

RESEARCH ARTICLE

Passive monitoring of phenological acoustic patterns reveals the sound of the camouflage grouper, *Epinephelus polyphekadion*

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Abstract

1. Passive acoustic monitoring (PAM) is a non-invasive technique that uses hydrophones to monitor populations and ecosystem dynamics. Although many applications of PAM have been developed in recent years, it has never been used to identify a calling marine species.
2. The south pass of Fakarava Atoll, French Polynesia, hosts spawning events of many reef fish species, including the camouflage grouper *Epinephelus polyphekadion*, with a spawning aggregation abundance exceeding 17 000 individuals during the full moons of June and July.
3. The current study aimed to use PAM to distinguish camouflage grouper sounds among the vocal activities of all fish recorded during the aggregation periods. Audio recordings analysis resulted in the identification of 29 sound types, some of which showed diel and lunar patterns.
4. Temporal analysis of these sounds in relation to spawning activities allowed the identification of camouflage grouper calls. These calls can be described as a single pulse or a series of 'boom(s)' with a pulse duration of ~44 ms and a low dominant frequency of 103 ± 31 Hz. Video recordings show that the camouflage grouper produces the 'booms' to initialize spawner ascent and to promote synchronous gamete release into the water column.
5. The study highlights for the first time that PAM can be used to identify the previously unknown sound of a fish species. Moreover, we can use it to understand the phenology of some biological activities for improving the resolution of fish biodiversity assessments.

KEYWORDS

biodiversity, coral, fish, lagoon, monitoring

1 | INTRODUCTION

More than 800 fish species from over 100 families have been documented to produce sounds (Bass & Ladich, 2008; Ladich & Fine, 2006), but this number is most probably an underestimate (Fine & Parmentier, 2015). Sounds are produced in different kinds of behavioural contexts, including territorial contexts and food competition or predatory attacks (Hawkins & Amorim, 2000; Lagardère, Millot, & Parmentier, 2005; Myrberg, Mohler, & Catala, 1986). Sound production associated with reproductive behaviour has been the most studied social context in fish bioacoustics, however (Amorim, 2006). These sounds are generally produced by males to attract mates in their territory (Longrie et al., 2013; Parmentier, Kéver, Casadevall, & Lecchini, 2010), to synchronize spawning events at fish spawning aggregation sites (Erisman & Rowell, 2017; Lobel, 1992; Rowell, Nemeth, Schärer, & Appeldoorn, 2015), and to promote the simultaneous release of gametes (Lobel, 2002). As sounds can be used to highlight the phenology of species activity (Ruppé et al., 2015), phenological events such as spawning activities could in turn also be used to identify unknown sounds of vocal species, and may be used to inform conservation management strategies (Rowell et al., 2015).

Fish spawning aggregations (FSAs) are defined as an annual or seasonal gathering of conspecifics for the purpose of reproduction, with higher fish densities than those observed during non-reproductive periods (Domeier & Colin, 1997). The south pass of Fakarava Atoll, French Polynesia, is known for its fish density and diversity, and because it hosts FSAs of many fish species, e.g. *Acanthurus triostegus* (the convict surgeonfish) and *Lutjanus gibbus* (the humpback red snapper) (EP, pers. observ.). Among aggregating species, FSAs of Epinephelidae (groupers) have been the most extensively documented and studied (Sadovy de Mitcheson et al., 2008). In many aggregation-forming grouper species, including *Epinephelus polyphkadion* (the camouflage grouper), individuals make extensive seasonal migrations to form large spawning aggregations at specific locations (Colin, Shapiro, & Weiler, 1987; Nemeth, 2005; Nemeth, Blondeau, Herzlieb, & Kadison, 2007; Rhodes, McIlwain, Joseph, & Nemeth, 2012; Sadovy, Rosario, & Román, 1994). The camouflage grouper is a gonochoristic species (Rhodes, Taylor, & McIlwain, 2011) that inhabits coral reefs (Heemstra & Randall, 1993) and forms large (100–1000s of individuals) transient FSAs at specific times and places (Rhodes, Nemeth, Kadison, & Joseph, 2014; Rhodes & Sadovy, 2002b, 2002a; Robinson, Aumeeruddy, Jörgensen, & Öhman, 2008). Within their distributional range, the timing of camouflage grouper FSAs varies with respect to their lunar and seasonal periodicity, with spawning typically occurring at either a new or a full moon (Rhodes & Sadovy, 2002b). The same reproductive behaviour has been described in several locations, including Palau (Johannes, Squire, Graham, Sadovy, & Renguul, 1999), Pohnpei (Rhodes & Sadovy, 2002b, 2002a), the Seychelles (Robinson et al., 2008), the Solomon Islands (Hamilton, Giningele, Aswani, & Ecochard, 2012), and Papua New Guinea (Hamilton, Potuku, & Montambault, 2011). Camouflage groupers typically aggregate on spawning sites for around 1–2 weeks each month over a reproductive season of 2–3 months (Rhodes, 2012). During

