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Evidence of vertical stratification in marine environments: insights from passive acoustic monitoring in French Polynesia

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Abstract

The stratification of species distribution in marine environments is well-documented, reflecting the influence of depth-related factors such as light availability, temperature, pressure, and habitat structure on the organization of marine communities. This study aimed to determine whether this stratification can also be highlighted using Passive Acoustic Monitoring (PAM), a technique proven effective in the study of various marine habitats. Sounds were recorded at 300 m in July 2022 off Moorea Island (French Polynesia) using a SNAP acoustic recorder. These data were compared to both those collected at shallower depths at Moorea Island (20, 60, and 120 m) and to data from other Polynesian islands obtained during a previous, non-concurrent study. Fish sounds in the recordings were manually identified. Richness and abundance of sounds from 20 m to 300 m depth were compared to assess whether fish communities in the altiphotic reef, upper mesophotic reef, lower mesophotic reef, and rariphotic zone could be distinguished based on the sounds they produce. Comparisons between zones over a 24-hour period revealed for the first time the existence of acoustic stratification, with a fourfold decrease in species richness, from the altiphotic reef to the rariphotic zone, along with a general decline in sound abundance. However, this general pattern was not uniform in terms of abundance throughout the day, as sound abundance increased with depth at dusk from 950 sounds per hour at 20 m to 3,600 at 300 m. It further confirms that diel activity patterns were also evident in light-deprived zones. This first exploration of vertical acoustic stratification based on fish sounds highlights the undeniable contribution of PAM to studies on the ecology of deep-sea communities.

Significance statement

This study demonstrates the existence of previously unquantified vertical acoustic stratification of fish communities across different marine zones, from the altiphotic and mesophotic reefs to the rariphotic zone at 300 meters depth. This stratification is characterized by a decrease in richness of fish sound types and sound abundance over a 24-hour cycle and by the development of new sound types at depth. However, the lower diversity of sound types at 300 meters contrasts with moments of the day when sound abundance is greater at depth than at the surface. The results align with previous studies based on visual data, thereby underscoring the potential of Passive Acoustic Monitoring (PAM) as a high-resolution, non-invasive tool for deep-sea biodiversity monitoring.

1. INTRODUCTION

Indigenous peoples have recognized for millennia that sounds reflect the activities of animals within their environments (Gray et al., 2001). However it is only in recent years that the scientific community has conducted studies to quantify sounds present in an environment and to understand how they interact with each other (Rice et al., 2023). Compared to visual surveys, Passive Acoustic Monitoring (PAM) offers significant advantages. These include the ability to operate continuously at lower cost over long periods (Tittensor et al., 2010, Bolgan 2025) regardless of weather conditions or depth (Lammers et al., 2008; McCauley et al., 2017). This technology has allowed investigation of numerous habitats. It has generated extensive datasets that are essential for conducting innovative studies in ecology and biology, including for habitat monitoring and assessment purposes (Rice et al., 2023). On the other hand, one of the limitations of the method is its reduced effectiveness in highly anthropogenic, noisy environments, as well as the challenge of distinguishing between acoustic absence and actual biological absence.

Soundscapes are stable acoustic environments that can be defined as collections of sounds composed of three acoustic sources: geophony, anthrophony, and biophony (Schafer 1977, Krause 2008, Pijanowski et al. 2011). Passive acoustic studies have demonstrated that soundscapes can characterize soniferous fish communities. For example, by identifying spawning periods (Bolgan et al., 2020) or locations (Wall et al., 2012, Bolgan et al. 2023). Several studies have also focused on relationships between soundscapes and specific habitats (Di Iorio et al., 2018) or their temporal variations, such as the day-night cycle (Staaterman et al. 2014, Kéver et al. 2016, Laboury et al., 2023, Raick et al., 2023a). To the best of our knowledge, however, it has never been determined whether soundscapes can provide information about the vertical stratification of marine communities.

