sound category, 25 sounds were selected for fine acoustic characterization. Temporal features were measured from oscillograms, while spectral features were obtained from power spectra. The measured acoustic

features were chosen for each sound category in order to be tailored to its specific acoustic characteristics. All sounds categories were characterized by measuring the following acoustic features: (i) sound duration (ms, measured from the onset of the first pulse to the onset of the last pulse); (ii) peak frequency of the call (Hz, frequency with the highest energy); (iii) frequency 5% (Hz, the frequency that divides the spectral content into two intervals containing 5% and 95% of the energy); (iv) center frequency (Hz, the frequency that divides the spectral content into two intervals of equal energy), and (v) frequency 95% (Hz, the frequency that divides the spectral content into two fine intervals containing 95% and 5% of the energy). For pulsed sounds, additional features were measured: (i) number of pulses and (ii) pulse period (ms, interval between the peaks of two consecutive pulses in a sound). For *Ophidion rochei*-like sounds (Parmentier *et al.*, 2010), additional measured features were (i) alternation start (the pulse number where the pulse period alternation pattern begins); (ii) long pulse period (ms, time between two consecutive pulses after the alternation start characterized by long pulse period); and (iii) short pulse period (ms, time between two consecutive pulses after the alternation start characterized by short pulse period). Details about the acoustic features measured for the two unknown biological sounds (TFPT, *Train of Fast Pulse Trains*, and STFRP, *Stereotyped Trains of Fast Repeated Pulses*) are shown in Supplemental Fig. 1.¹

2. Ambient noise characterization

Long-term spectrograms of the entire recordings achieved at each SAM station were built with routines developed on MATLAB (R2014b) in order to visualise and to inspect the soundscape in the fish auditory range (0–2 kHz; Supplemental Fig. 2).¹ Power spectral densities representing the 0.10, 0.50, 0.90 percentile of the soundscape were generated using MATLAB (R2014b). For each recording station, acoustic data were divided in night-time and day-time hours in order to evaluate the shift in PSD due to boat traffic, which is usually more enhanced during day-time hours. To relate signal detection and ambient noise levels, the PSD graphs were superimposed with the RL of sounds of suspected biological origin recorded during the SAM deployments.

III. RESULTS

A. Fish sounds

Considering all datasets, biological sounds were detected in 38% of the audio files. Ten sound types (or sound type categories), for a total of more than 9000 sounds, with characteristics similar to those emitted by known vocal fish species were found (Fig. 2). In particular, two sound types were recorded by both deployment configurations (SAM and MAM; i.e., *Ophidion rochei*-like sounds and STFRP), three sound types were identified only in the SAM datasets (i.e., *Pulse Series 1*, PS1, *Cloud* sound, C, and *Single Beat*, SB) and five other sound types were recorded by MAM (i.e., *Low Frequency DownswEEP*, LDS; *Fast*

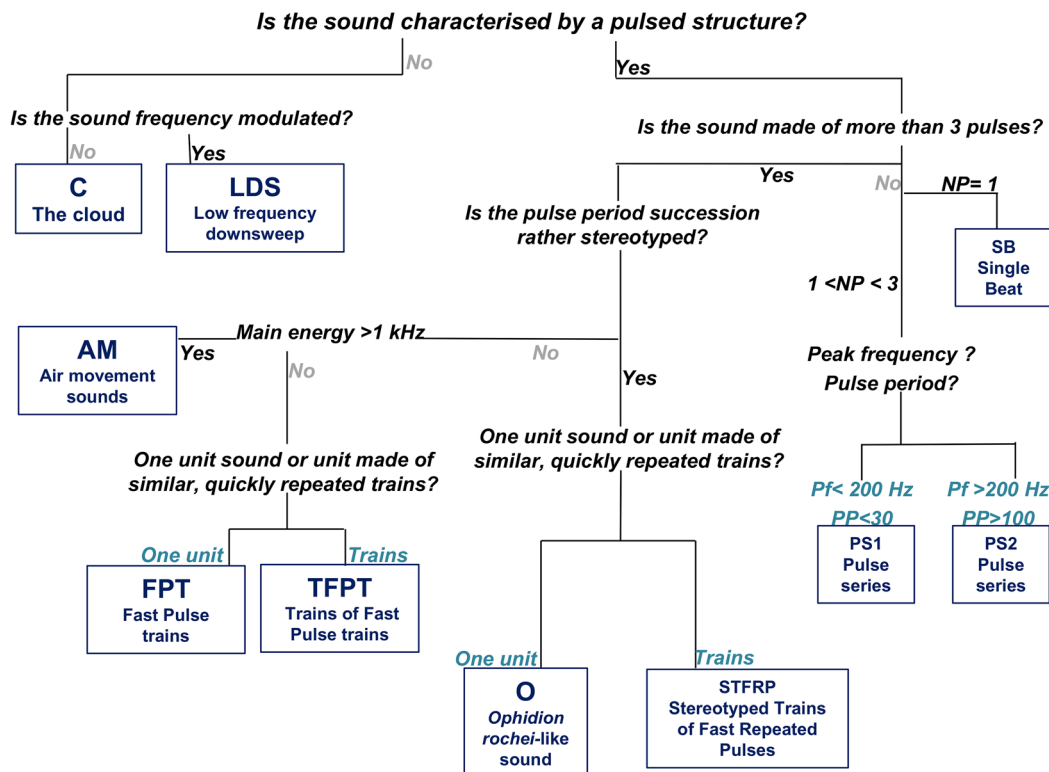


FIG. 2. (Color online) Dichotomy of fish sound types based on signals properties identified as part of this study (theoretical framework developed by Desiderà *et al.*, 2019 and adapted for this study). NP = number of pulses; Pf = peak frequency.

