

Diel cycle of two recurrent fish sounds from mesophotic coral reefs

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Summary: Mesophotic coral ecosystems (MCEs) are the deepest part of tropical coral reefs, ranging from depths of 30 to over 170 m. Despite their significance, MCEs remain largely unexplored due to the challenges associated with accessing these depths. However, the application of passive acoustic monitoring methods (PAM) is a suitable approach for studying fish communities within these unique habitats. In French Polynesia, recent PAM studies have unveiled a higher occurrence of frequency-modulated fish sounds in MCEs than in shallower reef environments. This study aims to further enhance our understanding of fish sounds in MCEs by examining their diel patterns, focusing specifically on the two most abundant frequency-modulated fish sounds that were recorded at depths of 60 and 120 m at six Polynesian islands. Both sound types occurred predominantly during the beginning and the end of nocturnal periods. The presence and abundance of these sounds exhibited variation between the islands, highlighting potential regional disparities in vocal activity or the bathymetric distribution of the sound-producing species. By characterizing the diel cycles and bathymetric differences in relation to their geographical distribution, this study offers preliminary insights into identifying the potential sound-producing species.

Keywords: French Polynesia; mesophotic coral ecosystems; passive acoustic monitoring; bioacoustics; biophony; fish sounds.

Ciclo diurno de dos sonidos recurrentes de peces en arrecifes de coral mesofóticos

Resumen: Los Ecosistemas de Coral Mesofótico (MCEs, por sus siglas en inglés) representan la parte más profunda de los arrecifes de coral tropicales, con profundidades que van desde los 30 metros hasta más de 170 metros. A pesar de su importancia, los MCEs siguen siendo en gran parte inexplorados debido a los desafíos asociados con el acceso a estas profundidades. Sin embargo, la aplicación de métodos de Monitoreo Acústico Pasivo (PAM, por sus siglas en inglés) presenta un enfoque adecuado para estudiar las comunidades de peces dentro de estos hábitats únicos. En la Polinesia francesa, estudios recientes de PAM han revelado una mayor ocurrencia de sonidos de peces de modulación de frecuencia en los MCEs en comparación con los ambientes de arrecifes menos profundos. Este estudio tiene como objetivo mejorar aún más nuestra comprensión de los sonidos de los peces en los MCEs mediante el examen de sus patrones diurnos, centrándose específicamente en los dos sonidos de peces de modulación de frecuencia más abundantes que fueron registrados a profundidades de 60 metros y 120 metros en seis islas distintas de la Polinesia. Ambos tipos de sonidos ocurrieron predominantemente al comienzo y al final de los períodos nocturnos. La presencia y abundancia de estos sonidos mostraron variaciones entre las diferentes islas, resaltando posibles disparidades regionales en la actividad vocal o en la distribución batimétrica de las especies que producen los sonidos. Al caracterizar los ciclos diurnos y las diferencias batimétricas en relación con su distribución geográfica, esta investigación ofrece conocimientos preliminares para identificar las posibles especies que producen estos sonidos.

Palabras clave: Polinesia francesa; Ecosistemas De Coral Mesofótico; Monitoreo Acústico Pasivo; bioacústica; biofonía; sonidos de peces.

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INTRODUCTION

Tropical coral reefs are traditionally classified into two main zones: the photic part (from the surface to 30 or 40 m) and a deeper part (from 30 or 40 m down to 150 to 172 m) (Pyle et al. 2016, Baldwin et al. 2018, Rouzé et al. 2021) referred to as mesophotic coral ecosystems (MCEs). Research on fish communities has predominantly focused on shallow coral reefs, resulting in limited data availability for MCEs (Raick et al. 2023a). However, it is known that fish assemblages within MCEs are generally segregated between the shallower part (between 30-40 and 60-90 m) and the deeper part (below 60-90 m) (Kahng et al. 2016, Pinheiro et al. 2016).

In teleosts, soniferous behaviour has been observed in 175 out of 470 families (Rice et al. 2022). Estimations focusing on Polynesian coral reefs have indicated that half of the fish families in the region have at least one known sonic species (Parmentier et al. 2021). MCEs are known to harbour numerous vocal fish species, suggesting that passive acoustic monitoring (PAM) can serve as a valuable tool for studying fish communities in these challenging-to-access environments (Raick et al. 2023a). A study conducted in South African submarines caves at a depth of 113 m demonstrated that sonic activity allowed for a clear distinction between diurnal and nocturnal fish assemblages (Ruppé et al. 2015). Furthermore, the study found that nocturnal fish sounds did not overlap at the main calling frequency, in contrast to diurnal fish sounds, indicating that acoustic

communication may serve as a complementary mode of communication to visual displays in diurnal species, while playing a particularly crucial role in nocturnal species for effective communication and species differentiation (Ruppé et al. 2015). Although diel cycles of fish from photic reefs are relatively well documented, with vocal activity peaking at sunset (Mooney et al. 2016, Rountree et al. 2018, Smith et al. 2018), sunrise (Parmentier et al. 2010), before sunrise (Parmentier et al. 2016) or after sunset (Di Iorio et al. 2018), limited knowledge exists regarding the sounds produced by fish from MCEs (Ruppé et al. 2015, Pichon 2019, Raick et al. 2023a).