aggregation periods, the density rapidly increases and peaks a few days prior to reproduction. Actual spawning typically occurs over brief periods during one or two successive days, before fish quickly disperse and the density rapidly decreases as fish return to their home reefs (Rhodes et al., 2011; Rhodes & Sadovy, 2002b). This sequence continues until the reproductive season is concluded.

In Fakarava, previous visual censuses revealed that up to 17 000 camouflage groupers come from the surrounding atoll and aggregate to spawn at the mouth of the south pass every year (Mourier et al., 2016; Robbins & Renaud, 2016). This spawning takes place exclusively during the full moons of June and July. Previous data have shown that at least some groupers use this pass as a spawning aggregation site over multiple years (Mourier, Ballesta, Clua, & Planes, 2019). The site is within a United Nations Educational, Scientific and Cultural Organization (UNESCO) biosphere reserve, where fishing activities are entirely restricted. As several grouper FSAs have shown a decrease in fish numbers over time or have simply disappeared from some atolls in French Polynesia, the protection of the Fakarava southern pass is critical for the collection of basic functional information to maintain healthy FSAs. This type of information, which includes understanding the phenology of reproducing species using this pass, is thus essential for management actions that will secure the long-term health and persistence of local grouper populations (Mourier et al., 2019). Within the Epinephelidae, acoustic signals have been associated with courtship behaviour and are likely to be related to the spawning activity of many species, including *Epinephelus guttatus* (the red hind) (Mann, Locascio, Schärer, Nemeth, & Appeldoorn, 2010), *Epinephelus itajara* (the goliath grouper) (Mann, Locascio, Coleman, & Koenig, 2009), *Epinephelus marginatus* (the dusky grouper) (Bertucci, Lejeune, Payrot, & Parmentier, 2015), *Epinephelus morio* (the red grouper) (Nelson, Koenig, Coleman, & Mann, 2011), *Epinephelus striatus* (the Nassau grouper) (Schärer, Rowell, Nemeth, & Appeldoorn, 2012), *Mycteroperca bonaci* (the black grouper) (Schärer, Nemeth, Rowell, & Appeldoorn, 2014), *Mycteroperca jordani* (the Gulf grouper) (Rowell, Aburto-Oropeza, Cota-Nieto, Steele, & Erisman, 2018), and *Mycteroperca venenosa* (the yellowfin grouper) (Schärer, Nemeth, et al., 2012). To our knowledge, however, vocalizations have not been assessed for any Pacific grouper species to date, including the camouflage grouper.

Passive acoustic monitoring (PAM) and eco-acoustics can uncover both broad and fine-scale ecological patterns, and can capture natural as well as anthropogenic sound sources and their dynamics simultaneously (Sueur & Farina, 2015). Acoustics are already used to assess terrestrial biodiversity (Sueur, Pavoine, Hamerlynck, & Duval, 2009; Towsey et al., 2014). Until recently, this approach has rarely been used in the marine environment to conduct environmental or biological surveys (Kaplan, Mooney, Partan, & Solow, 2015; McWilliam & Hawkins, 2013). PAM involves the use of hydrophones to record all components of underwater soundscapes, including biological sounds. It can provide information on ecosystem functioning by documenting the activities and dynamics of soniferous species over a wide range of temporal and spatial scales (Gannon, 2008; Parmentier et al., 2017; Rountree et al., 2006). It has been used to highlight fish phenology

(Ruppé et al., 2015), the presence of cryptic species (Kéver, Lejeune, Michel, & Parmentier, 2016; Picciulin, Kéver, Parmentier, & Bolgan, 2019), to delimit spawning seasons (Luczkovich, Pullinger, Johnson, & Sprague, 2008; Picciulin et al., 2013; Rowell et al., 2015), to investigate changes in community richness and diversity (Bertucci, Parmentier, Lecellier, Hawkins, & Lecchini, 2016; Desiderà et al., 2019), or to locate spawning sites (Lowerre-Barbieri et al., 2008; Walters, Lowerre-Barbieri, Bickford, & Mann, 2009), for example. Although PAM has been used in many applications over the past few years, it has never been used to identify the call of a focal species in coral reefs.