Pulse Train, FPT; Air movements sounds, AM; and Pulse Series 2, PS2).

1. SAM

In the SAM datasets, four different sound types of potential biological origin were identified during night-time hours

- (i) *Ophidion rochei*-like sounds were found in 13% of the files (71 out of 529), with an average of 2 ± 1 sounds (range = 1–8) per 5 min file (Table II, Fig. 3, SuppPubmm1.wav¹). The pulse period increased gradually during the first seven to 15 pulses, separating the call into two parts. The pulse period in the second part of the sounds exhibited alternation between short (median: 121 ± 28 ms) and long (median: 137 ± 22 ms) pulse periods that differed significantly (Mann–Whitney $U = 0.000$, p -value < 0.001). Although the latter characteristic is consistent with calls emitted by *Ophidion rochei*, some characteristics slightly differ: the alternation pattern is not as regular and the PSD profile shows only one peak of energy (Fig. 3) versus the typical two peaks profile of *O. rochei*. *Ophidion rochei*-like sound production started at 10 pm, peaked at 1 am, to then decreased up to 4 am (Fig. 3). *Ophidion rochei*-like sounds were not detected in October 2016 (station A), while only two *Ophidion rochei*-like sounds were detected between 8 and 9 pm on October 2017 in station C.

- (ii) A sound called “PS1” (Table III, Fig. 4, SuppPubmm2.wav¹) was detected four times at 11 pm during October 2016 in Station A.
- (iii) “C” were recorded in Station B (Table III; Fig. 4, SuppPubmm3.wav¹). The Cs were detected from 1 to 5 am, with a peak of 23 sounds per hour at 4 am (Fig. 4).
- (iv) The sound type named “SB” (Table III; Fig. 4, SuppPubmm4.wav¹) was detected during October 2016 in both Station A and B. The SBs were emitted in trains from 11 pm to 2 am, with a peak of 257 sounds per hour at midnight (Fig. 4).
- (v) The last sound type, named STFRP was recorded in all stations (Table III, Fig. 4, Supplemental Fig. 1; SuppPubmm5.wav¹). The STFRP consisted of a train of 7 ± 2 bursts of fast repeated pulses (Supporting Information Fig. 1, Table III; Fig. 4). The STFRP were emitted from 9 pm to 7 am with a peak of 681 sounds per hour at 4 am in Station C (Fig. 4).

2. MAM

In the glider dataset, a total of seven sound types of potential biological origin were identified (Fig. 5). Two of these sound types, namely *Ophidion rochei*-like sounds and STFRP (Tables II and III), were also recorded by the SAM. The highest fish acoustic richness (i.e., number of sound types) was found at the head of the canyon (between –80 and –150 m, Figs. 5 and 6). Here, three additional sound types were recorded, namely, (i) the “LDS” (Table III, Figs.

TABLE II. Descriptive statistics (mean, standard deviation, SD, and coefficient of variation, c.v.) of sound features characterizing *Ophidion rochei*-like sounds ($N_{\text{sounds}} = 25$ for the SAM data and $N_{\text{sounds}} = 25$ for the glider data). Statistical significances are indicated with * (Mann Whitney U test).

| | Duration (ms) | Number of pulses | Alternation start | Long Pulse Period (ms) | Short Pulse Period (ms) | Peak frequency (Hz) |
|------------------------|---------------|------------------|-------------------|------------------------|-------------------------|---------------------|
| SAM data | | | | | | |
| Mean | 5921.4 | 51.4 | 10.7 | 131.8 | 109.5 | 277.3 |
| SD | 656.0 | 10.2 | 2.1 | 22.4 | 28.1 | 36.2 |
| c.v. (%) | 11 | 20 | 20 | 17 | 25 | 13 |
| Glider data | | | | | | |
| Mean | 4905.3 | 40.2 | 12.1 | 127.5 | 106.8 | 215.2 |
| SD | 1735.9 | 11.8 | 2.0 | 13.7 | 7.3 | 70 |
| c.v. (%) | 35 | 29 | 17 | 11 | 7 | 33 |
| Statistical comparison | | | | | | |
| U | 65 | 53 | 81.5 | 94 | 76 | 58 |
| p-value | 0.02* | 0.001* | 0.07 | 0.20 | 0.52 | 0.007* |

5 and 6, SuppPubmm6.wav¹), (ii) the “FPT” (Table III, Figs. 5 and 6, SuppPubmm7.wav¹), and (iii) the “TFPT” (Table III, Figs. 5 and 6, SuppPubmm8.wav¹).

