Depth-dependent dynamics and acoustic niche partitioning of fish sounds in mesophotic coral reefs

Running page head: Depth-dynamics and acoustic niches

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Abstract

According to the acoustic niche hypothesis, the soundscape is a finite resource, theoretically implying that soniferous species whose sounds compose it within a given habitat must share this resource to minimize competition. However, depth-related patterns in this partitioning are still poorly understood. This study aims to compare the diel dynamics and realized acoustic niches of fish sounds at two depths (60 and 120 m) in mesophotic coral reefs of the Tuamotu Archipelago, French Polynesia, over a 62-hour period. Two complementary objectives are pursued: (1) to investigate depth-related patterns in the diel cycle of fish sounds using generalized additive models, and (2) to assess whether their realized acoustic niches change between depths. Although most sound types were shared between 60 and 120 m, the study revealed that the dynamics of fish sounds varied significantly between the two depths. It also supported clear diel patterns. As depth increased, frequency-modulated sounds became more prominent at night, while the opposite trend was observed for pulse series sounds. At the community level, acoustic activity was more concentrated during short time periods at night at 120 m. Different sound types were either produced at distinct times or differed in pulse period range or frequency spectrum during periods of temporal overlap. The structure of realized acoustic niches also differed between the two depths. The consistent increase in the abundance of frequency-modulated sounds under reduced light conditions (both at night and in deeper waters) may reflect the need for more stereotyped acoustic signals, suggesting a potential adaptation to low-light environments.

Keywords

Mesophotic Coral Ecosystems, Passive Acoustic Monitoring, Ecological Niche, Biophony, Acoustic Niche Hypothesis

1. INTRODUCTION

Tropical coral reefs can be divided into two parts based on their depth: a shallow part called the altiphotic reef (ranging from the surface to ~30-40 m deep), from which a deeper part extends, known as mesophotic coral ecosystems (MCEs, ranging from ~30-40 m to over 170 m deep) (Kahng et al. 2017, Baldwin et al. 2018, Rouzé et al. 2021). MCEs represent approximately 80% of habitable space for coral in tropical coral reef ecosystems (Pyle & Copus 2019). In addition to this division mainly based on corals, variations in ichthyological diversity based on depth have been documented (Pyle et al. 2019). MCEs consist of an ‘upper’ zone (from 30 to 60 meters) where ichthyological communities are mainly similar to those of altiphotic reefs (Wagner et al. 2014, Kahng et al. 2017), and a ‘lower’ zone (from 60 to over 150 meters) that often possesses its own fish assemblages (Pinheiro et al. 2016, Kahng et al. 2017), where the overlap zone is an interval between 60 and 90 meters deep within which a shift in faunal community is observable (Pyle et al. 2016, Pinheiro et al. 2016, Baldwin et al. 2018). Finally, the zone just below the lower MCEs is called the rariphotic zone, and these two zones share similarities in terms of ichthyofauna (Baldwin et al. 2018).

Our knowledge of MCEs and their functioning remains limited due to numerous logistical, human, and financial constraints (Kahng et al. 2010, Pyle et al. 2016) resulting in significant gaps in various areas, particularly in ecology (Pyle & Copus 2019). Today, advancements in underwater technology enable the study of MCEs through less invasive methods (Armstrong et al. 2019) and acoustic approaches have been developed to study the ichthyological communities of these ecosystems (Raick et al. 2023a, 2023c).

Passive Acoustic Monitoring (PAM) is a technique used to non-intrusively, and with high temporal resolution, collect various types of sounds (e.g., biological and anthropogenic sounds) that are useful for inferring ecological conditions (Luczkovich et al. 2008, Mooney et al. 2020) by focusing on soniferous species. Across marine realms, PAM can be used to study a specific species (Picciulin et al. 2013, Bertucci et al. 2015, Higgs & Humphrey 2020, Darras et al. 2025), a group of species (Wall et al. 2013, Di Iorio et al. 2018), or to approach the study of the entire soniferous fish community living in a particular location (Staaterman et al. 2014, Ruppé et al. 2015, Bertucci et al. 2020, Raick et al. 2021a, 2023c, Minier et al. 2023, Raick 2024, 2025). Given that species-specific sounds produced intentionally are widely recognized in fish (Crawford et al. 1997, Kihslinger & Klimley 2002, Lamml & Kramer 2006, Raick et al. 2020, 2021b, 2023b). Studies using PAM often operate under the assumption that each sound identified as a fish sound corresponds to a specific species. While we follow this approach for the purposes of our analysis, we do so with caution, acknowledging that some fish species are known to produce a variety of sound types (Dos Santos et al. 2000, Amorim et al. 2008, Amorim & Vasconcelos 2008, Parmentier et al. 2010, 2022, Kéver et al. 2014, Raick 2015), which may complicate species-level attribution.

The detection of various types of sounds within a given soundscape shows that the related ecosystem should harbor numerous species of sound-producing fish. These species must have developed diverse strategies to communicate effectively and avoid cacophony (Thorson & Fine, 2002; Ruppé et al. 2015). However, fish can adopt different strategies to cope with this. First, the ‘Lombard effect’ is a strategy in which producers increase the intensity of their emitted sounds to enhance reception by the receiver and avoid masking effects caused by background noise (Lombard 1911, Brumm & Slabbekoorn 2005, Holt & Johnston 2014). This effect is known but poorly documented in fish (Brown et al. 2021). A second strategy involves producing sounds at different times of the day or at different frequencies. Although fish acoustic activity is often higher at specific periods such as dusk and night (Connaughton & Taylor 1995, Locascio & Mann 2011, Wall et al. 2013, Carriço et al. 2020), not all vocalizations are produced at the same time within one site (Ruppé et al. 2015, Bertucci et al. 2020). Indeed, some species vocalize more during the day (Wall et al. 2012, Staaterman et al. 2013), others vocalize both during the day and at night (Nelson et al. 2011, Bertucci et al. 2020), and some vocalize primarily at night (McCauley & Cato 2000, Staaterman et al. 2014). Further subdivisions of each part of the day may exist, with some species producing sounds only for a few hours (Bertucci et al. 2020, Bolgan et al. 2022). This time partitioning within a community aims to decrease competition for acoustic resources and prevent misidentification between different species in challenging conditions due to a cacophony masking emitted signals (Farina 2014, Ruppé et al. 2015) and impairs reception. Different species' utilization of acoustic resources in a mature ecosystem is the foundation of the acoustic niche hypothesis (ANH) (Krause 1993).