The present study aimed to record and describe the phenology of vocal activities at the FSA site in Fakarava, and to discern the sound production of the camouflage grouper *E. polyphemadion*. This goal has been achieved in three steps. First, every fish sound recorded in 2017 in the pass has been discriminated and the most abundant signals were selected, highlighting some temporal variations. Second, this dataset has been compared with diver observations to identify the sound of the focal grouper. Lastly, the selected signals have been validated from video recordings in 2018. This original methodology allowed the validation of the alternative use of PAM in the detection and study of vocal species and provides important conservation applications.

2 | MATERIALS AND METHODS

2.1 | Underwater recordings

Passive acoustic recordings were made in the south pass of Fakarava Atoll, French Polynesia ($-16^{\circ}52'S$, $-145^{\circ}46'W$), during the reproductive period of the camouflage grouper in June and July 2017. Two autonomous long-term acoustic recorders (Loggerhead Instruments, Sarasota, FL) connected to HTI96-min hydrophones (sensitivity of -170 dB re: 1V for a sound pressure of $1\mu Pa$ and with a flat frequency response range between 2Hz and 30kHz; High Tech Inc., Long Beach, MS) were deployed at two different locations at the aggregation site at 30 and 40 m of depth. Recorders were secured to a stand ~ 1 m above the reef. The devices were programmed to record for 5 min with 20-min intervals at a sampling rate of 48 kHz (16-bit resolution) from 4 June to 18 June, and for 10 min duration with 30-min intervals from 3 July to 12 July. These recording periods included the full moon of both aggregating months in 2017 (9 June and 9 July). Data were stored on a 64-Gb micro SD memory card and downloaded following retrieval at the end of each recording period.

Additional audio and video recordings were made with a Cyclops camera (Loggerhead Instruments) in June 2018 in the southern pass between 26 June (09:30 h) and 28 June (13:29 h) (the full moon occurred on 27 June). The Cyclops audio recorder (44.1 kHz, 16-bit resolution) triggered simultaneous high-definition video recordings, both of which were scheduled to record for a 30-sec duration at 5-min intervals.

2.2 | Recordings analysis

Data from 2017 were analysed from 4–12 June (i.e. 5 days before and 3 days after the full moon), and from 6–12 July (i.e. 3 days before and 2 days after the full moon). One 5-min file was analysed every 2 hours. This effort was increased by analysing one 5-min sample every hour at the full moon (9–10 June and 9–10 July). In order to focus on fish vocal activity, audio samples were first down-sampled to a 6-kHz rate and a 20-Hz high-pass filter was further applied. With the higher background noise in the low frequencies in July, a band-pass filter of 50–3000 Hz was applied. Sounds were detected by visual and aural inspections of spectrograms (fast Fourier transform (FFT), 512 points, Hamming window) using AVISOFT SASLAB PRO 5.2.07 (Avisoft Bioacoustics e.K., Glienicke/Nordbahn, Germany). First, every biological sound that could be attributed to a fish was labelled based on its distinct features, such as the number of pulses, pulse period, frequency, oscillogram shape, etc. (Table 1). Each category referred to a known sound-producing family (e.g. Pomacentridae), identified from existing literature, or to a descriptive name or onomatopoeia (e.g. growl, pulse train, boom) if it could not be identified. Unknown sound types were considered as representative of either a single species or a group of species with similar sounds, such as members of a single fish family. Second, the occurrence of each sound type was plotted against time to identify temporal patterns in their production.

The audio files from 2018 were analysed the same way to validate the results from PAM and, potentially, to link the audio data with behaviours shown in the videos. Temporal and spectral characteristics of the sounds associated with specific behaviours of the grouper were also analysed.

2.3 | Ethical note

The positioning and retrieving of the recording devices in this UNESCO biosphere reserve were made under the agreement of the Direction de l'Environnement (DIREN) of French Polynesia and performed by professional divers of the Gombessa IV expedition.

3 | RESULTS

3.1 | Detection of the different sound types

A total of 11 524 fish sounds were identified in June and grouped into 29 sound types. On average (mean $\pm$ SD), 122 ± 33 sounds, belonging to 14 ± 2 sound types were detected every 5 min. Thirteen types of sound representing 95% of the total sounds (Figure 1) were selected. The 16 remaining sounds, accounting for less than 1% each, were all grouped in the category 'others' and were removed from the analysis.