This stratification of communities, however, has been documented by direct observation and sampling with nets and traps. It forms the basis for subdividing marine environments into distinct zones (Semmler et al. 2017; Baldwin et al. 2018; Stefanoudis 2019a). In tropical coral reef regions, the depth range from the surface to 300 m is generally divided into three zones, though the precise boundaries may vary depending on the location (Baldwin et al., 2018). These are identified as the altiphotic, mesophotic, and rariphotic zones. The altiphotic zone, which extends from the surface to a depth of 30–40 m, is well-lit and well-known to recreational divers and has been the subject of numerous PAM studies (Lin et al., 2021; Lobel et al., 2010; Minier et al., 2023; Raick et al., 2021a). Altiphotic reefs are also called shallow-water coral reefs. Within tropical hermatypic reefs, mesophotic coral ecosystems (MCEs) are reefs located below the recreational diving limit, i.e., below 30 to 40 m depth (Baldwin et al., 2018). MCEs are partly-lit and extend to the depth at which the growth of photosynthesizing symbionts associated with corals is no longer possible (Van den Hoek et al., 1978). This limit varies with location and water clarity (Baldwin et al., 2018; Pyle and Copus, 2019; Turner et al., 2017). It is generally considered to be around 150 m (Rouzé et al., 2021). Below the MCEs lies the rariphotic zone, which is partly dimly lit and partly unlit. It begins with the disappearance of hermatypic corals and forms part of a depth continuum of discrete faunal zones for tropical reef fishes (Baldwin et al., 2018). It extends from approximately 150 m to 300 m in depth, thereby overlapping both the photic and aphotic oceanic compartments. The rariphotic zone can therefore straddle both the so-called 'photic' oceanic layer and the 'aphotic' layer, where light intensity is less than 1% of that at the surface.

The rariphotic zone remains relatively understudied worldwide, as it is more challenging to access compared to MCEs. However, it has been demonstrated that this distinct zone, which exhibit strong depth-dependent structuring, are used by different fish and benthic invertebrate communities (Stefanoudis et al., 2019b). Loss of hard coral cover is partly responsible for the faunal break between upper and lower parts of the reefs (Stefanoudis et al., 2019a) while the presence of key deeper species such as branching black coral seems to play key ecological roles in lower MCEs (Rosa et al., 2016). In the rariphotic zone, a significant faunal change separates fish of the upper rariphotic zone (130–190 m) from those of the lower rariphotic zone (190–309 m) (Baldwin et al., 2018; Semmler et al., 2017; Stefanoudis et al., 2019a). Changes in fish trophic guilds with depth are well-documented, with herbivores dominating altiphotic reefs and zooplanktivores prevailing in MCEs (Bejarano et al., 2014). Variation in zooplankton abundance with depth seems to be a key factor in the rariphotic zone, as fish biomass in the rariphotic zone surrounding Bermuda has been shown to be predominantly composed of planktivorous fish (Stefanoudis et al., 2019b).

These studies were based on visual observations, while potential insights from acoustic data were largely overlooked. While few studies have focused on soundscapes of MCEs (Bertucci et al., 2017; Raick, 2023 ; Raick et al., 2023a, 2023c, 2024, 2025a, 2025b, 2025d) or of deeper waters in the aphotic zone (Cato, 1978; Erbe et al., 2015; Lin and Kawagucci, 2024; Mann and Jarvis, 2004; McCauley and Cato, 2016; Wall et al., 2014), none has investigated the rariphotic zone meaning that acoustic stratifications reflecting marine-life communities have never been quantified.

Quantifying fish sounds vertical stratification is key to validating the relationship between fish communities and their soundscape. This knowledge can provide essential insights into the functioning of unexplored ecosystems. This study aimed to describe the fish acoustic activity in the lower rariphotic reef at Moorea Island (300 m). Additionally, it aimed to provide the first description of vertical acoustic stratification of fish sounds at depths of 20, 60, 120, and 300 m.

2. RESULTS

Vertical stratification patterns

Based on daily recording period, the comparison of zones indicated that the abundance and richness of fish sounds decreased with depth (Fig. 1A). In the mesophotic zone (MCE), we identified between 68 (at 60 m) and 69 (at 120 m) different sound types, whereas only 16 distinct sound types were recorded at a depth of 300 m. Among these 16 sound types, eight were also recorded in MCEs. Six other sound types appeared to be similar to those recorded in MCEs but their low occurrence at either 300 m or shallower depths – 60 and 120 m – did not provide sufficient data for robust comparisons. The two last sounds were not found in shallow-waters. This observation indicates mainly a tangible decrease in the soniferous activity, likely linked to the number of soniferous species, accompanied by a very low rate of renewal at depth. However, these general observations do not account for temporal variations throughout the day. During the sunset period (5 to 7 PM), the rariphotic zone exhibited the highest number of fish sounds per unit of time, with more than 3,600 sounds per hour, compared to fewer than 950 sounds per hour in the altiphotic reef (Fig. 1B). However, while the rariphotic zone showed the highest abundance of sounds at sunset, it had the lowest richness in comparison with other zones. The high abundance in the rariphotic zone during sunset was primarily driven by one dominant sound type (see next section).