The acoustic niche is one of the subsets of the ecological niche and can be defined as a multidimensional abstraction encompassing spectral and temporal features of a sound type, as well as its diel pattern of occurrence while the 'realized acoustic niche' can be defined as 'the range of acoustic resources effectively exploited by a specific sound type along at least three axes: diel timing of calling activity, call spectral features and call temporal features' (Bolgan et al. 2022) observed at a specific moment and location. The realized acoustic niche is always a subset of the acoustic niche and is the result of both biotic and abiotic constraints on the acoustic niche. The ANH has been demonstrated in birds (Popp et al. 1985, Chitnis et al. 2020, Hart et al. 2021), frogs (Duellman & Pyles 1983, Sinsch et al. 2012, Allen-Ankins & Schwarzkopf 2021), and arthropods (Sueur 2002, Henry & Wells 2010). Regarding marine ichthyofauna, it is known that fish sounds do not occupy the same temporal periods (Ruppé et al. 2015, Bertucci et al. 2020) and can be partitioned into nocturnal and diurnal acoustic communities (Ruppé et al. 2015) (i.e., temporal aggregation of species acoustically interacting (Schafer 1977, Gasc et al. 2013)). Additionally, within the nocturnal acoustic community, which is typically more diverse than the diurnal one (Ruppé et al. 2015, Bertucci et al. 2020), the sounds show less overlap in many acoustic characteristics (e.g., peak frequency and pulse period) (Ruppé et al. 2015). In marine temperate ecosystems, the allocation of acoustic resources (both temporal and frequency ranges) increases when acoustic richness increases (Bolgan et al. 2022). Unfortunately, studies on how an entire ichthyological community occupies the soundscape in coral reefs are relatively few (Staaterman et al. 2014, Bertucci et al. 2020, Wilson et al. 2020), and our knowledge on this topic in MCEs is extremely limited (Raick et al. 2023a c).

However, a recent study focusing on the biophony of MCEs in French Polynesia showed that the composition of acoustic communities varied with depth since differences in the relative proportions of sound types were found (Raick et al. 2023c). Pulse series (PS) sounds were dominant in the altiphotic zone, while frequency-modulated (FM) sounds were more abundant in the lower mesophotic zone (Raick et al. 2023c). Regarding the temporal distribution of fish sounds in MCEs, a second study focusing on the two most abundant FM sounds in the MCEs of French Polynesia showed a higher presence of these sounds during the night (Raick et al. 2023a). However, how the entire fish community shares the soundscape along the diel cycle within MCEs has never been studied.

The objective of this research is to explore depth-related differences in the diel cycle and realized acoustic niches of fish sounds in MCEs in the Tuamotu archipelago (French Polynesia). Specifically, two lines of investigation were pursued. (*1*) Assessing how depth shapes the diel cycle of fish sounds in the upper (60 m) and lower (120 m) parts of the MCEs. (*2*) Analyzing the realized acoustic niche of the most abundant sound types at both depths.

2. MATERIALS AND METHODS

2.1. Sampling

The acoustic data collection was conducted between March and November 2018 at three atolls in the Tuamotu Archipelago (French Polynesia): Rangiroa (30th October – 2nd November), Raroia (2nd – 5th March), and Tikehau (15 – 18th October, Fig. 1, Table A.1). The acoustic similarity among the three islands was assessed in a previous study by Raick et al. (2023c).

During fieldwork, sunrise was between 5:50 and 6:09 AM and sunset was between 5:21 and 5:43 PM (https://www.sunrise-and-sunset.com). Sampling was carried out as part of the Under The Pole III expedition (https://underthepole.org) by professional divers using closed-circuit rebreathers. On each atoll, recordings were conducted simultaneously at depths of 60 m and 120 m along the outer slope as detailed in Raick et al. (2023). At each depth, a SNAP autonomous acoustic recorder (Loggerhead Instruments; Sarasota, FL, USA) connected to an HTI96 hydrophone (sensitivity ranging from −170.5 to −169 dB re 1 V for an acoustic pressure of 1 µPa, flat frequency response from 2 Hz to 30 kHz) was deployed. The recorders were vertically mounted on a 60 cm tripod, weighted down with 4 kg, and placed on the seafloor. All recorders were programmed to capture 1-minute recordings every 10 minutes over a 62-hour period, with a sampling frequency of 44.1 kHz (16-bit resolution) and a gain of +2.05 dB. While a longer sampling period would have strengthened this study, it leverages a unique dataset recorded in a remote region, making it an ideal exploratory proof-of-concept study.