Among the 13 sound types selected, two types could be attributed to a fish family (Figure 1), i.e. the Pomacentridae and the Holocentridae (Parmentier, Lecchini, & Mann, 2016; Parmentier, Vandewalle, Frédéric, & Fine, 2006). The remaining sound types were

TABLE 1 Brief description of the 13 dominant sound types

Sound type	Main frequency interval	Description
Pomacentridae	600–800 Hz	Series of various numbers of pulses. Short inter-pulses (30 ms). Sometimes sequence of series separated by a longer inter-pulse of >100 ms.
Holocentridae	100–200 Hz	Series of 3 to >30 pulses. Inter-pulses of 100–200 ms. Sometimes with harmonics.
Low-frequency knock series	200–280 Hz	Series of ≥ 3 knocking sounds with inter-pulses of 100–150 ms. Rarely exceeding 10 knocks.
High-frequency knock series	280–600 Hz	Series of ≥ 3 knocking sounds with quite even slow inter-pulses (often ≥ 200 ms). Rarely exceeding 10 knocks.
Single boom	30–190 Hz	A very low-frequency sound.
Boom series	30–190 Hz	Series of up to 5 booms.
Fast pulse series	180–280 Hz	Series of 3 to ≥ 30 pulses with short inter-pulses in the middle (~ 30 ms) and often longer inter-pulses at the end and/or at the beginning (~ 100 ms) of the series.
Fast pulses, 3–5	200–400 Hz	Series characterized by the last inter-pulse longer than the previous one(s), i.e. 120 ms, 120 ms, and 160 ms.
Series of high-frequency pulses	750–900 Hz	Series of ≥ 3 pulses with inter-pulses of generally ≥ 200 ms.
Fast series of high-frequency pulses	750–900 Hz	Series of ≥ 3 pulses with inter-pulses shorter than the series of high-frequency pulses (≤ 150 ms).
Growling	150–500 Hz	Series of low-frequency pulses (>10 pulses) with short inter-pulses (<80 ms), leading the pulses to overlap in an almost tonal groan sound.
Growl	150–500 Hz	Growling of very short duration with no distinction in the composing pulses.
Click series	900–1200 Hz	Short, high-frequency sound, often with 3 pulses.

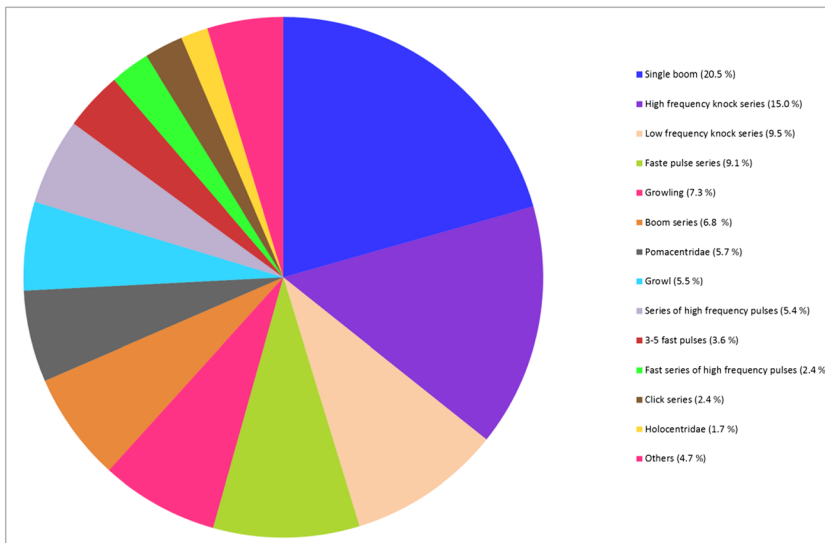


FIGURE 1 Pie chart of the relative proportions of the 13 dominant (95.3%) and 16 minor (4.7% combined in 'Others') sound types recorded during 4–12 June 2017

classified as described in Table 1. (See Figure S1 for the oscillogram and spectrogram of each sound type.)

3.2 | Temporal patterns of the sound types

Pomacentridae sounds and 'click series' showed a diurnal pattern in sound production (Figure 2a, b), whereas the 'high-frequency knock series' and 'high-frequency fast pulse sequences' showed a nocturnal pattern (Figure 2c, d). In addition to the daily pattern, the 'click series' (Figure 2b) and the 'high-frequency fast pulse sequences' (Figure 2d) varied according to lunar periodicity: the number of 'click series' and 'high-frequency fast pulse sequences', respectively, increase and decrease after the full moon. Additional data will be required to validate these observations, however. The other sound types, excluding booms, did not show any clear diel or lunar patterns during the recorded time period (Figure S2).