Another sound category was encountered only when the glider was reaching the surface but over a wide geographical range (e.g., from -500 m depth inside the canyon to the canyon head, Table III, Figs. 5 and 6). The sounds of this category were “Air movements sounds” (AM, SuppPubmm9.wav¹). Air movement sounds are a wide category of sound types emitted by physostomes fishes (i.e., fishes that have a pneumatic duct connecting the gas bladder to the alimentary canal; Rountree *et al.*, 2018b). Within this wide category, the best known are probably the “Fast Repetitive Ticks” (FRT, SuppPubmm10.wav¹ Table III).

Finally, one sound type named “PS2” (Table III, Figs. 5 and 6, SuppPubmm11.wav¹) was recorded inside the canyon at depths reaching more than -1000 m when the glider was running in the water column (glider depth between -100 and -200 m, Figs. 4 and 5).

B. Ambient noise characterization

During day-time hours, the presence of boat traffic noise resulted in an increase of Sea Ambient Noise in all three SAM stations (Fig. 7). In particular, during daytime hours, the noise level in the frequency band in which fish hearing is most enhanced (i.e., from 0 to 2 kHz) was found to be from 10 to 15 dB m higher than during night-time hours, where the maximum shift occurred during August 2017 (Fig. 7). Under spherical transmission loss assumption, this implies that signal detection and acoustic space are reduced by a factor 3 to 5 during daytime hours (Supplemental Table I¹).

IV. DISCUSSION

A. Fish sounds

To the best of our knowledge, this is the first description of fish sounds recorded at depths greater than -40 m anywhere in the Mediterranean Sea. The highest acoustic richness was detected at the head of the canyon (around ca. -100 m depth), while one sound type was recorded when the glider was in the mid-water (ca. from -100 to -200 m

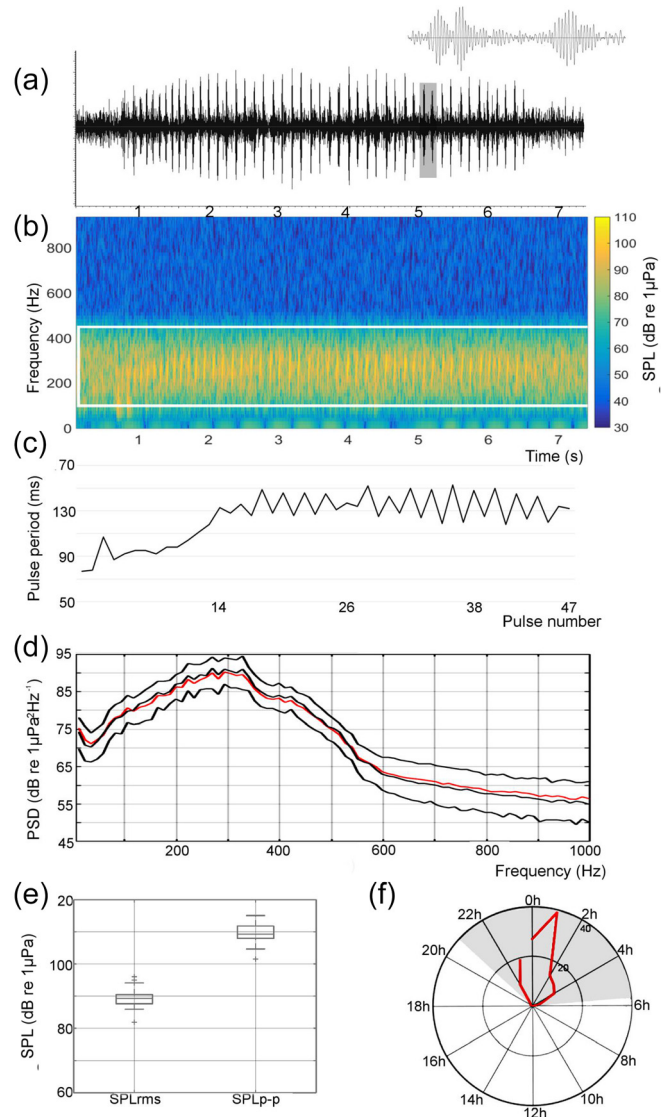


FIG. 3. (Color online) *Ophidion rochei*-like sound; acoustic features and diel pattern of emission. (a) Waveform (bandpass filter = 50–400 Hz) of the sounds and of two pulses (grey selection; upright); (b) spectrogram (sample rate = 4000 Hz, FFT = Hanning window 256); (c) pulse period (ms) succession within the sound; (d) PSD (dB re $1 \mu\text{Pa}^2 \text{Hz}^{-1}$; 0.25, 0.5 in red, 0.95; sample rate = 4000 Hz, FFT = Hanning window 256) of the sound; (e) received SPL levels (dB re $1 \mu\text{Pa}$) of the sound, SPLrms and SPLp-p; (f) diel pattern of emission (n of sounds per hour).