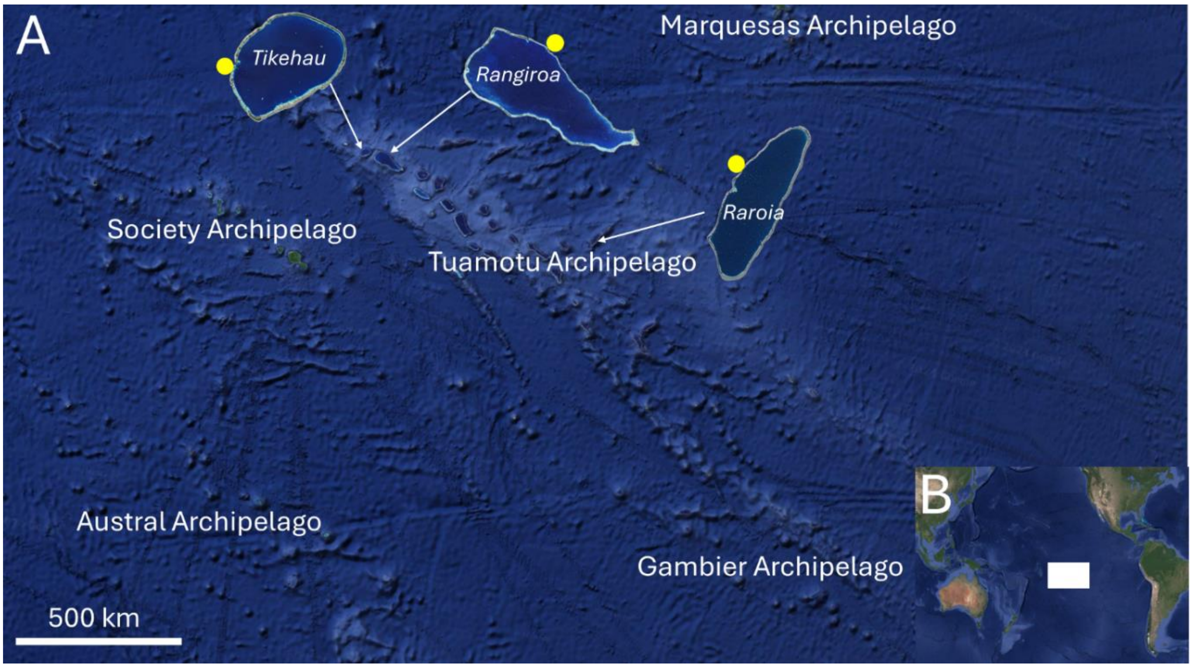

Figure 1. (A) Location of sampling sites with zoomed-in views of the three studied islands and (B) location of French Polynesia in the Pacific Ocean. Yellow dots indicate sampling sites. The white rectangle outlines French Polynesia. Images from SIO, NOAA, U.S. Navy, NGA, GEBCO 2021, Maxar Technologies, LDEO-Columbia, NSF, NOAA 2021, CNES / Airbus.

2.2. Data analysis

The audio files were downsampled to 4 kHz to assess fish sounds (Raick et al. 2021, 2023b, 2023c). The audio files (totaling 37.2 hours) were visually and audibly inspected using the acoustic analysis software Raven Pro 1.5. (Cornell Lab of Ornithology; Ithaca, NY, USA). The audio files contained recordings from three nights and two days. Fish sounds were classified into categories referred to as 'sound types' (Fig. 2 and 3) using a dichotomous key adapted from a pre-existing key from Raick et al. (2023c) (Fig. A.1 and Key A.1). A sound type incorporates sounds with similar acoustic characteristics, such as peak frequency or pulse period, and can be produced either by a single species (Amorim & Hawkins 2000) or can contain sounds from multiple related species (Di Iorio et al. 2018, Mélotte et al. 2019, Raick et al. 2022), i.e., species using similar soniferous mechanisms. Only sound types with at least ten occurrences were used for analysis, resulting in a total of 52,255 sounds classified into 69 different fish sound types and grouped into three broad sound categories referred to as ‘acoustic categories’ (Fig. A.1): pulse series (PS), frequency modulations (FM), and arched sounds (AS, grouping non-FM tonal calls and ultra-fast pulse series with pulses too closely spaced to be perceived as PS) as described in Raick et al. (2023c). FM can be subdivided into upsweeps (FM_{US}), downsweeps (FM_{DS}), and complex sounds (i.e., sounds with both upsweeping and downsweeping parts, FM_{CS}).