3.3 | Sound type attributed to the camouflage grouper

Among the different sound types, the 'booms' are particularly interesting for their acoustic characteristics (Figure 3) and for their strong relationships with the lunar phase in both June (Figure 4a) and July (Figure 4b) 2017. 'Booms' were recorded from 4 June through to the end of the aggregation period. Before spawning, a higher sound production rate was recorded during the daytime (Figure 4a). The sounds made at night began to increase regularly from 40 to 70 booms per min on the night of the full moon, however, and peaked at 05:00 h (with 75–90 booms per min). This peak was followed by a dramatic decrease in the number of sounds around sunrise (06:24 h). At that time the rate declined to less than 10 booms per min. Around noon, the boom rate returned to a similar level as observed prior to the full moon. A second peak occurred at 05:00 h the following day. On

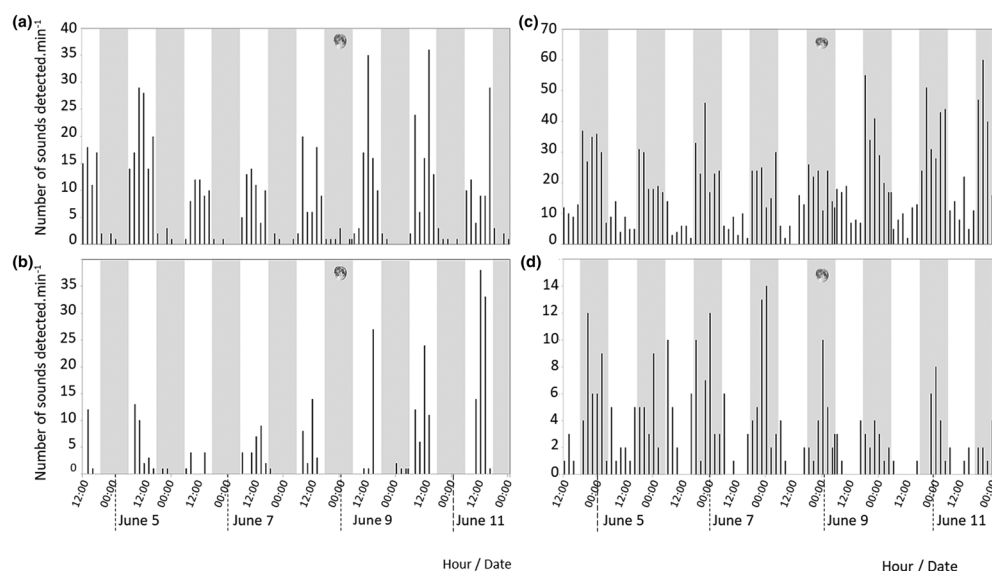


FIGURE 2 Sound types displaying a diel cycle in sound production: (a) Pomacentridae; (b) click series; (c) high-frequency knock series; and (d) high-frequency fast pulse sequence. The grey bands indicate night times. The circle corresponds to the full moon

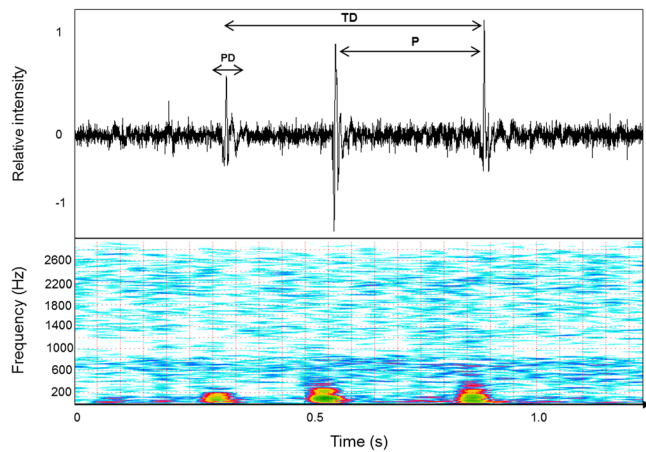


FIGURE 3 'Boom' characteristics. Oscillogram (top) and spectrogram (bottom) of a 'boom series'. The sound intensity colour scale goes from blue through red to green, with green being the highest intensity and blue being the lowest. Abbreviations: P, period; PD, pulse duration; and TD, total sound duration. Note the increasing frequency of each successive boom

subsequent days after the full moon, fewer than 10 booms per min were recorded (Figure 4a). Notably, the occurrence of these two peaks of sonic activity corresponded to observations of spawning activity made by scuba-divers (diving every day prior to the upcoming full

moon), i.e. a first small spawning on 9 June and then a major spawning event, together with massive gamete release, on 10 June at c. 05:30 h. Although less intense, the same trend in sound production was observed on both 9 and 10 July 2017. At c. 05:30 h on 9 July, the sound production of the camouflage grouper peaked simultaneously with the diver-observed spawning (Figure 4b). A second smaller peak occurred on 10 July, suggesting a second spawning the following day; however, the actual spawning was not directly observed by the divers. In each case, the most notable change in the data is that at the time of spawning the sound production drops around sunrise, from 80–90 to 10 booms per min in June and from 50 to 10 booms per min in July (Figure 4).