TABLE III. Descriptive statistics (mean, SD, and c.v.) of sound features characterizing the unidentified, suspected fish sound types recorded during the SAM deployments and by the hydrophone-integrated glider. LDS; FPT, which falls (within the AM sounds category); TFPT; STFRP. N.a., features not applicable to that specific sound type.

| Sound type | | 5% Frequency (Hz) | Center Frequency (Hz) | Peak Frequency (Hz) | 95% Frequency (Hz) | Duration (ms) | Number of pulses | Pulse period (ms) | Train duration (ms) | Train period (ms) | Number of trains |
|-----------------|----------|-------------------------|-----------------------------|---------------------------|--------------------------|------------------|---------------------|-------------------------|---------------------------|-------------------------|---------------------|
| PS1 (N = 4) | mean | 140.3 | 276.7 | 249.9 | 1191.2 | 249.5 | 3.5 | 122.0 | n.a. | n.a. | n.a. |
| | SD | 0.4 | 4.7 | 43.9 | 60.5 | 2.1 | 0.7 | 1.4 | | | |
| | c.v. (%) | 0.2 | 1.0 | 18.0 | 5.0 | 1.0 | 20.0 | 1.0 | | | |
| C (N = 25) | mean | 161.1 | 262.0 | 257.0 | 399.0 | 9964.0 | n.a. | n.a. | n.a. | n.a. | n.a. |
| | SD | 5.1 | 10.3 | 41.0 | 18.9 | 3032.0 | | | | | |
| | c.v. (%) | 3.0 | 4.0 | 16.0 | 4.0 | 30.0 | | | | | |
| SB (N = 25) | mean | 313.0 | 455.0 | 466.3 | 624.0 | 20.7 | n.a. | n.a. | n.a. | n.a. | n.a. |
| | SD | 0.0 | 98.4 | 103.4 | 198.0 | 4.3 | | | | | |
| | c.v. (%) | 0.0 | 21.0 | 23.0 | 31.0 | 20.0 | | | | | |
| PS2 2 (N = 25) | mean | 113.3 | 249.7 | 179.4 | 624.7 | 64.5 | 2.3 | 26.2 | n.a. | n.a. | n.a. |
| | SD | 115.4 | 253.6 | 182.9 | 634.4 | 65.5 | 2.3 | 26.2 | | | |
| | c.v. (%) | 101.9 | 101.6 | 102.0 | 101.6 | 101.5 | 100.5 | 100.2 | | | |
| LDS (N = 17) | mean | 106.8 | 276.0 | 224.6 | 1282.6 | 147.6 | 16.8 | 8.8 | n.a. | n.a. | n.a. |
| | SD | 29.6 | 90.2 | 126.3 | 280.3 | 76.6 | 8.7 | 2.9 | | | |
| | c.v. (%) | 27.8 | 32.7 | 56.2 | 21.9 | 51.9 | 51.5 | 33.3 | | | |
| FPT (N = 25) | mean | 44.3 | 233.1 | 137.4 | 538.7 | 39.6 | 11.5 | 3.2 | n.a. | n.a. | n.a. |
| | SD | 9.1 | 121.0 | 135.3 | 96.8 | 24.0 | 6.2 | 1.5 | | | |
| | c.v. (%) | 20.6 | 51.9 | 98.5 | 18.0 | 60.6 | 53.5 | 46.3 | | | |
| FPT (N = 25) | mean | 38.5 | 745.3 | 374.0 | 1657.8 | 261.3 | 11.3 | 20.4 | n.a. | n.a. | n.a. |
| | SD | 51.8 | 689.9 | 630.9 | 152.7 | 97.8 | 7.2 | 15.5 | | | |
| | c.v. (%) | 134.4 | 92.6 | 168.7 | 9.2 | 37.4 | 63.8 | 76.0 | | | |
| TFPT (N = 3) | mean | 54.7 | 207.1 | 187.5 | 1168.0 | 717.5 | 5.0 | 6.8 | 30.0 | 92.0 | 6.5 |
| | SD | 11.0 | 149.1 | 132.5 | 878.4 | 111.0 | 1.4 | 0.4 | 1.8 | 26.4 | 0.7 |
| | c.v. (%) | 20.2 | 72.0 | 70.7 | 75.2 | 15.5 | 28.3 | 5.2 | 6.1 | 28.7 | 10.9 |
| STFRP (N = 25) | mean | 270.4 | 607.0 | 380.6 | 1319.0 | 1433.0 | 7.3 | 3.4 | 106.0 | 153.0 | 7.3 |
| | SD | 5.0 | 59.8 | 232.0 | 24.3 | 200.0 | 1.6 | 1.0 | 24.0 | 93.2 | 1.6 |
| | c.v. (%) | 2.0 | 10.0 | 61.0 | 2.0 | 13.0 | 22.0 | 30.0 | 23.0 | 61.0 | 22.0 |

depth) at a bottom depth of more than -1000 m. The analysis of the SAM datasets provided information about diel patterns of fish vocal production at the head of the canyon; all sound types analyzed as part of this study were emitted during night-time hours, which is in accordance with what known for coastal areas (e.g., Picciulin *et al.*, 2013; Desiderà *et al.*, 2019). This seems to indicate that shifts in daylight regime influence vocal communication also in fish species inhabiting habitats with reduced light penetration. In a study conducted in the Perth canyon (Australia), evening choruses were detected at depths greater than -400 m, where light penetration is further reduced (McCauley and Cato, 2016). The diel pattern of fish choruses could correspond with daily, vertical migrations undertaken by several zooplankton and small fish species, which spend the day at high depths and rise up in the evening to forage in the photic zone of the upper water column (McCauley and Cato, 2016). Similarly, diel patterns in fish sound production might also be present in deeper Mediterranean environments.