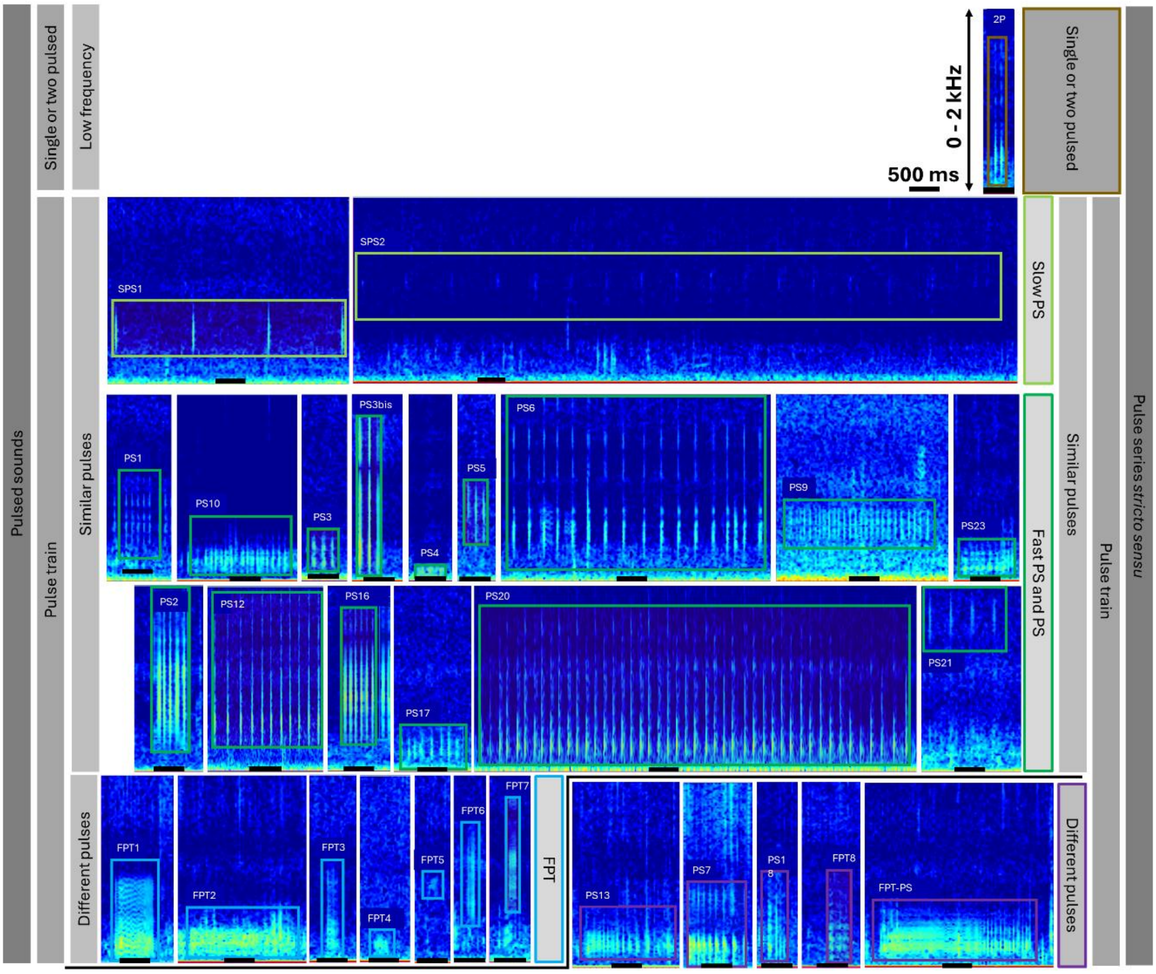

Figure 2. Diversity of fish sounds in Polynesian mesophotic reefs. The classification on the right of the figure is adapted from (Raick et al. 2023c) and the one on the left from (Puebla-Aparicio et al. 2024). Sampling frequency: 4 kHz. FFT = 256. PS = pulse series, FPT = fast pulse train. DS = downsweeping sound. US = upsweeping sound. CS = complex sound. UFPS = ultra-fast pulse series. The structure of the figure is inspired by (Puebla-Aparicio et al. 2024) (Fig. 3). ‘kwa-like’ sounds are a sub-category of ‘arched sounds’ also named ‘non-FM tonal sounds and UFPS. In the spectrograms, the hotter the color, the more intense the sounds are (no calibration was performed on Raven).

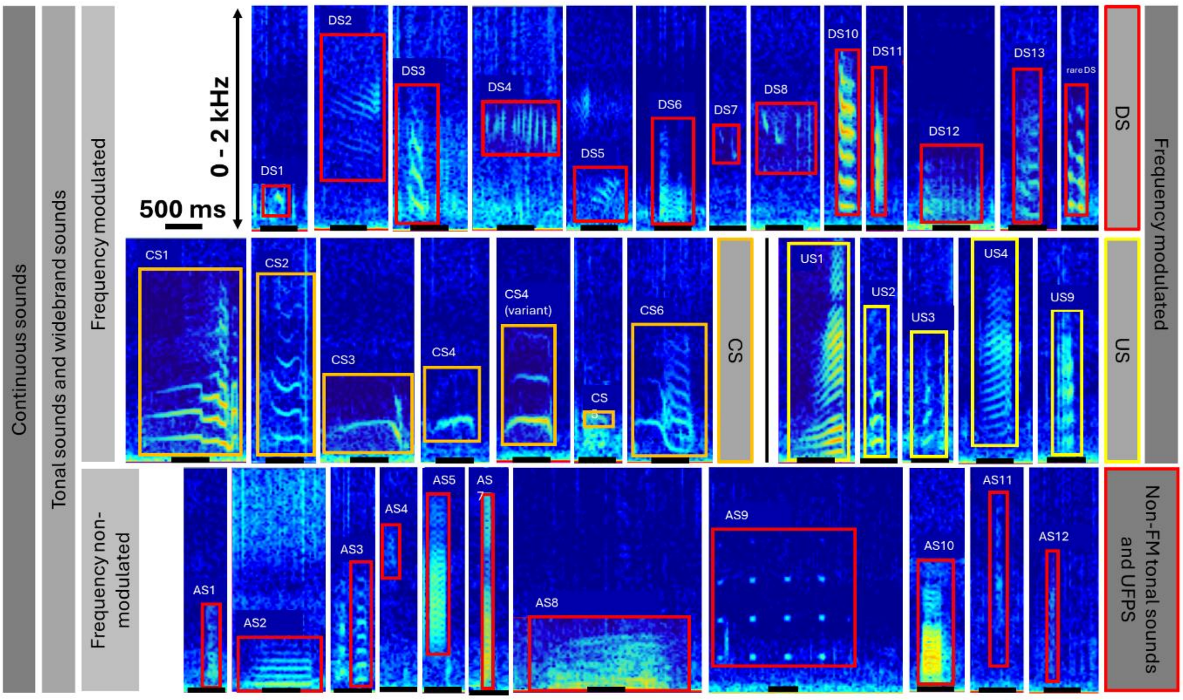

Figure 3. (continuation of Figure 2) Diversity of fish sounds in Polynesian mesophotic reefs. The classification on the right of the figure is adapted from (Raick et al. 2023c) and the one on the left from (Puebla-Aparicio et al. 2024). Sampling frequency: 4 kHz. FFT = 256. PS = pulse series, FPT = fast pulse train. DS = downsweeping sound. US = upsweeping sound. CS = complex sound. UFPS = ultra-fast pulse series. The structure of the figure is inspired by (Puebla-Aparicio et al. 2024) (Fig. 3). ‘kwa-like’ sounds are a sub-category of ‘arched sounds’ also named ‘non-FM tonal sounds and UFPS. In the spectrograms, the hotter the color, the more intense the sounds are (no calibration was performed on Raven).

All the sound types were used to examine the diel pattern of sound activity for the entire acoustic community. In contrast, for the diel cycle of each sound type and the niches analyses, we specifically focused on sound types with a total minimum of 1,000 occurrences. Of all the sound types detected in the MCEs of the three atolls, 13 met this criterion. These 13 types comprised a total of 42,578 sounds, representing ca. 80% of the total sounds detected. Among the 13 types, there were three AS (AS4, AS5, and AS1), seven PS (PS3, PS17, PS16, PS18, FPT1, FPT2, and FPT4), and three FM sound types: one FM_{CS} (CS1), one FM_{DS} (DS2), and one FM_{US} (US1). Among these 13 sound types, 12 had already been described (Raick et al. 2023c). The thirteenth sound type, named PS18, is an undescribed sound type composed of two distinct parts separated by a time interval. The first part consists of a single pulse with multiple peaks, while the second part is a series of regular pulses (i.e., constant pulse period) with a single peak. A detailed description of ten sounds with a good signal-to-noise ratio that allowed for the characterization of sound types was carried out for each of the 13 sound types. The pulse period (i.e., the period between consecutive pulses) was measured on oscillograms with Avisoft SAS Lab Pro (Avisoft Bioacoustics; Glienicke/Nordbahn, Germany). This feature was needed for the realized acoustic niche analysis, and it was not automatically measured by Raven.