Booms were mainly produced as single pulses but were also found in series of up to five pulses (Table 2). The pulse duration was 44 ± 14 ms ($n = 70$) with a quite irregular period of 321 ± 213 ms ($n = 36$). The dominant pulse frequency was 103 ± 31 Hz ($n = 70$) (Figure 3).

3.4 | Behaviour potentially linked with the 'booms'

Two spawning events were observed from the videos made in 2018, one on 27 June and one on 28 June, both at 06:00 h. A series of booms (or single booms made by several individuals simultaneously) was produced preceding the ascent of camouflage groupers in the

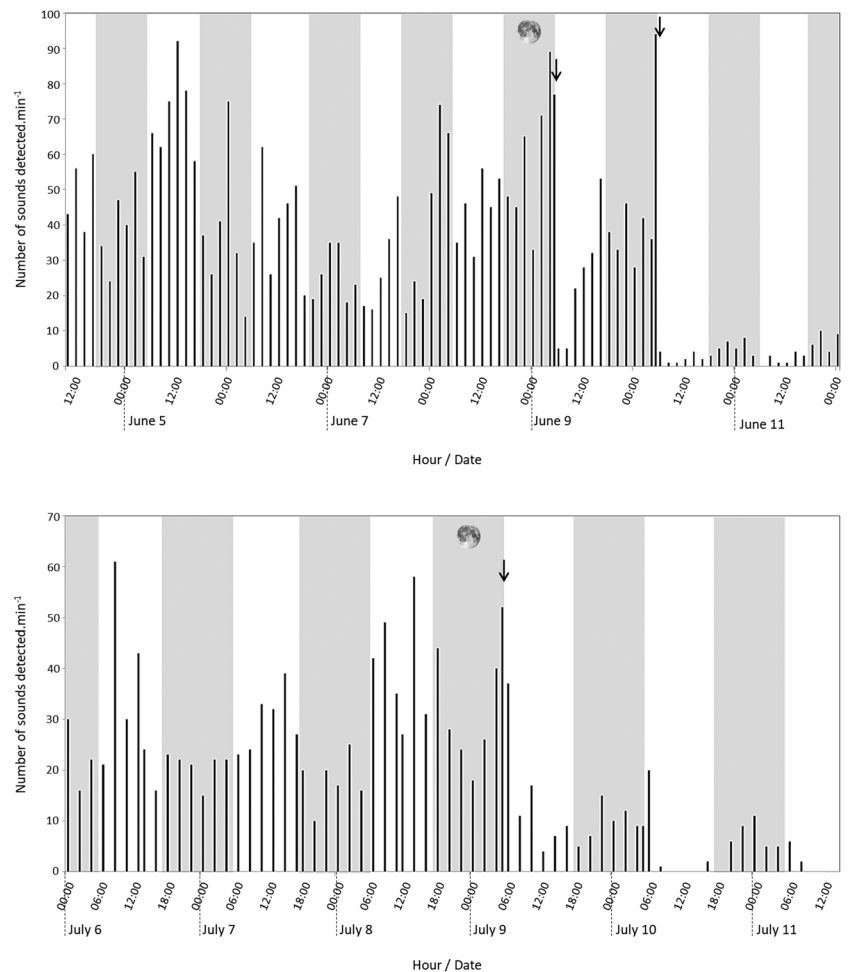


FIGURE 4 Occurrence of the 'boom': (a) 4–12 June 2017; (b) 6–11 July 2017. The grey bands indicates night times; the arrows indicate the spawning events observed by scuba-divers. The circle corresponds to the full moon

TABLE 2 Acoustic characteristics of the 'boom' based on 34 sound samples. See Figure 3 for a representative oscillogram

	Mean $\pm$ SD	Min.–max.
Total duration (ms)	527 $\pm$ 481	31–1787
Number of pulse	2 $\pm$ 1	1–5
Pulse duration (ms)	44 $\pm$ 14	20–86
Pulse period (ms)	321 $\pm$ 213	69–900
Dominant frequency (Hz)	103 $\pm$ 31	32–185

water column to release their gametes. These booms showed similar acoustic features to the sounds recorded in 2017. The mean pulse duration of the booms recorded in 2018 was 37 ± 16 ms ($n = 9$) and the mean dominant frequency was 126 ± 14 Hz ($n = 9$).