Detailed description of the four most abundant fish sound types

Over the complete investigated period, 7,477 fish sounds were recorded at 300 m and subsequently classified into 16 distinct types. The distribution of these sound types was not uniform, with four sound types accounting for 98.3% of all recorded fish sounds. These four sound types were recorded more often at 300 m but some of them were already found in shallower depths (Fig. 2A).

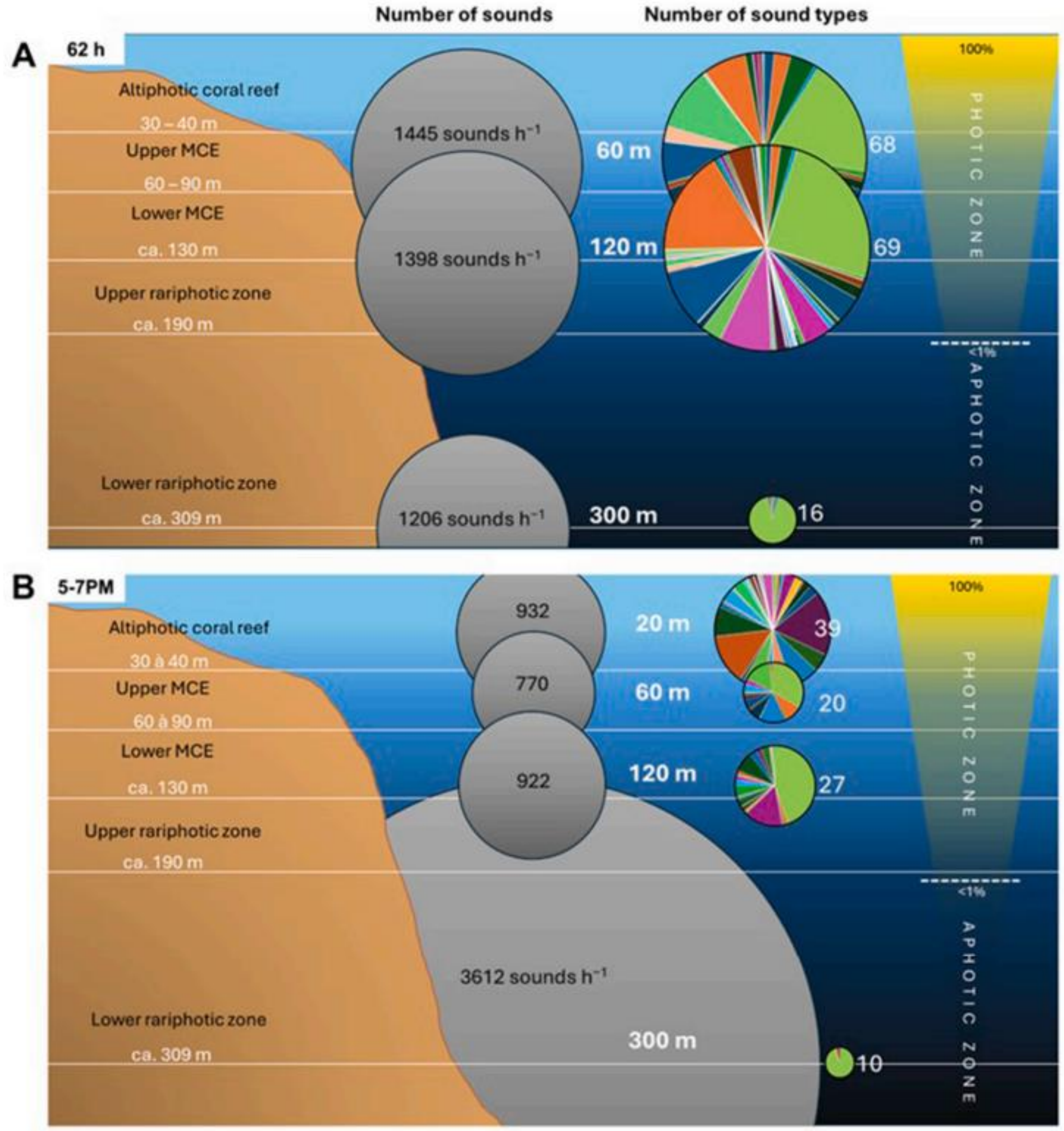

Fig. 1 Vertical acoustic stratification of fish sounds. Grey circles represent the number of fish sounds per hour for each studied depth (from top to bottom: 20, 60, 120, and 300 m). The diameter of the circles is proportional to the abundance of sounds. Colored circles represent the richness of fish sound types per hour for each studied depth, with the size of the circles indicating the number of sound types. Each sound type is assigned a distinct color. (A) Data for the entire diel cycle based on a recording of 62 hours (B) Data for the sunset period (5 to 7 PM). In panel A, values are from a different study conducted across several Polynesian islands (Raick et al., 2025a). The values for both altiphotic and MCEs in panel B are from a previous study in Moorea Island (Raick et al., 2023c).