In French Polynesia (South Pacific), recent acoustic recordings from MCEs have revealed a diverse range of fish sounds (Raick et al. 2023a). This study specifically focused on the sunset period (5 to 7 p.m.) and found that frequency-modulated sounds, which are sounds characterized by a changing frequency, were more abundant in MCEs than on photic reefs. Frequency-modulated (FM) sounds have been described in only a few marine taxa, such as Batrachoididae (Tower 1908, Bass et al. 1999, Rice and Bass 2009), Gobiidae (Lugli et al. 1997) and Serranidae (Lobel 1992, Bertucci et al. 2015, Desiderà et al. 2019). At a depth of 120 m, the two most common FM sounds recorded during sunset were a harmonic upsweep sound (i.e. a sound with a frequency increasing over time) referred to as US1 and a longer harmonic complex sound exhibiting both upsweeps and downsweeps referred to as CS1 (which repre-

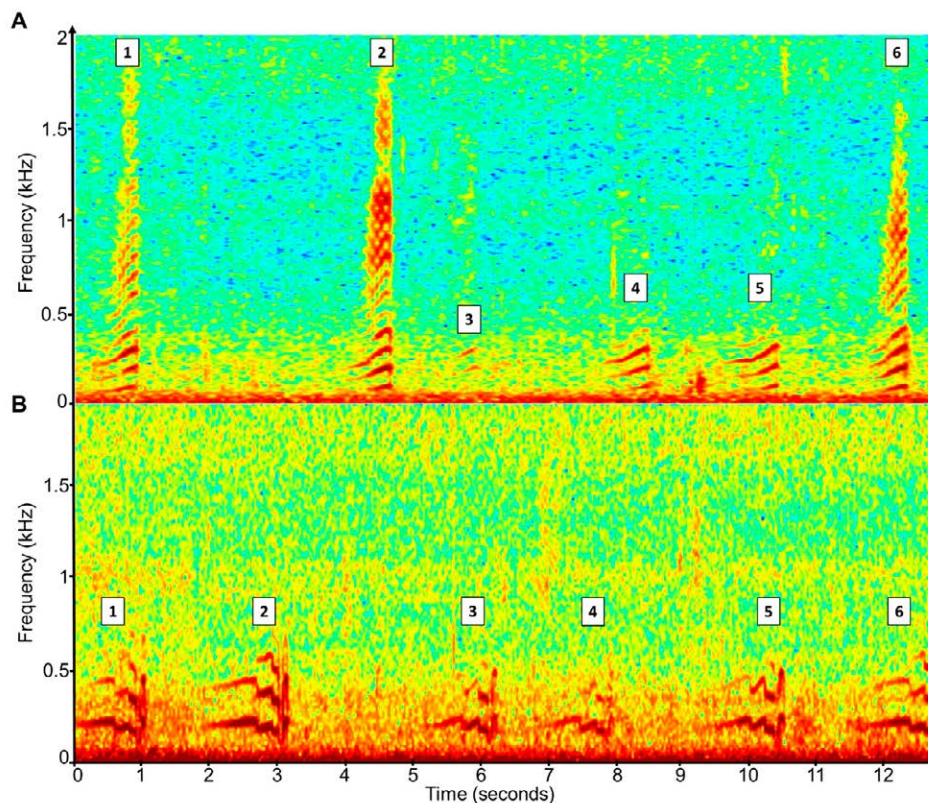


Fig. 1. – Spectrogram of six US1 sounds (A) and six CS1 sounds (B). FFT=256 points. Window=Hann. The colour code indicates energy levels, with warmer colours representing higher energy.

sented 61% and 18% of all FM sounds, respectively) (Raick et al. 2023a). US1 consists of approximately 32 ± 6 peaks with a peak frequency of around 225 ± 49 Hz (Fig. 1A) (Raick et al. 2023a). CS1, also known as *whoot* in a previous study conducted in the same geographic area (Bertucci et al. 2020), exhibits two frequency peaks around 200 Hz and 400 Hz (Fig. 1B) (Raick et al. 2023a). The objective of this study was to characterize the acoustic variability, geographical variation and diel cycle of US1 and CS1 in Polynesian MCEs. Determining the most prolific period of activity will assist future research in identifying the species responsible for their production.

MATERIALS AND METHODS

Sampling

Recordings were conducted between March 2018 and April 2019 on six islands in French Polynesia (Fig. 2). Three of the islands were atolls from the Tuamotu Archipelago, Rangiroa, Raroia and Tikehau (sampled between March and November 2018), while the other three were high islands, Bora Bora and Moorea (both in the Society Archipelago, sampled in September 2018), and Mangareva (Gambier Archipelago, sampled in April 2019). The sampling activities were carried out as part of the Under The Pole III expedition (Concarneau, France; <https://underthepole.org/>). Considering the known faunal shift occurring between 60 and 90 m (Pinheiro et al. 2016, Pyle et al. 2016, Baldwin et al. 2018), two different depths were selected for sampling: one above and one below this depth range. Due to logistical constraints, the chosen depths were 60 and 120 m (except for Mangareva, where data are only available for 60 m depth).