Among the ten sounds types described in this study, one could be assigned to the *Ophidion* genus on the basis of acoustic similarities with sounds emitted by a species inhabiting shallow water environments. The alternation pattern of

pulse period duration is characteristic of *Ophidion rochei* adult male calls, reflecting a highly specialized sound production mechanism, which has been characterized in detail (Parmentier *et al.*, 2010; Kéver *et al.*, 2012; Kéver *et al.*, 2014). Although this acoustic structure matches the one described for *O. rochei*, the high variability found in the alternation pattern, in the pulse shape and in the PSD profile requires a careful approach when assigning these sounds to a specific *Ophidion* species. Two hypotheses should be further tested; (i) *O. rochei* sounds might present a wider variability than expected or (ii) the sounds recorded at the head of Calvi canyon might have been emitted by the co-generic *Ophidion barbatum*. In the Mediterranean Sea, *O. rochei* has been reported from shallow waters until -150 m (Nielsen *et al.*, 1999), while *O. barbatum* has been reported between -150 and -1456 m (Goren and Galil, 2002). These two species share the same kind of sound production mechanisms (i.e., swimbladder rebound model, see Parmentier and Fine, 2016) involving modified vertebrae, a “rocker bone” on the anterior portion of the swimbladder and three pairs of sonic muscles (Parmentier *et al.*, 2006; Parmentier *et al.*, 2010). Despite these similarities, Casadevall *et al.* (1996), Parmentier *et al.* (2006), and