2.3.Statistical analyses

To address the two objectives of this study, the analyses were divided into the study of the depth effect on (1) the diel cycle, and (2) realized acoustic niches. All statistical analyses were conducted using R software version 4.2.1 (R Core Team, 2022), and a significance level of $\alpha = 0.05$ was used.

2.3.1. Diel cycle

Raw abundance data of each sound type was converted into abundance per minute (number per min). For each depth studied, a cumulative graph of abundance per minute over time was generated for all sound types. To enhance visualization of rarer sound types, in addition to the graph of original values on a linear scale, graphs of relative values and the logarithm of abundance were employed. These graphs were useful to visualize the diel occurrence of all the sound types together.

Generalized Additive Models (GAMs) were used to assess the presence of temporal trends. GAMs are commonly used to study diel cycles (Adlerstein & Welleman 2000, Buscaino et al. 2020). The *gam* function from the *mcgv* package was used to create a model for the 13 most common sound types. For each model, we only used data with a minimum of 30 sounds per depth per island. The model predicted the abundance of sounds based on the spline of time by depth, the depth itself, and the island (site). Poisson distributions were initially used for all the models (Bischof et al. 2014). Subsequently, the dispersion of residuals was computed using the model's residuals, the number of observations, and the number of predictors in the model. When the dispersion of residuals was below 1.5 (Zuur 2012), the Poisson model was retained. When the residuals indicated overdispersion, the same model was employed, but with a negative binomial distribution. Thus, all final models exhibited appropriate residual dispersion (minimum value obtained: 0.59, maximum value obtained: 1.23). The relationship between predictors and the dependent variable (i.e., the abundance per minute of each sound type) is described in part through the effective degrees of freedom (edf), which estimate the 'complexity' of each smooth term (spline). An edf value close to 1 implies a linear relationship, while a higher value indicates a non-linear relationship (complex and undulating curve). Finally, the model-predicted values along with a 95% confidence interval were exponentiated (due to the log link used in the model) and presented alongside the original abundance data (Wood 2017).

2.3.2. Realized acoustic niches

We examined the partitioning of acoustic resources within fish communities across three key axes, commonly referred to as ‘niche dimensions’ in ecological studies: (1) the period of acoustic activity (time), (2) the peak frequency, and (3) the pulse period (Bolgan et al. 2022). These features were selected as they are relevant for fish and relatively stable in their environment. Duration has not been used, as it does not seem relevant for fish niche assessment. For fish, it could simply be the same train of pulses with just more pulses. Duration has still a meaning as male capable of emitting more pulses may be more attractive especially if they do it over long periods –duration is a sexual selection trait in animal acoustics–(Brumm et al. 2004). However, in terms of the utilization of the acoustic space, it does not appear as a differentiation axis. Then, in marine coastal environments, bandwidth is not stable with distance, making it currently unsuitable for niche assessments in fish.

The realized acoustic niche was studied for each of the two depths, focusing on the 13 most abundant sound types. Because only two days of data were available for each island and for each depth for daytime, only two nighttime periods out of three were used. The excluded night was always the first one. For each axis (diel acoustic activity, frequency, and pulse period), we determined the range of acoustic resources (i.e., utilized resources classes, (Bolgan et al. 2022)). Each hour of the day represented a temporal resource. Concerning the frequency resources classes, we first measured the minimum and the maximum peak frequency of all the fish sounds, respectively 15 and 1815 Hz. Then, we divided this range in 100 Hz intervals, obtaining 18 resource classes. The number of resources for pulse period was obtained by dividing the range of pulse periods (i.e., the difference between maximum and minimum periods duration) by the range of each class (logarithmic scale 0.1 ms classes ranging from 0.1 to 2.9 ms). The peak frequency was automatically measured in Raven. The pulse period data for each regular sound type (all types except PS18) were estimated by dividing the total sound duration (automatically measured in Raven) by the average number of pulses for pulse series, or by the average number of consecutive peaks for more tonal or FM sounds according to Bolgan et al. (2022), (manually measured in Avisoft). Because of its irregularity, only the regular part of the PS18 was considered for the measurement.

The number of acoustic resource classes used varied based on the three axes: 24 for the temporal axis (axis I), 18 for the frequency axis (axis II), and 28 classes for the pulse period axis (axis III). The sizes of each resource class (1 h, 100 Hz, and 0.1 ms respectively for axes I, II, and III) were identical to those of Bolgan et al. (2022).

The data for each axis was organized into a resource matrix, where each row represented a sound type and each column represented a resource class. For each sound type and resource axis, the relative percentage of the number of sounds belonging to each resource class was displayed with a color scale. Furthermore, the acoustic community space (i.e., the range of acoustic resources exploited by the entire acoustic community) was calculated by summing all sound types present in each resource class across the three axes (Bolgan et al. 2022). Finally, the realized acoustic niche breadth (NB), measuring the level of resource class occupation, was calculated using the inverse of the Simpson diversity index (using the *diversity* function from the *vegan* package) and standardized (NB*) as follows: NB* = (NB – 1) / (r – 1), where r is the number of resource classes. When NB* is equal to zero, the sound type is considered a specialist meaning it only exploits one resource class, while when NB* is equal to 1, the sound type exploits all resource classes (Colwell & Futuyma 1971, Sinsch et al. 2012). The standardized realized acoustic niche breadth for each sound type was calculated separately for each niche axis (NB_{temp}* = standardized realized acoustic niche breadth for the temporal axis; NB_{freq}* = standardized realized acoustic niche breadth for the frequency axis; NB_{pp}* = standardized realized acoustic niche breadth for the pulse period axis), as well as for the overall realized acoustic niche (NB_{tot}*). For each axis, the overlap between each pair of sound types was calculated using the *overlapEst* function from the *overlap* package. The minimum overlap value among the three calculated axes was then determined.