4 | DISCUSSION

Coral reef fish often have lengthy spawning seasons with species-specific variation in timing and duration that are often related to interactions between temperature and photoperiod (Pankhurst & Porter, 2004), or to lunar phases (Biggs & Nemeth, 2016; Johannes, 1978). The specific phenology (Colin & Clavijo, 1988) of spawning events could be related to conditions that may increase the chances of larval survival and can vary among species, with daily, monthly, and annual cycles. In parallel with spawning events, fish can also show sound production patterns with diurnal, crepuscular, or nocturnal calling activities (McCauley & Cato, 2000; Staaterman, Paris, DeFerrari, Mann, & Rice, 2014). This study allowed the collection of a large variety of sounds in a marine protected area showing phenological patterns at different temporal scales, from hourly to daily to lunar cycles. This study also noted that the majority of sounds produced by many putative soniferous species remain unknown, however.

Marine soundscapes and their cycles of production may also be informative for understanding biodiversity patterns (Pieretti, Martire, Farina, & Danovaro, 2017). In Fakarava, temporal cycles were identified for six sound types with a mix of diurnal and nocturnal patterns, that show fishes shared their acoustic space on a temporal basis (Ruppé et al., 2015). Sound types also increased or decreased relative to the full moon, information that can be used to identify sympatric species based on differences in their reproductive activity patterns (Robertson, Green, & Victor, 1988). Seven dominant sound types did not show any clear pattern during this short-term study and the remaining sounds, accounting each for less than 1% of the total sounds recorded, may be produced by species that were in very low densities at the time of the recordings, rely less on acoustic signals to communicate, or produce more frequent sounds during other periods of the year. As it seems unlikely that fish produce sounds continuously, longer time-series of PAM recordings will most likely capture novel sound cycles made by different species. The discrimination of species-specific sounds in the field remains quite difficult, however, as similar acoustic signals can be shared by different species (Colleye, Vandewalle, Lanterbecq, Lecchini, & Parmentier, 2011; Myrberg, Spanier, & Ha,

1978; Parmentier, Lecchini, Frederich, Brie, & Mann, 2009). One approach would be to identify and catalogue the vocalizations of fish species in the south pass of Fakarava and develop a comprehensive repertoire of fish sounds at this important biosphere reserve, which can then be used for comparative purposes at other sites.

The catalogue of identified sounds of different soniferous fish species in Fakarava and elsewhere can be increased by combining underwater field observations and PAM. This was accomplished in 2017 when unique sounds from the fish soundscape were extracted and related to movements of specific fish groups in the field. The booming sound can be attributed to the camouflage grouper for several reasons. First, the sound features (Table 1) are similar to those of other grouper species (Bertucci et al., 2015), and seem to be related to specific behaviours. According to diver observations, the fish started to aggregate at least 9 days before the full moon of June in Fakarava south pass, reaching the highest density a couple of days prior to spawning, similar to studies performed elsewhere (Rhodes & Sadovy, 2002b). During the full moon, sonic activity peaked in the morning when groupers were observed spawning. Fish, and consequently the booming sounds, rapidly dispersed the day after the spawning event. This spawning period corresponded precisely to the falling tide, with the water outflow favouring egg dispersion into the ocean (Barlow, 1981). These patterns of abundance were also observed by camouflage grouper tracked with acoustic transmitters in Fakarava (Mourier et al., 2019). The frequency of 'booms' around the full moons of July 2017 followed these same temporal trends and declined rapidly after the second spawning event (Figure 4). A similar match in behaviour and sound production was also observed in *E. guttatus*, where variations in sound levels corresponded to increases in fish density, with maximum levels occurring around spawning at sunset (Rowell et al., 2012). Higher rates of sound production prior to or during spawning have been observed in several fish species, such as *M. venenosa* (Schärer, Rowell, et al., 2012) and *Atractoscion nobilis* (the white weakfish) (Aalbers, 2008; Aalbers & Drawbridge, 2008), which could indicate an intensification of the behaviours related to spawning. Moreover, the video recordings suggest that sounds could be emitted to synchronize the spawners, as they were produced just prior to their ascents in the water column. The role of sounds in synchronizing individuals has also been suggested by Bertucci et al. (2015) in *E. marginatus*, where boom series were associated with behaviours occurring in the initial stage of spawning, preceding vertical ascents. As 'booms' were also recorded in the days before the spawning events, the sounds could be used during other behaviours associated with reproduction, such as territory defence or hierarchic positioning, with male confrontations.