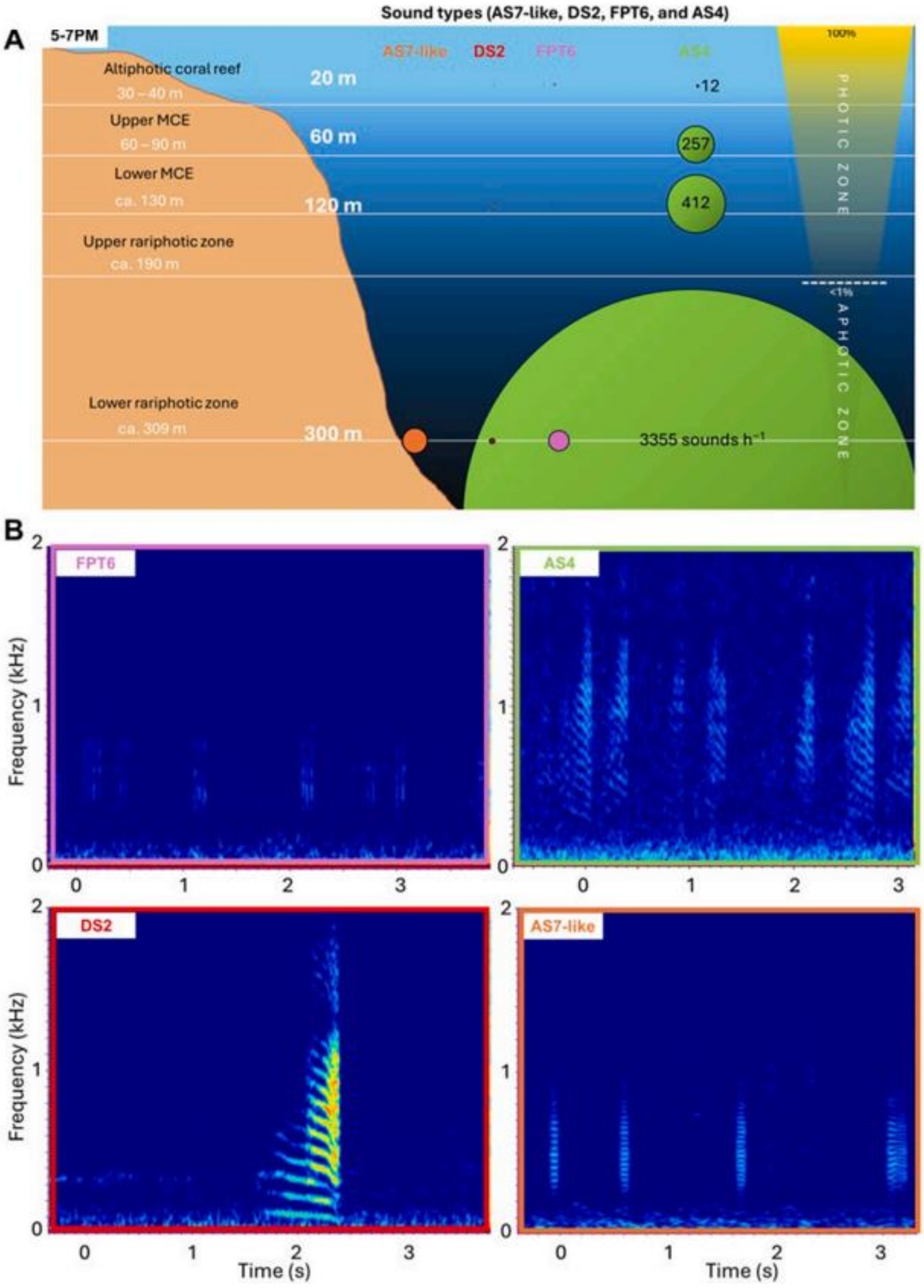

Fig. 2 Vertical acoustic stratification of the four most abundant fish sounds recorded in the rariphotic zone at Moorea Island. Circles represent the number of fish sounds per hour for each studied depth (from top to bottom: 20, 60, 120, and 300 m). The diameter of the circles is proportional to the abundance of sounds. Each sound type is assigned a distinct color, and the color code is consistent with that used in the spectrograms in part B. Spectrograms were generated using a 256-point FFT with a frequency resolution of 15.6 Hz and a 94.9% overlap. The contrast has been increased by 20% for better visualization. The use of a 94.9% overlap for visual representation in this figure, compared to a 50% overlap for routine inspection, results in a noticeable difference in the visualization of FPT6. In this figure, the individual pulses are clearly distinguishable, whereas they are not as evident with a 50% overlap. The hotter the color on the spectrogram, the more intense the sounds (on a relative scale). Although they are not easily discernible due to the scale, note the presence of DS2 and FPT6 at shallow depths. Audio files of all the low frequency sound types from altiphotic reefs and MCEs can be assessed on-line (DOI: 10.5281/zenodo.12570714). The oscillograms and power-spectra of the sound types can be assessed in Raick et al. 2023c (Supplementary materials). Raw audio data from the rariphotic zone can be assessed on-line (DOI: 10.5281/zenodo.12580170).