3. RESULTS

3.1. Diel cycle

When examining all the sound types together, a general trend was observed with abundance generally peaking after sunset and/or before sunrise (see Fig. 2 & Fig. 3 for the sound types and Fig. 4 for the diel patterns). Regardless of the depth, the abundance of fish sounds gradually increased at sunset (Fig. 4, Fig. 5, Table A.2, Fig. A2, and Fig. A.4) with a shift from a ‘diurnal acoustic community’ dominated by PS sound types to an ‘early nocturnal acoustic community’ dominated by AS4 (27% AS increase at 120 m, 23% AS increase at 60 m between 5:40 and 5:50 PM). Subsequently, this acoustic activity decreased, marking the transition to a ‘late nocturnal community’ which started later at 120 m than at 60 m and characterized by an increase in FM_{CS} sound types such as CS1.

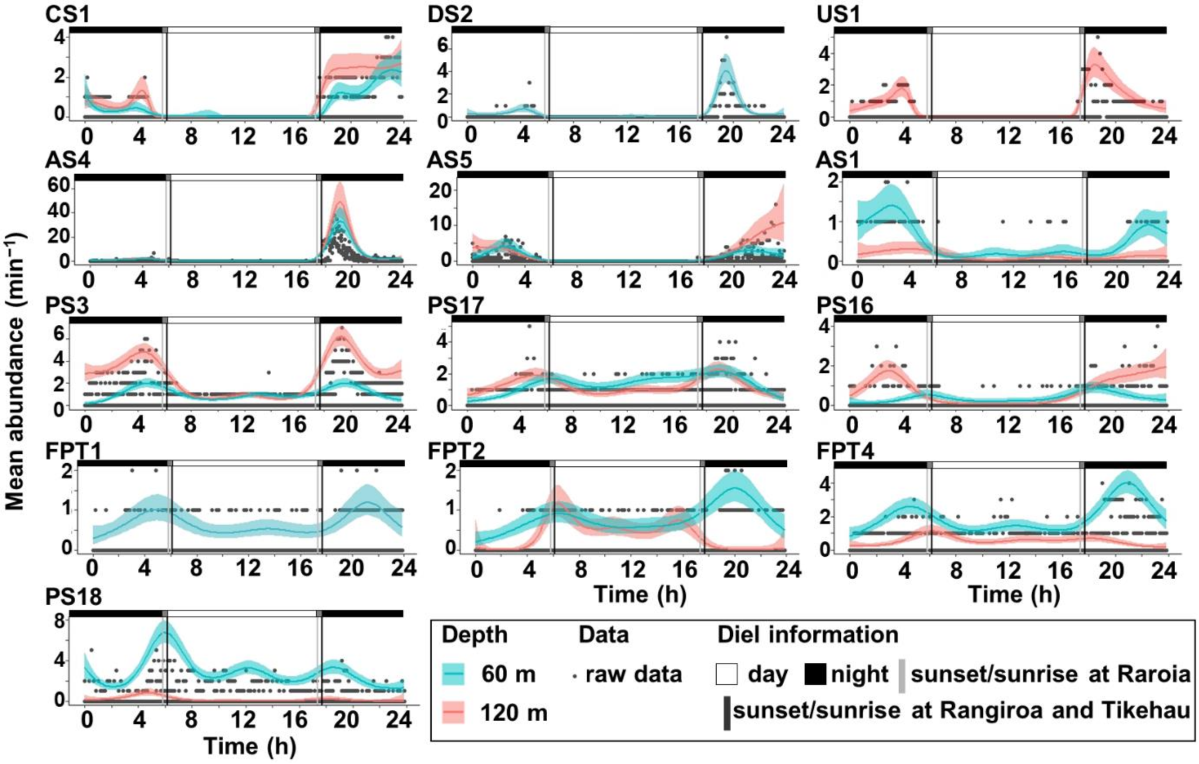

Figure 4. Temporal variations in sound type abundance for the 13 most abundant sound types. Predicted values from GAM models depicted by curves, with blue curves representing 60 m depth and red curves representing 120 m depth. Each curve is accompanied by a band illustrating the corresponding 95% confidence interval. Dots signify raw data points. Vertical grey lines denote sunrise and sunset at Raroia (5:50 AM and 5:21 PM), while vertical black lines denote sunrise and sunset at Tikehau and Rangiroa (6:09 AM and 5:43 PM).