Acoustic recordings

Recordings were conducted using SNAP recorders (Loggerhead Instruments, Sarasota, FL, USA) connected to HTI-96 hydrophones (sensitivity ranging from -170.5 to -169.7 dB re 1 V, flat frequency response from 2 Hz to 30 kHz, sampling rate of 44.1 kHz, gain of 2.05, 16-bit resolution). The recording schedule was set to capture 1 min recordings every 10 min for a total duration of 62 h (2 days and 3 nights). The diel cycle was divided into four periods: the sunset period (between 5 and 6:59 p.m., $n=3$), night (7 p.m. to 4:59 a.m., $n=3$), sunrise period (5 to 6:59 a.m., $n=3$), and daytime (7 a.m. to 4:59 p.m., $n=2$).

Acoustic analysis

The analysis focused on frequencies below 2 kHz (Raick et al. 2021a, 2023a, 2023b), because most fish sounds are commonly found within this frequency range (Parmentier et al. 2017, 2019, Raick et al. 2020), including CS1 and US1 (Bertucci et al. 2020, Raick et al. 2023a). The files were subsampled at 4 kHz using a MatLab® R2014b routine (MathWorks, Natick, MA, USA). Spectrograms were visualized using Raven Lite 2.0.3 (Cornell Lab of Ornithology, Ithaca, NY, USA; FFT=256). All files were audited and visually inspected to identify US1 and CS1 sounds. The number of sounds per file was then calculated.

Statistics

Temporal series of the total number of sounds were used to visualize diel cycles. Differences between depths and islands were visualized using boxplots. Given that the number of replicates was lower for the day than in other temporal periods ($n=2$ vs. $n=3$),

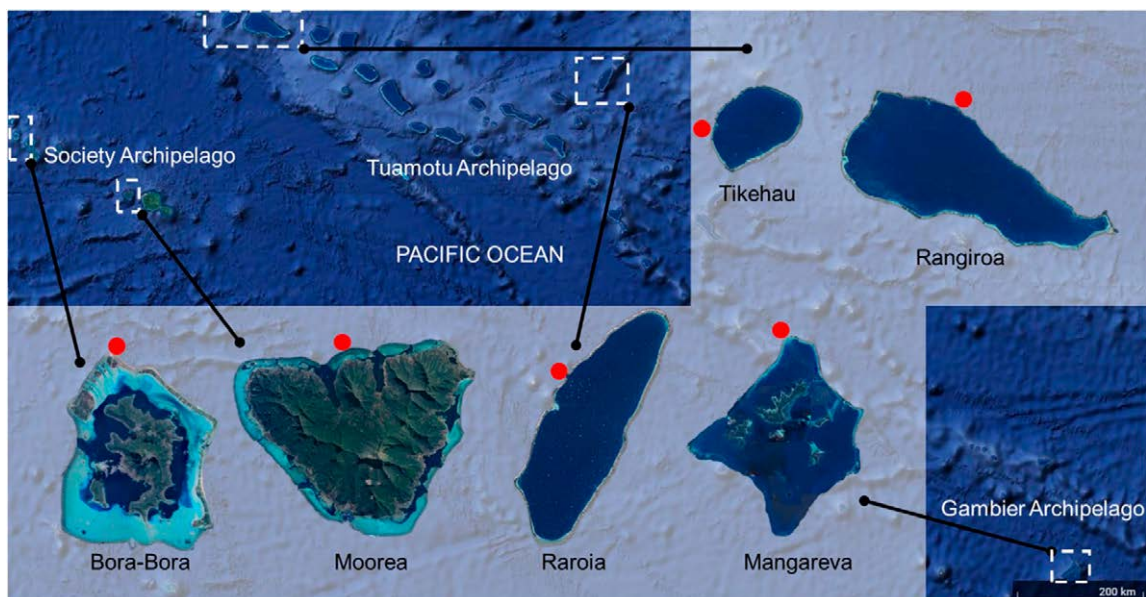


Fig. 2. – Map of the studied islands in part of French Polynesia. Data SIO, NOAA Image ©, U.S. Navy, NGA, GEBCO Image © Maxar Technologies, Data LDEO-Columbia, NSF, CNES / Airbus, Image Landsat / Copernicus.

boxplots were created summing data from the night, sunset and sunrise periods (i.e., between 5 p.m. and 7 a.m.), in addition to boxplots using raw data. The results were similar for both methods. Only the first method is presented in the results. Normality was assessed using Shapiro-Wilk tests, and homogeneity of variances was assessed using the *F*-test of equality of variances ($n_{\text{groups}}=2$, to compare the number of sounds at 60 and 120 m) or Bartlett tests ($n_{\text{groups}}>2$, to compare the number of sounds between islands). Because neither of the two conditions was met, non-parametric tests were employed. The number of sounds at 60 vs. 120 m was compared using Mann-Whitney tests. To compare the number of sounds between islands, Kruskal-Wallis tests followed by Dunn post hoc tests were conducted for each depth separately. *P*-values were corrected using the Benjamini-Hochberg method. All statistical analyses were performed using R 4.0.5 (R Core Team, 2021) with $\alpha=0.05$.