The most abundant sound, representing 93.38% (n = 6,982) of all fish sounds detected at 300 m, was a type of ultra-fast pulse series. It had a duration of 141 ± 35 ms (n = 10 for all the measurements) and a dominant frequency of 928 ± 194 Hz (Fig. 2B). It was as a series of 10.6 ± 2.8 pulseswith a pulse period of 13.6 ± 3.4 ms. This sound statistically corresponds to the AS4 sound found in the altiphotic and mesophotic compartment (Raick et al., 2023c)(Table SP2). At these shallower depths, AS4 peaked in occurrence at 7 PM (Raick et al., 2023a, 2023c), which corresponded to the period of high sound production observed at 300 meters. At 300 m, AS4 has a clear diel cycle (GAM, $p < 0.0001$, Fig. 3 & Table SP2), with a primary activity peak between 6 and 9 PM and a smaller peak between 3 and 6 AM. When considering the 5 – 7 PM period at Moorea Island, the AS4 sound type was 15 times more abundant at 300 m (300 m: 3355 h^{-1} *vs*. 120 m: 412 h^{-1}, 60 m: 257 h^{-1}, 20 m: 12 h^{-1}). When considering available data for the entire diel cycle, it was 3.6 times more abundant at 300 m (300 m: 1126 h^{-1} *vs*. 60-120 m: 310 h^{-1}).

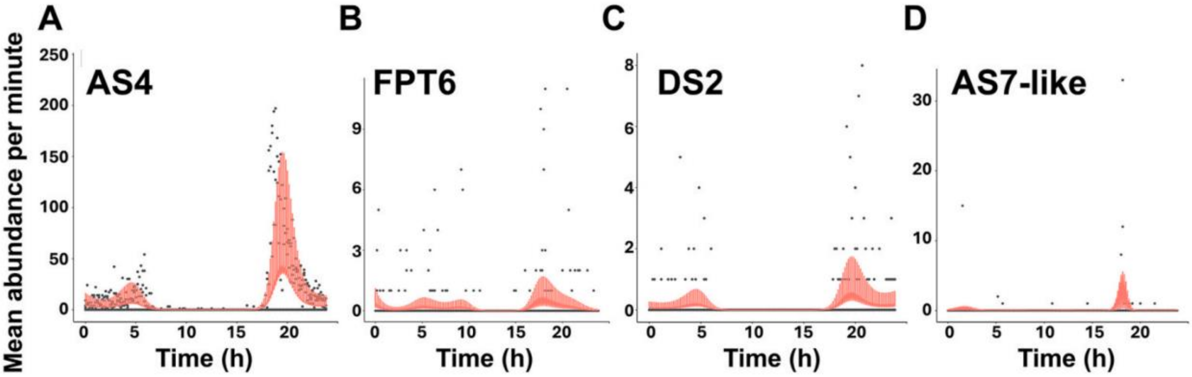

Fig. 3 Average number of sounds at 300 m, for four different sound types, per minute as a function of the time of day. The curve represents the data predicted by the GAM model. The vertical red lines around the curve indicate a 95% confidence interval.