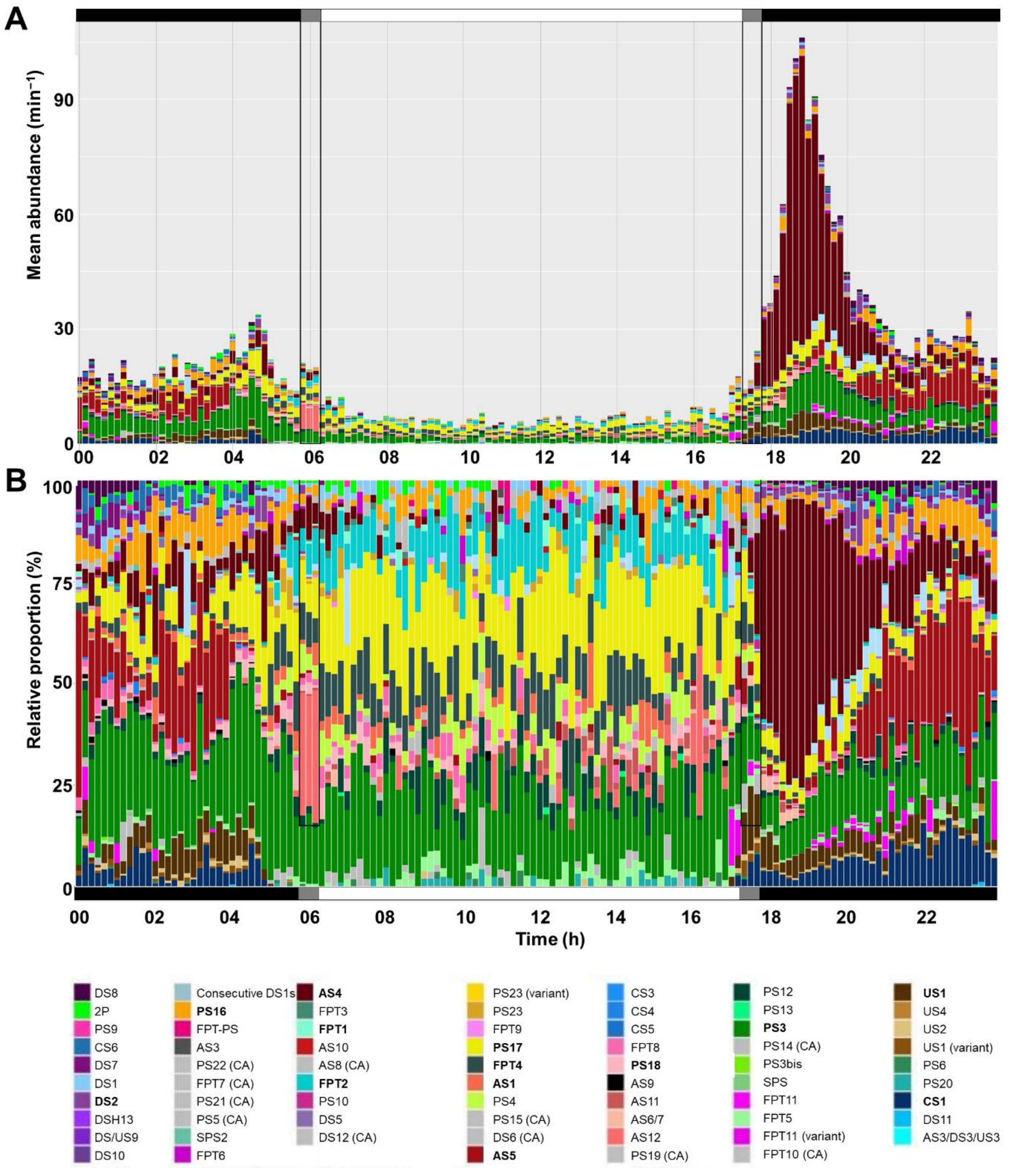

Figure 5. Cumulative graph of abundance over time for all sound types at 120 m depth: absolute values (A) and relative proportion (B). Less abundant sound types lacking a clear diel cycle are colored in grey for ease of interpretation. The legend includes the annotation 'CA' (Cycle Absent) for such sounds. The 13 most abundant sound types, utilized in the models, are highlighted in bold.

During sunrise, there was a second increase in the abundance of PS sound types to a level almost as high as their first peak. This second abundance peak was reached an hour earlier at 120 m and was equal to the first one. Following sunrise, the abundance of PS sound types gradually returned to daytime values. The abundance and relative proportion of PS sound types during the daytime was lower at 120 m. Conversely, the predominance of FM sound types at night and during sunset was more pronounced at greater depth.

The GAM models applied to the 13 most abundant sound types demonstrated a significant influence of the time of day on the abundance of all studied sound types at both depths (all $P < 0.001$; Fig. 4 and Table 1). Eleven out of 13 sound types could be characterized as nocturnal (i.e., with an abundance peak between 7 PM and 5:59 AM). Among them, some such as AS4, are part of an early nocturnal community (5:50 PM – 8:30 PM), while others such as AS5 are part of a later nocturnal acoustic community (7:40 PM – 5:40 AM, Fig. 5 and Fig. A.2). Other sound types, such as PS3 and PS17 have one abundance peak before 7:40 PM and another during the second half of the night (Fig. 4 and Table 2), placing them in both the early and late nocturnal acoustic communities at both depths.

Table 1 Summary of GAM model results for the 13 most abundant sound types. '/' = insufficient number of sounds to perform the model. Edf = effective degrees of freedom. GAM = Generalized additive model. NB = Negative binomial.

	GAM Model	**Adjusted R^2**	**Edf**		**P-value**		**Dispersion of residuals**	**N**
			60 m	**120 m**	**60 m**	**120 m**		
AS4	NB	0.75	8.70	8.63	< 0.001	< 0.001	0.77	11550
AS5	NB	0.09	6.90	6.63	< 0.001	< 0.001	0.59	4067
AS1	Poisson	0.42	8.42	7.02	< 0.001	0.00069	0.65	1039
PS3	Poisson	0.64	8.10	9.00	< 0.001	< 0.001	1.23	6168
PS17	Poisson	0.47	7.29	8.12	< 0.001	< 0.001	1.085	4446
PS16	Poisson	0.20	7.35	7.32	< 0.001	< 0.001	1.19	1665
PS18	Poisson	0.64	8.98	6.90	< 0.001	< 0.001	1.16	2967
FPT1	Poisson	0.40	7.40	/	< 0.001	/	0.82	1352
FPT2	Poisson	0.30	6.30	8.48	< 0.001	< 0.001	0.83	1599
FPT4	Poisson	0.55	7.80	7.58	< 0.001	< 0.001	1.12	3563
CS1	Poisson	0.40	8.89	8.88	< 0.001	< 0.001	1.05	1883
DS2	Poisson	0.62	8.74	/	< 0.001	/	0.68	1098
US1	Poisson	0.48	/	8.45	/	< 0.001	0.86	1181

Table 2 Mean abundance per minute predicted by the GAM models for the 13 most abundant sound types. '-' = no peak abundance detected. '/' = insufficient number of sounds to perform the model.