RESULTS

Sound description

A total of 4318 sounds were detected in the audio files: 2318 CS1 and 2000 US1. The majority of US1 (91.65%) exhibited a classical pattern (Fig. 3), while others displayed variations of the classic pattern: 0.1% had a higher frequency distribution, and 8.25% were followed by one or several pulses (Fig. 3). These pulse series consisted, on average, of 4.5 ± 0.85 pulses (mean \pm SD, measured in ten sounds) with a pulse period of 127 ± 35 ms. The peak frequency of these pulses varied, but it always corresponded to the fundamental frequency (94 ± 22 Hz) or the first harmonic frequency (215 ± 7 Hz) when measured at the end of the classical pattern. The occasional presence of pulses after the main part of the sound was reported by Raick et al. (2023a).

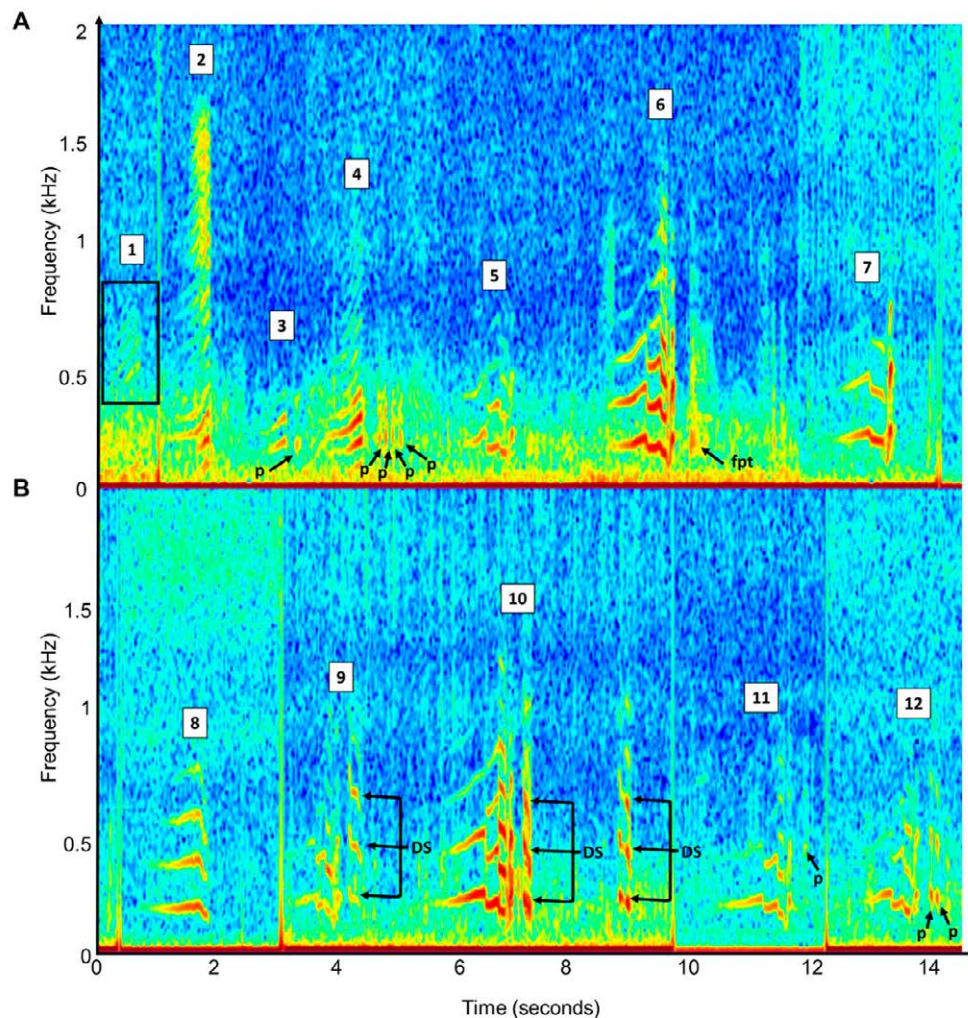


Fig. 3. – A, spectrogram illustrating variations in the sound pattern of US1 (a to d) and CS1 (e to g) sounds. a, US1 with a higher frequency distribution (black box); b, classic US1; c, US1 followed by a pulse (p); d, US1 followed by a series of pulses (in this example, 4); e, classic CS1; f, CS1 followed by a *fast pulse train* (fpt); g, CS1 with only one inflexion point. B, spectrogram illustrating variations in the sound pattern of CS1 (h to l) sounds. h, CS1 with only one inflexion point, a longer first part, and without the classic second part; i, CS1 followed by a *downsweep* (DS); j, CS1 followed by several *downsweeps*; k, CS1 followed by a pulse (p); and l, CS1 followed by a series of pulses (in this example, 2). FFT=256. The warmer the colour code, the higher the energy.