The three next most abundant sound types were FPT6, DS2, and AS7-like. They had total counts of 160, 118, and 91 over the entire investigated period. The second most abundant sound type was a fast pulse train (FPT). It had an average duration of 149 ± 66 ms, composed of 4.7 ± 2.5 pulses with an associated period of 35 ± 9 ms and a dominant frequency of 516 ± 108 Hz (Fig. 2B). This sound corresponded to the FPT6 sound described at lower depths (Raick et al., 2023c) (Table SP2). The highest abundance of this sound occurred at 6 PM (Fig. 3, $p < 0.0001$, Table SP1). When considering the 5 – 7 PM period at Moorea Island, this sound type was 11 times more abundant at 300 m (300 m: 90 h^{-1} vs. 20-60-120 m: 8 h^{-1}). When considering available data for the entire diel cycle, it was 3.2 times more abundant at 300 m (300 m: 26 h^{-1} vs. 60-120 m: 8 h^{-1}).

The third most abundant sound type was a frequency-modulated downsweep. Its characteristics, determined from ten high-SNR sounds, included an average duration of 428 ± 230 ms and a dominant frequency of 690 ± 241 Hz. It consisted of a series of pseudo-harmonics (Fig. 2B) with 20 ± 7 pulses and an associated period of 15 ± 7 ms. This sound was statistically equivalent to the DS2 sound described in shallower waters (Raick et al., 2023c) (Table SP2). Similarly to the observations for AS4, elevated abundance was noted primarily between 7 and 9 PM and secondarily from 3 to 5 AM (Fig. 3, $p < 0.0001$, Table SP1). When considering the 5 – 7 PM period at Moorea Island, this sound type was 11.5 times more abundant at 300 m (300 m: 23 h^{-1} vs. 20-60-120 m: 2 h^{-1}). When considering available data for the entire diel cycle, it was 1.5 times less abundant at 300 m (300 m: 19 h^{-1} vs. 60-120 m: 29.5 h^{-1}).

The fourth most abundant sound type exhibited pseudo-harmonics (Fig. 2B). Its characteristics included an average duration of 104 ± 16 ms, a dominant frequency of 579 ± 35 Hz, and was consisted of 3.6 ± 0.5 pulses separated by pulse intervals of 25 ± 4 ms. Despite similarities to AS7 sounds, statistical analysis revealed significant differences, particularly in the dominant frequency, which was twice as high as that of AS7 sounds ($p = 0.003$, Table SP2). This sound was named ‘AS7-like’. The higher abundance was observed between 5 and 7 PM (Fig. 3, $p < 0.0001$, Table SP1).

3. DISCUSSION

This study represents a significant advancement in the exploration of marine environments using PAM, as it demonstrates the presence of acoustic stratification in fish sounds. Sound diversity decreased with increasing depth. Only 16 distinct sound types were recorded at 300 m, compared to over four times this number near the surface. Furthermore, when both daytime and nighttime are considered, the total number of sounds per hour was significantly higher close to the surface, decreasing with increasing depth. This decline in both sound richness and abundance provided quantitative evidence supporting the hypothesis that fish sounds contribute to the soundscape at depths beyond 300 m, as previously suggested theoretically (Bolgan and Parmentier, 2020).

The transition to greater depths not only corresponded to a decrease in some sound types but also to changes in the relative contribution of the remaining sound types to the soundscape. This is because sounds mainly found in mesophotic reefs (Raick et al. 2023c) and the rariphotic zone (reference: this study) were not the most abundant in altiphotic reefs and vice versa. While the majority of the phenomenon is linked to a significant reduction in existing sound types, it is also important to highlight our discovery of new sound types unique to the rariphotic zone. These new sounds suggest that the animals producing them either do not live shallower or that they only produce these sounds when they are in deeper water. We postulate these three aspects, the decrease in number of fish sound types, the modifications in fish calls contribution, and the appearance of new sound types, reflect changes in the composition of the fish assemblage across the depth gradient. It is also important to highlight that the recordings were not all performed simultaneously, which introduces a temporal aspect to the comparison. The lack of acoustic data from Polynesian MCEs and the rariphotic zone remains a limitation, as only short-term recordings are currently available. Long-term recordings conducted at multiple depths and across several islands for replication would allow us to confirm or refute the observed results and refine our understanding of these ecosystems.