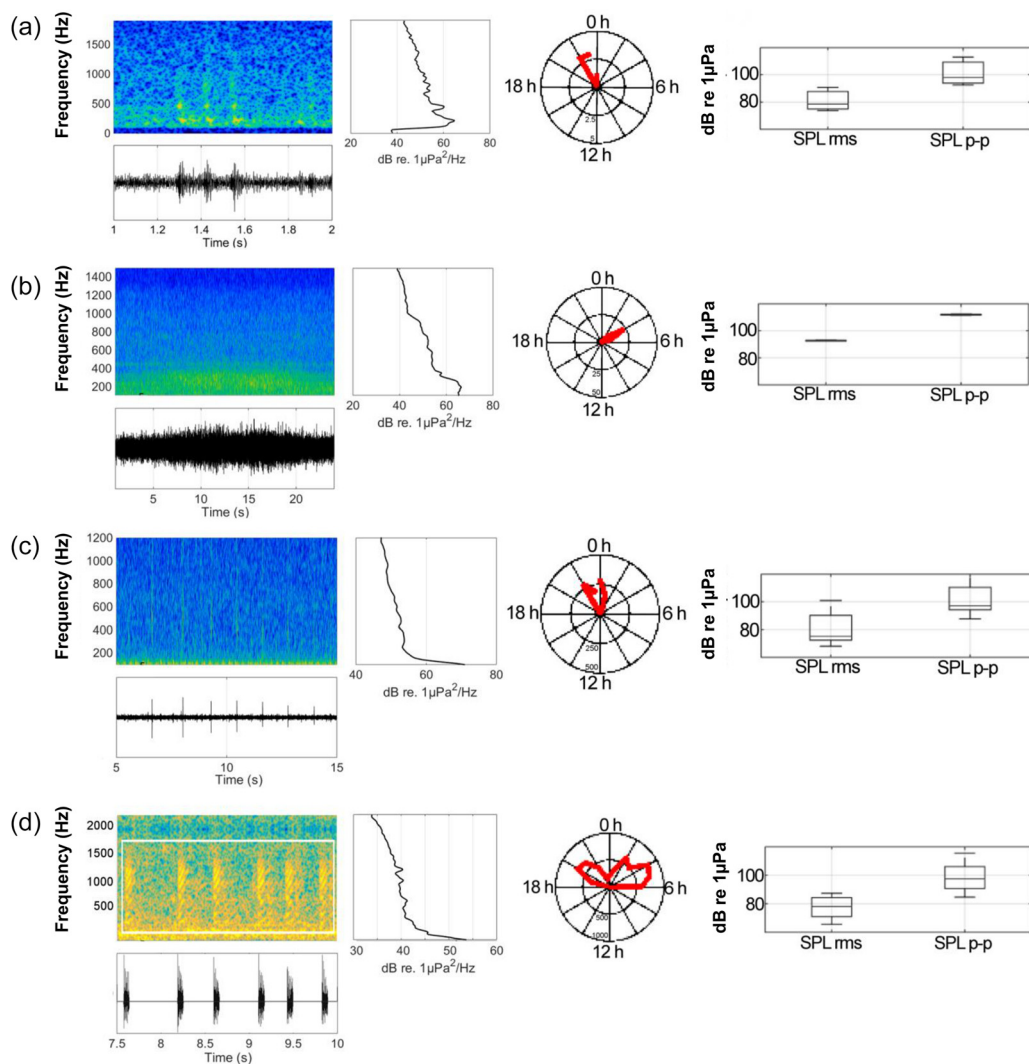


FIG. 4. (Color online) Waveform, spectrogram (sample rate = 4000 Hz, FFT = Hanning window 256), mean PSD (dB re $1 \mu\text{Pa}^2/\text{Hz}^{-1}$), diel pattern (n of sounds per hour), and Received SPL levels (dB re $1 \mu\text{Pa}$) of unidentified, suspected biological sounds recorded during the SAM deployments. (a) PS1; (b) C; (c) SB; and (d) STFRP.

Parmentier *et al.* (2010) highlighted prominent morphological differences between the sound production apparatus of these two species: *O. barbatum* has a smaller swimbladder lacking both anterior neck, posterior valve, and inner tube (Parmentier *et al.*, 2006). However, sounds of *O. barbatum* have never been recorded and cannot be compared with the canyon sounds.

The hypothesis that *Ophidion rochei*-like sounds recorded as part of this study might have been the result of transmission loss on sounds emitted by *Ophidion rochei* in coastal areas has also been considered (Supplemental Tables II, III, and IV¹). In absence of synchronized hydrophone arrays, a rough estimation of the distance of the source (fish) to the receiver (hydrophone) can be calculated if the source levels of the signal and the propagation properties of the medium are known. Thanks to captive acoustic recordings of *O. rochei* previously collected and data reported in literature, and by assuming a mixed spreading model, a hypothetical distance of the fish emitting the *Ophidion rochei*-like

sounds recorded by the deepest hydrophone was inferred (Supplemental Tables II–IV¹). The estimated range was below -250 m (Supplemental Table IV¹). In this context, it has to be underlined that *Ophidion* spp. are exclusively benthic fishes, as shown by the presence of highly modified pelvic fins, capable of chemoreception and mechanoreception which are suited for bottom living and dwelling habits (Codina *et al.*, 2012). Although this estimation does not allow to precisely locate the fish emitting the sound or to accurately estimate its distance from the recording device, it nevertheless suggests that *Ophidion rochei*-like sounds were most likely emitted by fishes living at or close to the head of the canyon and not at the coast, which is located at ca. 265 m distance.

The air movement sounds emitted by physostomous fishes have been described in Clupeiformes (Wahlberg and Westerberg, 2003; Wilson *et al.*, 2004) and, more recently, in two other orders of fishes, i.e., Cypriniformes and Salmoniformes (Rountree *et al.*, 2018b). Rountree *et al.*

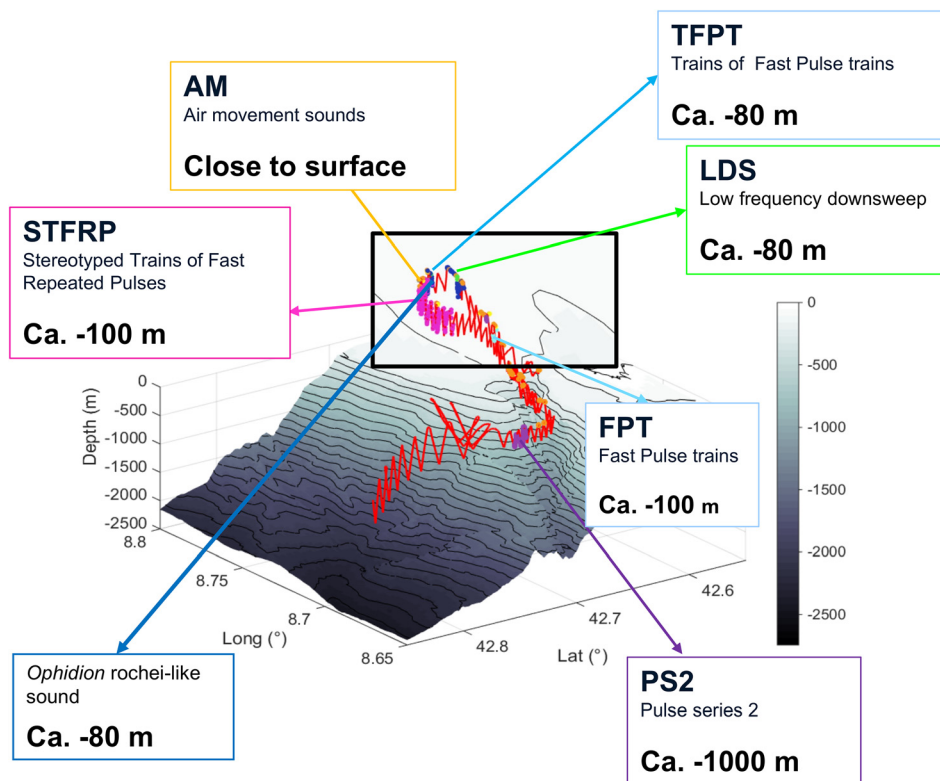


FIG. 5. (Color online) Glider trajectory in the Calvi canyon (red line) and zoom on the head of the canyon; suspected fish sound types recorded by the hydrophone-integrated glider are depicted in accordance with the glider position when these were detected.