Of the CS1 sounds, 99.6% exhibited a classical pattern, 0.09% were followed by one or several pulse(s), 0.09% by one or several downsweeps (i.e. sounds with a frequency that decreases over time) and 0.04% by a fast pulse train. All the elements following the classical CS1 patterns had a harmonic structure with the same harmonic interval as the one measured at the end of the classical pattern. Additionally, the peak power (dB re one dimensionless sample unit) was equivalent for those elements. Furthermore, 0.13% of CS1 sounds had only one inflexion point and a longer first part of the sound (Fig. 3).

Diel cycle and depth differences

The number of sounds exhibited a pronounced diel pattern (Table 1, Figs 4 and 5). Both CS1 and US1 were predominantly present at sunset and during the night but were less common (sometimes even absent) during the day and sunrise periods (Table 1). At sunset, the number of sounds increased by a factor of 7 to 17

compared with daytime. CS1 sounds were two to three times more abundant in the first part of the night (7 to 11:59 p.m.) than in the second part of the night (12 to 4:59 a.m.) regardless of the depth. An increase was also observed for US1, but only at 120 m. In fact, the recorded sound counts were not homogenous across depths. Considering the entire diel cycle, US1 sounds were more abundant by a factor of 28 at 120 m than at 60 m. This difference was less significant for CS1: the number of sounds was higher by a factor of 1.3 at 120 m than at 60 m.

Inter-island variability in the number of sounds

Although general diel patterns existed, there was a variability in the number of sounds recorded on the different islands (Fig. 6). At 120 m, for the entire diel cycle, the number of US1 varied between 44.8 ± 13.1 per hour (at Tikehau) and 134.5 ± 23.7 per hour (at Raroia) (Fig. 6A). At 60 m, for the entire diel cycle,