Using acoustic data, a gradual shift in sound composition was observed with increasing depth that aligns closely with recent classical ecological studies (Stefanoudis et al., 2019a). In these studies, it has been shown that depth-related changes in biotopes corresponded to different fish assemblages (Pinheiro et al., 2016; Rosa et al., 2016). While we lack direct data on fish richness and abundance in MCEs and in the rariphotic zone of Moorea Island, our findings align closely with visual observations from other parts of the world such as Bermuda (Stefanoudis et al., 2019a). In Bermuda, the rariphotic zone (150-300 m) has been shown to host a distinct assemblage, with both depth-specialists and depth-generalists observed along the depth gradient axis. A decline in fish abundance with increasing depth is well-documented (Asher et al., 2017; Bejarano et al., 2014; Fukunaga et al., 2016; Pinheiro et al., 2016; Sih et al., 2017; Thresher and Colin, 1986), and a change in species richness along with a decrease in biomass from shallow reefs to depths of 300 m has also been confirmed (Stefanoudis et al., 2019a). This decline can be attributed to the reduced availability of light and its effect on photosynthetic organisms, including those associated with scleractinian corals.

Using PAM, it appears that changes in sound assemblages across depth zones resulted primarily from the disappearance of soniferous species. It allows those that remain (particularly the one producing AS4) to occupy a larger portion of the acoustic space. New sound types seem to show that certain species from the rariphotic zone at Moorea Island are not found in the altiphotic and mesophotic reefs. Previous studies on mesophotic and rariphotic fauna have relied exclusively on visual approaches. Notably, our acoustic approach is similar to these findings in terms of diversity and abundance. It strongly supports the potential of PAM to provide valuable data for monitoring populations and understanding ecosystem ecology. While PAM as deployed here did not offer an exhaustive census of fish species present at different depths, it will serve as a reliable proxy for ecological studies, especially when the fish species involved are identified.

In addition to documenting acoustic stratification, this study aligns with previous studies highlighting diel changes in shallower acoustic communities (Bertucci et al., 2020; Raick et al., 2023a, 2023c; Ruppé et al., 2015; Staaterman et al., 2014). It reveals that specific variations in the biophony at 300 m also occur within a daily period, despite the absence of light at that depth. This is in line with the presence of rhythmic patterns, such as evening choruses, which could act as a circadian time cue in the aphotic zone (Lin and Kawagucci, 2024). Further fieldwork is required to identify the species producing the different sounds detected at our Moorea study site and elsewhere, for example using camera and hydrophone arrays (Mouy et al., 2018) or ROV technology (Rountree et al., 2002). Once this is accomplished, PAM-based monitoring will provide unparalleled opportunities for ecological monitoring and conservation of these fragile tropical systems.

4. METHODS

Data collection

Acoustic data were collected at 20, 60, 120, and ca. 300 m. At 300 m, data were collected over a ten-day period, from July 8 to 17, 2022, at a site on the northern coast of Moorea Island, French Polynesia (17°32'00.0"S 149°34'00.0"W). Data from the other depths were not collected simultaneously but available as open-access resources (10.5281/zenodo.11960305) and originate from previous studies (Raick, 2023; Raick et al., 2023a, 2023c, 2024, 2025a, 2025b). Within these studies, we can distinguish between those analyzing data from Moorea Island during the 5–7 PM period and those analyzing the entire diel cycle in the Tuamotu Archipelago. Data from Moorea Island at depths of 20, 60, and 120 m were collected from September 4 to 7, 2018, while data from the Tuamotu Archipelago were collected at Rangiroa from October 30 to November 2, 2018; at Raroia from March 2 to 5, 2018; and at Tikehau Island from October 15 to 18, 2018.

All the recordings, both at 300 m and those realized shallower, were realized with a SNAP autonomous acoustic recorder (16-bit, + 2 dB gain; Loggerhead Instruments; Sarasota, FL, USA) connected to an HTI96 hydrophone (High Tech Inc.; Long Beach, MS, USA), which has a flat frequency response between 2 Hz and 30 kHz, a ca. −170 dB re 1 V sensitivity. Continuous recording was conducted at a sampling rate of 44.1 kHz. The recorder was attached to an AR701 acoustic release (iXblue, Saint-Germain-en-Laye, France) (Fig. SP1). A 20 kg weight was held by the hook, while a deep-sea buoy capable of withstanding ambient pressure of 29-32 bar was attached to the upper side. The system was retrieved using a TT701 remote control (iXblue, Saint-Germain-en-Laye, France). As seawater is a dense medium that favors long-distance sound propagation, fish sounds can be detected from considerable distances—though still much less so than sounds produced by other taxa, such as cetaceans. This effect is noticeable when considering the total energy within the frequency band associated with fish sounds, but is much less pronounced when focusing on identifiable fish sounds with a high signal-to-noise ratio, as done in this study. This suggests that the majority of fish sounds recorded were produced relatively close to the recorder. The resulting bias is consistent across all studied depths, allowing for valid comparisons.