(2018b) suggested a generalized air movement sound production behavior for physostomous fishes that includes a rise to the surface, air gulp event, dive to depth, and resumption of normal behavior at a presumed acclimation depth. Air movement sounds were recorded in this study only when the glider was running close the surface, which is in accordance with the generalized behavioral pattern proposed by Rountree *et al.* (2018b). Although a precise species-specific identification was not possible, it is likely that these sounds were emitted by schooling Clupeidae fishes.

A specific identification was not feasible for the other detected sound types, but these sounds are promising and deserve further investigation. The *Pulse Series* (PS1, recorded at the head of the canyon and the PS2, recorded in the mid-water inside the canyon) shows one of the most typical structures of known fish sounds, i.e., low frequency and rhythmic pulses, suggesting that they are biological and likely emitted by fish. The *Cs* lack the typical pulsed structure characterizing many fish calls, and it is arguable that this sound is a communication signal emitted by a fish. However, the *Cs* have been detected also in shallower waters, in presence of *O. rochei* (e.g., SuppPubmm12.wav¹). It is therefore possible that the *Clouds* are related to the presence of *Ophidion* sp. In this regard, it is interesting to compare the diel pattern of *Ophidion rochei*-like sounds with that of the *Clouds*; the abundance of *Clouds* increases at 4 am, when the production of *Ophidion rochei*-like sounds falls. It remains to be determined if the *Clouds* are related to the vocal behavior of *Ophidion* spp. or if they

are an involuntary noise associated with their activities (e.g., sand dwelling, see SuppPubmm13.wav¹). This question should be further investigated as, although the *Clouds* might not be voluntarily emitted and might not be a vocalization *per se*, it has already been demonstrated that noises resulting from the activity of certain fish species can be used as proxies for informing about their presence in a specific area (Bolgan *et al.*, 2017; Straight *et al.*, 2014).

The *SB* sounds present some similarities with the *POP* sound described in *Sebastes* spp: a single, discrete acoustic beat with spectral content mainly below 500 Hz (Nichols, 2005; Širović and Demer, 2009; Širović *et al.*, 2009). The Sebastidae *Helicolenus dactylopterus* has been reported as abundant in the canyon of Calvi and between -200 and -600 m depth in the entire Western Mediterranean (D'Onghia *et al.*, 2004). It can be hypothesized that *H. dactylopterus* emit sound for communication purposes and that its sounds have similar features to those of other Sebastidae spp. previously described (i.e., *SB*). Considering that *H. dactylopterus* is a commercial species, further investigations in this sense are strongly encouraged. It must be considered that even in environments that have been acoustically investigated for longer periods of time than underwater canyons (e.g., coastal areas), a huge proportion (if not the majority) of sound types remains to be identified (Rountree *et al.*, 2018a). Considering that fish acoustic communication has never been investigated in Mediterranean underwater canyons, it is not surprising that nine out of ten potential sound occurrences could not be identified at the species level.

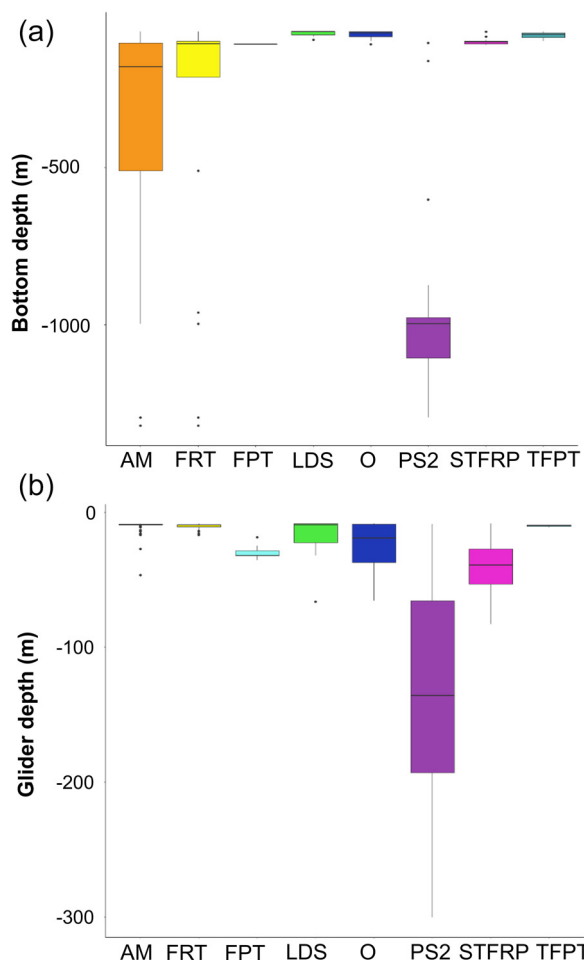


FIG. 6. (Color online) Bottom depth (a) and glider depth (b) range for each suspected fish sound type recorded by the hydrophone-integrated glider. For abbreviations significance, refer to Fig. 2 and note that FRT is a subcategory of the AM sounds.