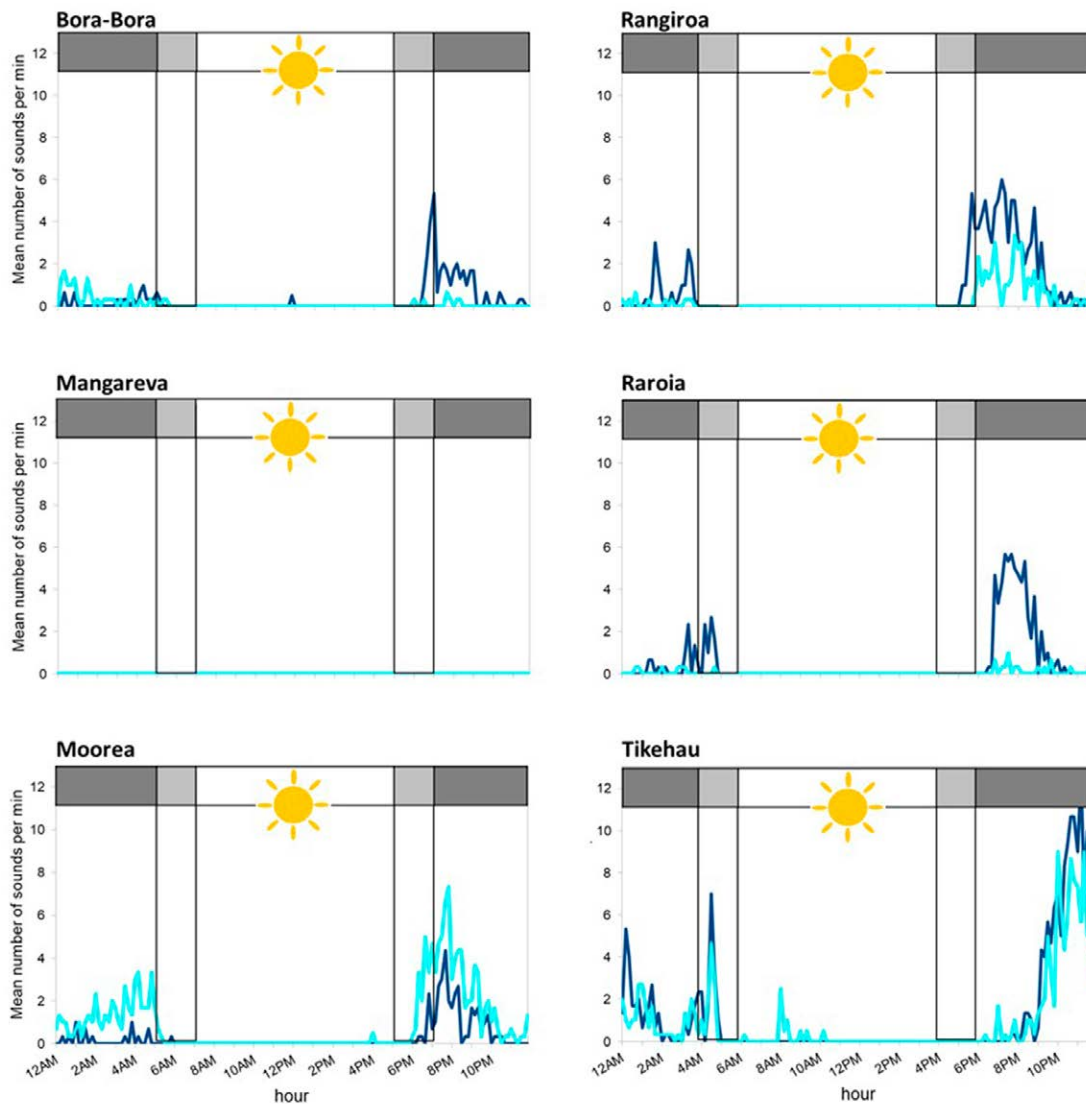


Fig. 4. – Diel cycle of the number of CS1 sounds min^{-1} for each studied island. Light blue, 60 m; deep blue, 120 m (unavailable for Mangareva). Red boxes represent two-hour sunrise and sunset periods centred around the official sunrise and sunset hours.

Table 1. – Number of sounds per hour for each diel period (combined data from all islands).

		CS1				US1			
		60 m		120 m		60 m		120 m	
	h	mean	SD	mean	SD	mean	SD	mean	SD
Sunrise	5 – 6:59 a.m.	20	13.25	10	5	0	0	51.65	25.65
	7 – 11:59 a.m.	7.34	12.7	0.66	1.16	0.66	1.16	0	0
Day	12 – 4:59 p.m.	0.66	1.16	0	0	0	0	0	0
	5 – 6:59 p.m.	140	100.35	271.65	50.1	51.65	42.5	933.35	131.55
Night	7 – 11:59 p.m.	402.66	72.24	595.34	6.12	11.34	9.46	530.66	43.18
	12 – 4:59 a.m.	188.66	30.62	172.66	53.12	15.34	11.02	360.66	43