Other groupers, i.e. *E. striatus*, *M. bonaci*, and *M. venenosa*, produce more complex sounds including a series of pulses followed by a long tonal section (Rowell et al., 2018; Schärer et al., 2014; Schärer, Nemeth, et al., 2012; Schärer, Rowell, et al., 2012). Some species also exhibit more specific sound production patterns. For example, *E. morio* increases its vocalizations in the late afternoon (Nelson et al., 2011), whereas *E. itajara* produces sounds based on a diel cycle, with the highest level between 01:00 and 03:00 h (Mann et al., 2009). The

camouflage groupers' simpler pattern may be explained by the characteristics of the Fakarava aggregation, which has been reported as being the world's largest, consisting of about 17 000 individuals (Mourier et al., 2019, 2016). This aggregation also attracts more than 600 reef sharks (Mourier et al., 2019) that may intercept communication signals (Myrberg, Gordon, & Klimley, 1976). The increased density of predators may disturb or stress fish species, such that they reduce their vocalizations to reduce predation pressure (Luczkovich et al., 2000; Remage-Healey, Nowacek, & Bass, 2006). The high density of groupers and sharks at Fakarava may provide unique insights into the dynamics of aggregating species and their sound repertoire at protected FSA sites. The pattern of reduced vocalizations suggests that no complex and repetitive callings are required to communicate at high-density spawning sites, as all of the individuals are in close proximity to one another (Mourier et al., 2019). Other cues can also be used. Males fighting and territory defence behaviour are associated with colour change (Rhodes & Sadovy, 2002b). Other behaviours involving physical contact rather than acoustic signalling, such as cheek-to-cheek position, pushing at the flanks, snout-to-snout snapping, and sidling have also been described (Johannes et al., 1999; Robinson et al., 2008).

The characterization of the courtship-associated sounds of camouflage grouper in this study indicates that this activity can be acoustically monitored and provides a unique opportunity for the conservation and management of this important species. As has been achieved for *E. itajara* (Mann et al., 2009) and *E. morio* (Wall et al., 2014), PAM can help to identify the location and duration of FSA sites. In the groupers *E. striatus*, *M. bonaci*, and *M. venenosa*, for example, the highest rates of courtship-associated sound production occurred prior to sunset and lasted for a period of 10 days, with lunar periodicity over three to five consecutive months (Rowell et al., 2015; Schärer et al., 2014). This information can be used to guide management in terms of defining MPA boundaries or temporary fishing closures during the reproductive season (Nemeth, 2012; Rowell et al., 2015). PAM and other remote-sensing equipment could help to elucidate the location of other possible aggregation sites for the camouflage grouper and other aggregating species (Kobara, Heyman, Pittman, & Nemeth, 2013).

Overall, the study provided further evidence that passive acoustic monitoring is an efficient tool for the survey of soniferous species populations at spawning aggregation sites. Although fish sounds are usually identified by means of recordings performed in tanks and/or by means of video analysis of isolated specimens, this study allowed us to determine for the first time the sound produced by camouflage grouper in the wild by means of PAM. As described above, PAM can help to locate previously unknown FSAs and support the creation of new marine protected areas. It confirms that sounds are an important part of the spawning behaviour of *E. polyphekadion*, but that silent waters may be required during the reproductive period, which is currently not the case in Fakarava, with excessive boat traffic transporting recreational scuba-divers. Moreover, recordings allowed the identification of clear diel and lunar cycles (Figure 2) in several detected sound types, probably related to the reproductive activity of several fish species, but this requires further investigation. It shows

that the continued monitoring of this spawning site will inevitably be beneficial for other sympatric calling species. Monitoring requires the collection of data over long periods, mainly for species like the camouflage grouper that spawn during short periods of the year (June and July). Because of its status as an UNESCO biosphere reserve, the sound data collected in Fakarava Pass provides an initial baseline for soundscapes from a relatively pristine location. We anticipate that data from Fakarava (Figure 4) can be used for comparative purposes with other locations under varying management levels or conservation agendas. It will provide a reference point for determining the levels of produced sounds and can help with both monitoring and determining the size of the grouper aggregation.

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SUPPORTING INFORMATION

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