B. Ambient noise

In recent years, marine traffic has increased at unprecedented rates and has become the most common and chronic source of ocean noise pollution (Rako-Gospic and Picciulin, 2018). Anthropogenic noise elicits a wide range of physiological, perceptual and behavioral effects on aquatic life (Slabbekoorn et al., 2010; Rako-Gospic and Picciulin, 2018). For example, an increase in background noise has been shown to reduce the communication space of littoral coastal fish species (Alves et al., 2016), to reduce the number of viable embryos (Sierra-Flores et al., 2015) and to induce shifts in female mate choice (de Jong et al., 2016). Our study calculated a hypothetical reduction of fish active acoustic space due to boat traffic by a factor 3–5 occurring during daytime hours. Although this calculation is merely speculative and has to be taken with care, especially because fish vocalizations seem to occur only at night, it cannot be excluded that potential physiological effects of anthropogenic noise could extend beyond the moment of noise exposure. Further studies should address the potential effects of anthropogenic noise on deep-sea

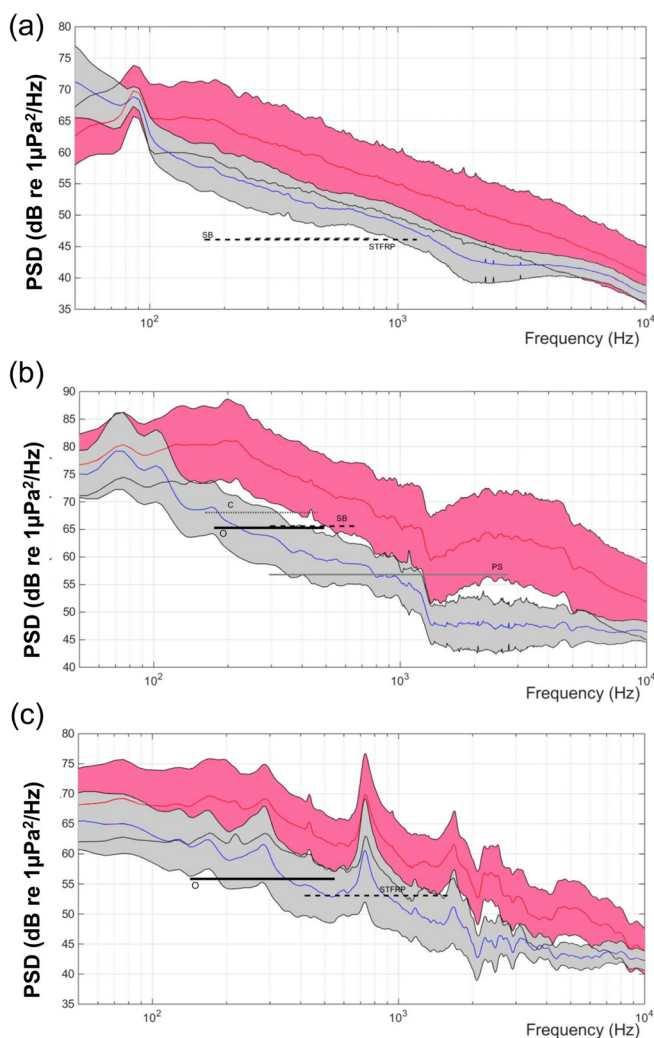


FIG. 7. (Color online) PSD; dB re $1 \mu\text{Pa}^2\text{Hz}^{-1}$, black lines = 0.10, 0.50, 0.90, blue (night) and red (day) lines = mean of night-time hours (grey) and day-time hours (pink) in the three SAM recording sites (a, b, c) with Received Levels (SPL, dB re $1 \mu\text{Pa}$, from min to max frequency) of suspected fish sound types. Black full line = *Ophidion rochei*-like sounds (O); grey full line = PS1; grey dotted line = C; black dashed line = SB and STFRP.

fish, which, at the current stage of knowledge, is a completely unexplored topic.

V. CONCLUSION

Deep-sea fish are slow-growing species, with a low rate of population increase and low fecundity (Priede, 2017). Despite this, deep-sea fish populations are already exploited by fisheries and their conservation is hampered by a severe scarcity of data (Mann and Jarvis, 2004; Morato et al., 2006; Priede 2017). Our study has shown that fish biophony exists in a Mediterranean submarine canyon, where SAM and MAM can successfully be applied for gaining complementary data on fish distribution and cycles of activities. In particular, SAM provides long-term information on diel and seasonal patterns while MAM informs on large-scale,

stratigraphic distribution of vocal fish populations. This study wishes to call for future, wider-scale, and longer-term ecoacoustic investigations of submarine canyons and of other deep-sea environments. The long-term monitoring of fish vocalizations and of the overall soundscape (including anthropogenic noise) could provide important information necessary for better understanding and, ultimately, protecting deep-sea fish populations.

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¹See supplementary material at <https://doi.org/10.1121/10.0001101> for supplemental audio files 1–13 and supplemental Tables I–IV.

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