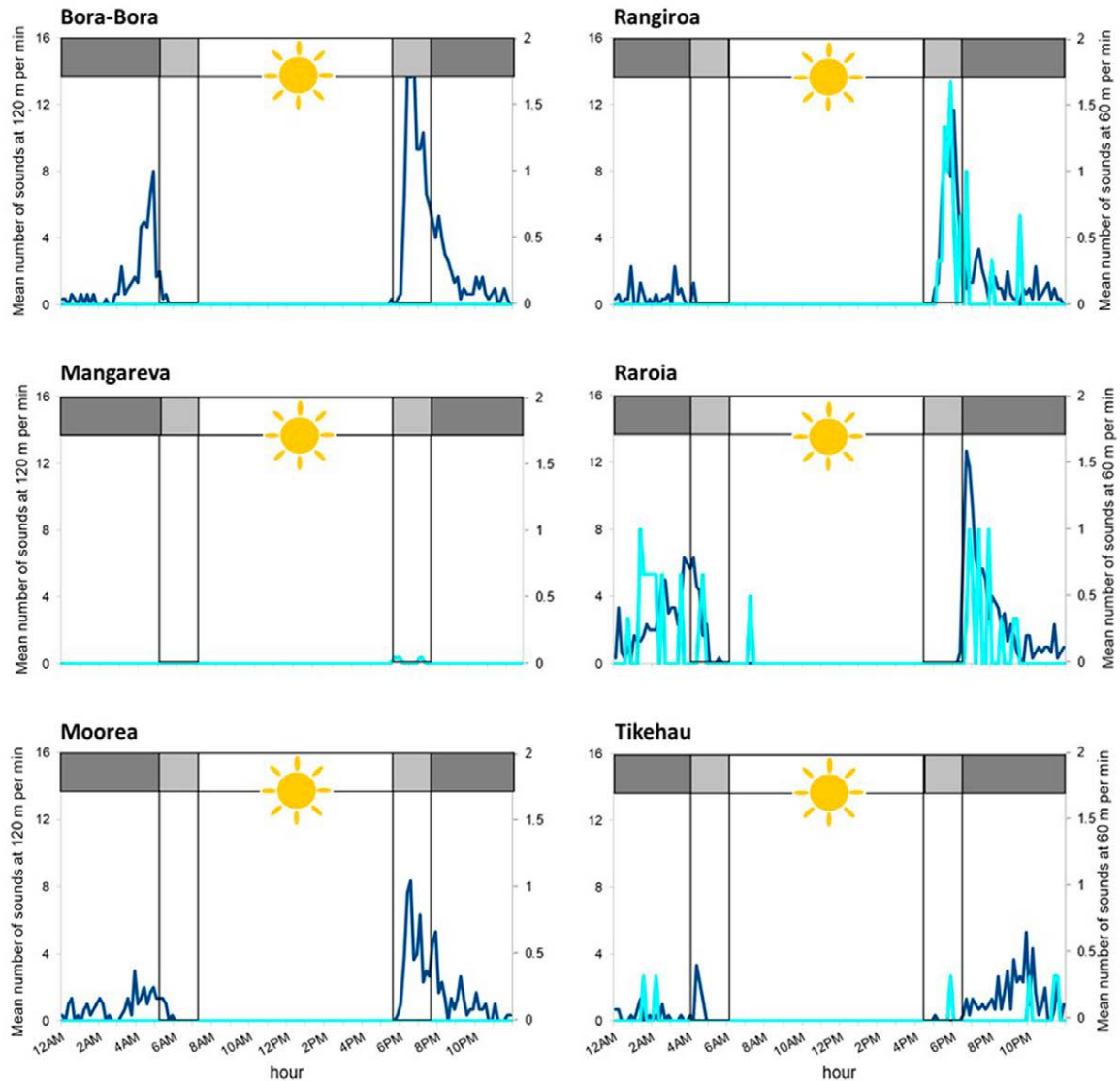


Fig. 5. – Diel cycle of the number of US1 sounds min⁻¹ along the diel cycle for each studied island. Light blue, 60 m (right axis); deep blue, 120 m (left axis, unavailable for Mangareva). Red boxes represent two-hour sunrise and sunset periods centred around the official sunrise and sunset hours.

Raroia was also the island with the highest number of recorded US1 (8.9±7.6 per h). There were significantly more US1 at Raroia than at all the other islands, both at 60 m (Kruskal-Wallis: $\chi^2=60.35$, $df=4$, $P<0.0001$; Dunn: $Z=[-6.38, -5.17, -6.38, -2.94, \text{ and } 4.92]$; $P=[<0.0001, <0.0001, <0.0001, 0.007, \text{ and } <0.0001]$) and at

120 m (Kruskal-Wallis: $\chi^2=44.50$, $df=4$, $P<0.0001$; Dunn: $Z=[-2.57, -3.89, -4.63, \text{ and } 6.28]$; $P=[0.02, 0.00033, <0.0001, \text{ and } <0.0001]$). No US1 were recorded at 60 m for Bora Bora and Moorea.

The number of CS1 also varied between islands, with Rangiroa and Tikehau showing the highest

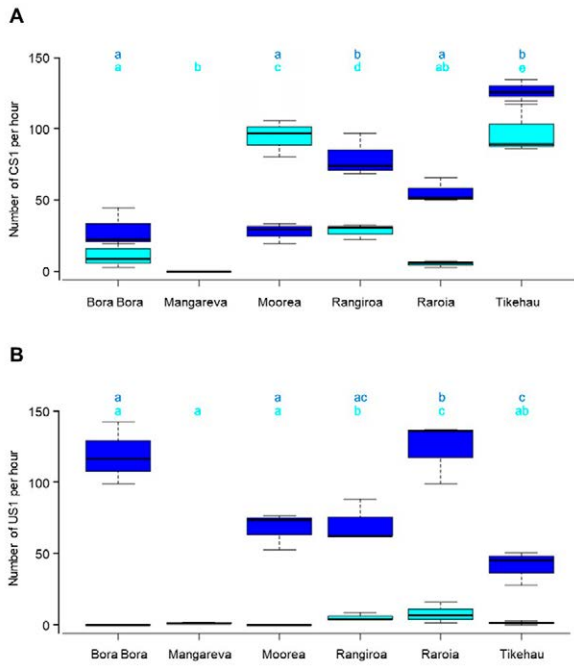


Fig. 6. – Boxplots representing the number of CS1 (A) and US1 (B) per hour between 5 p.m. and 7 a.m. for each island. The light blue colour represents the 60 m depth, while the dark blue colour represents the 120 m depth. Letters are used to indicate significant inter-island differences.

number of CS1 at 120 m (Fig. 6B) (Kruskal-Wallis: $\chi^2=38.41$, $df=4$, $P<0.0001$; Dunn's multiple comparisons test: $Z=-3.9$, -4.3 , and 2.8 for Rangiroa, $Z=-4.3$, -4.7 , and -3.2 for Tikehau; all $P \leq 0.009$). At 60 m, there were statistically significant differences in the number of CS1 between islands (Kruskal-Wallis: $\chi^2=281.9$, $df=5$, $P<0.0001$), ranging from 0 (at Mangareva) to over 90 per hour. Moorea and Tikehau had more sounds than the other four islands (Dunn's multiple comparisons tests: $Z=-13.2$, -10.1 , and 7.5 and 11.4 for Moorea; $Z=-8.1$, -11.2 , and -5.5 and -9.4 for Tikehau, all $P<0.0001$). Moorea was the only island with a higher number of CS1 at 60 m (93.3 ± 12.3 per hour) than at 120 m (27.1 ± 7.0 per h) (Mann-Whitney U test: $W=54256$, $P<0.0001$), while all other islands showed the opposite pattern ($W=74234$, 77450 , 78328 and 68256 , $P=0.0024$, <0.0001 , <0.0001 and 0.69 , with a non-significant result obtained for Tikehau).