Analysis

The acoustic analyses were carried out in the Raven software environment (Cornell Lab of Ornithology, Ithaca, NY, USA). Only sounds below 2 kHz that appeared to be emitted by fish were selected. These fish-like sounds are referred to as "fish sounds" throughout the document. Other sounds, such as higher-frequency signals (e.g., invertebrate-like sounds) or sounds within the same frequency range but produced by other taxa (e.g., baleen whale calls and songs), were not considered. No low-frequency sounds resembling those produced by invertebrates (e.g., Stomatopoda rumbles) were found. Fish sounds were analyzed from 4 kHz subsampled files over a 62-hour interval subsample. This duration was consistent with shallower data sampled at 20, 60, and 120 m on the same island (Raick, 2023; Raick et al.,2023a, 2023b, 2023c, 2024). One minute of audio file every ten minutes was used for the manual analysis. The analysis was carried out by a graduate student (M.V.) under the supervision of a bioacoustician (X.R.), who also supervised works at shallower depths. Sounds were classified into sound types using a dichotomous key (Raick et al., 2025a) based on several acoustic parameters, such as dominant frequency, pulse period, presence of harmonics or pseudo-harmonics, and frequency modulation characteristics. A sound type is defined as a category that contains sounds that share similar acoustic features (Raick 2024). The Avisoft SAS Lab Pro program (Avisoft Bioacoustics; Glienicke/Nordbahn, Germany) was used to characterize parameters of the most frequently heard fish sounds. For each of these sounds, the total duration (ms), dominant frequency (Hz), number of pulses, and pulse period (ms) were analyzed. Examples of how our team measure these features on fish sounds with Avisoft SAS Lab Pro can be found in the literature (Parmentier et al., 2017, 2021, 2022; Raick et al., 2020, 2021b, 2022, 2025c).

Statistics

Statistical tests were conducted on four acoustic features of ten fish sounds good signal-to-noise ratio for each sound type: duration (s), dominant frequency (Hz), number of pulses, and pulse period (s). These characteristics were compared to those calculated at 20, 60, and 120 m (Raick et al., 2023c), with the aim of confirming or refuting the hypothesis of similarity of these sounds. For this, data normality was assessed using a Quantile-Quantile plot. If the data distribution was not normal, a Mann–Whitney–Wilcoxon test was performed to test data proximity. If the data distribution was normal, homoscedasticity was tested using Fisher’s test. In cases of equal variances, a Student's t-test was used to measure the mean differences between two groups of sounds based on depth (i.e., one group represented the mean characteristics of sounds at 20, 60, and 120 meters, and the other group represented the characteristics of sounds at 300 meters). If homoscedasticity was rejected, a Welch’s t-test was performed. When results between features differed, the test was performed on the first principal component (PC1) from a Principal Component Analysis (PCA) conducted on the correlation matrix.

For sound types with a minimum daily occurrence of 15 (n = 7,351; 98,32% of all the sounds), diel cycles at 300 m were assessed using Generalized Additive Models (GAMs). GAMs are commonly employed to study activity cycles (Broitman et al., 2001; Irons et al., 2023; Papale et al., 2023), including fish sound production (Raick et al., 2025a). Initially, a GAM with a Poisson distribution was applied to each type of fish sound. Residual dispersion was then calculated. If the dispersion value was below 1.5 (Zuur, 2012), the model was retained; if it exceeded 1.5, the Poisson model was rejected, and a new model with negative binomial regression was performed. The model was retained if the newly calculated residual dispersion was below 1.5 aRaick et al., 2025a). All final models used in this study had a residual dispersion value below 1.5. For models with $R^2 > 0.50$, we calculated the normalized root mean square error (NRMSE, in %) using fivefold cross-validation. All statistical analyses were conducted using R version 4.3.0.

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Author contributions

Conceptualization, X.R and É.P..; methodology, X.R.; software, X.R.; validation, X.R. and É.P.; formal analysis, X.R. and M.V.; investigation, X.R. and M.V.; data curation, X.R.; writing—original draft preparation, X.R., É.P. and M.V.; writing—review and editing, X.R., É.P., and M.V..; visualization, X.R; supervision, X.R. and É.P.; project administration, X.R. Resources, D.L.

Conflict of interest

The authors declare no conflict of interest.

Data availability statement

The data underlying this study are openly available in Zenodo (doi: 10.5281/zenodo.12580170).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.dsr.2025.104548.

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