DISCUSSION

Diel cycle and depth differences

This study focused on investigating the diel cycle of two sound types, US1 and CS1, which were previously described in MCEs in French Polynesia. These sounds were known to occur between 5:00 and 6:59 p.m. on various coral reefs (Raick et al. 2023a). Additionally, in Moorea, CS1 sounds were documented to take place between 7 and 9 p.m. on the photic reef at a depth of 20 m (Bertucci et al. 2020). The find-

ings of our study reveal that US1 and CS1 sounds are predominantly produced during the night and sunset hours, rather than during sunrise and daytime (with US1 occurring 26 times more and CS1 50 times more during these periods). This observation suggests that the species emitting these sounds are likely nocturnal. Given the complex nature of the sounds, it was expected to record them primarily at night. Diurnal species typically use sounds to complement visual signals, whereas nocturnal species generally lack visual signals (Ruppé et al. 2015). Both CS1 and US1 exhibit harmonic characteristics, a trait found in several families of teleosts (Mélotte et al. 2019, Raick et al. 2020, 2021b, 2023c), and are FM, similar to the sounds produced by Batrachoididae (Tower 1908, Bass et al. 1999, Rice and Bass 2009), a family not known to occur in French Polynesia (Siu et al. 2017). FM sounds are less commonly observed in fish than pulse series. Some are known to be associated with species from various families, such as Batrachoididae (Tower 1908), Gobiidae (Lugli et al. 1997) and Serranidae (Lobel 1992). However, these specific families are not known to produce sounds resembling CS1 and US1. Understanding the diel cycle of US1 and CS1 should aid in identifying these nocturnal sound-producing species. Based on the results, to identify the vocal species, investigations should primarily be conducted during sunset or shortly after at a depth of 120 m for US1 and during the early part of the night at both 60 m and 120 m for CS1.

This study confirmed the depth preference of the species emitting the studied complex and FM sounds, as the number of US1 and CS1 was higher at 120 m than at 60 m. The effect of depth was more pronounced for US1, with a 30-fold difference between 120 m and 60 m. This finding aligns with the study conducted by Raick et al. (2023a), which indicated that the US and CS categories (to which US1 and CS1 belong) were 10 and 2 times more abundant, respectively, at 120 m than at 20 m (specifically studied between 5 and 6:59 p.m.). Therefore, US1 and CS1 are characteristic of the deeper part of MCEs. MCEs have distinct acoustic sources that are unique to them, as previously hypothesized by Bertucci et al. (2017), and are not merely propagated from the photic reef.

Inter-island variability of the diel cycle

The geographic distribution of recorded US1 and CS1 sounds was not uniform. There were extreme situations, such as the absence of US1 sounds in the recordings at 60 m in Bora Bora and Moorea. Moorea also stood out in terms of CS1 sounds: they were more abundant at 60 m than at 120 m. However, when comparing between islands, it is important to consider that the recordings were not made during the same time period for technical reasons, such as transporting a boat with rebreathers from one island to another, given the size of French Polynesia (5000000 km^2) (Rougerie et al. 1997).

If we focus on the sites at 120 m, fewer CS1 sounds were recorded at Moorea and Bora Bora than at the other three islands (Rangiroa, Raroia and Tikehau; there was no data available at 120 m for Man-gareva). Two factors could explain this difference: geographical variations (differences between archipelagos) or geomorphological differences (different types of islands: atolls vs. high islands). High islands are known to have a more variable bathymetric profile due to their younger age (Pichon 2019). However, it is not possible to distinguish between these two factors because Moorea and Bora Bora are the only studied islands belonging to the Society Archipelago, while all the other islands studied at 120 m belong to the Tuamotu Archipelago, and both Moorea and Bora Bora are high islands, whereas all the islands in the Tuamotu Archipelago are atolls.

The analysis of the boxplots also suggests that, for some islands, US1 may be more abundant where CS1 are less abundant (e.g. in Bora Bora) or vice versa (e.g. in Tikehau). However, this hypothesis requires further substantial observations to be confirmed in order to better understand the acoustic niche of each sound type.

CONCLUSION

This study concludes that the US1 and CS1 sounds found in MCEs of French Polynesia are predominantly produced at night and during sunset, indicating the presence of nocturnal emitting species. Additionally, these sounds occur more frequently at 120 m than at 60 m, with US1 showing a particularly higher occurrence. Inter-island comparisons revealed variability in the diel cycle, highlighting the need for further investigation to better understand the acoustic niche of each sound type and its relationship with habitat characteristics.

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DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are openly available online (doi: 10.5281/zenodo.7716945).

CONFLICTS OF INTEREST STATEMENT

The authors declare that there is no conflict of interest.

AUTHOR CONTRIBUTIONS

XR conceived and supervised the study. XR analysed and interpreted part of the data. PC analysed and interpreted part of the data under the supervision of XR. XR wrote the first version of the manuscript with inputs from PC. XR wrote the final version of the manuscript with inputs from EP, FB and DL. DL helped with funding acquisition. UTP performed the sampling. FB prepared the acoustic equipment for the sampling.

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