Sound type	**Depth (m)**	**Time of peak 1**	**Corresponding abundance**	**Time of peak 2**	**Corresponding abundance**
AS4	60	7:10 PM	33.15	-	-
AS5	60	9:10 PM	2.95	02:30 AM	4.14
AS1	60	10:20 PM	0.92	02:40 AM	1.40
PS3	60	7:30 PM	2	04:40 AM	2
PS17	60	7:00 PM	2.13	06:20 AM	1.68
PS16	60	06:30 PM	0.86	05:40 AM	0.54
PS18	60	06:30 PM	3.31	06:00 AM	6.75
FPT1	60	09:10 PM	1.20	05:00 AM	1.02
FPT2	60	08:00 PM	1.55	06:30 AM	0.92
FPT4	60	08:40 PM	4.01	04:30 AM	2.60
CS1	60	11:10 PM	2.35	03:50 AM	0.44
DS2	60	07:30 PM	4.01	04:10 AM	0.70
US1	60	/	/	/	/
AS4	120	07:00 PM	48.8	-	-
AS5	120	11:50 PM	10.92	01:10 AM	3.84
AS1	120	-	-	04:00 AM	0.30
PS3	120	07:20 PM	6.16	04:20 AM	4.81
PS17	120	06:40 PM	2.30	05:10 AM	1.90
PS16	120	11:50 PM	2	02:40 AM	1.76
PS18	120	-	-	04:40 AM	0.80
FPT1	120	/	/	/	/
FPT2	120	03:40 PM	0.75	06:20 AM	1.17
FPT4	120	-	-	06:10 AM	1.14
CS1	120	11:50 PM	2.70	04:20 AM	1.34
DS2	120	/	/	/	/
US1	120	06:30 PM	3.3	4:00 AM	1.78

The abundance of PS sound types was higher at 60 m than at 120 m during the later nocturnal acoustic community: 15.32 ± 4.72 PS sounds min^{-1} at 60 m (measured between 7:40 PM and midnight, mean ± standard deviation) vs.10.32 ± 3.12 PS sounds min^{-1} at 120 m (measured between 8:30 PM and midnight; Fig. 5 and Fig. A.2). At 120 m, the two most abundant sound types during the daytime were PS17 and PS3 (Fig. 5) while the three most abundant PS at 60 m are PS18, PS17, and FPT4 (Fig. A.2). This indicates that some sound types such as PS18 were associated with one depth (Fig. 4 and Table 2). Additionally, some PS exhibit abundance peaks at different times depending on the depth (Fig. 4 and Table 2). PS16 is part of the early nocturnal community at 60 m and the late nocturnal community at 120 m. In contrast, FPT2 is nocturnal at 120 m, and more diurnal at 60 m (Fig. 4 and Table 2).

3.2. Realized acoustic niches

3.2.1. Composition of the realized acoustic niches

The 13 most abundant sound types were differentiated along (at least) one of the three axes of their realized acoustic niche [overlap ≤ 0.5 for 76 out of 78 pairwise comparisons, with exceptions for PS18 vs. AS1 (minimum overlap = 0.61) and CS1 vs. PS17 (minimum overlap = 0.53)]. AS sound types differentiated well along both the temporal axis (Axis I) and the frequency axis (Axis II) but exhibited comparable pulse periods (Fig. 6, Fig. 7, and Fig. A3). This was true for both 60 m and 120 m depths (Fig. 7). Among PS at 60 m, PS18, FPT1, and FPT4 sound types exhibited different activity periods (Axis I) than other PS types, while at 120 m, only FPT2 and FPT4 types differed in their temporal axis (Fig. A3 and Fig. 7).

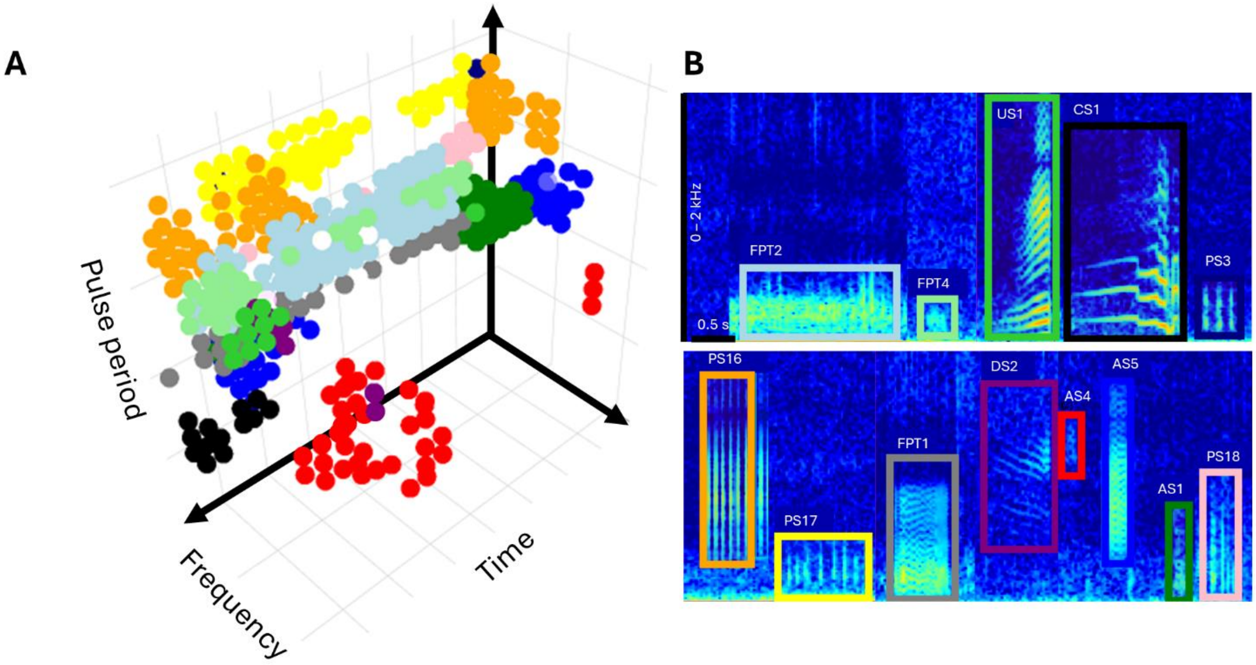

Figure 6. (A) Realized acoustic niche analysis of the 13 most abundant sound types (diel: 24 resource classes; frequency: 18 resource classes; pulse period: 18 resource classes). Data for each axis were organized in a resource matrix, where each row represented a sound type and each column a resource class. For each sound type and resource axis, the number of sounds associated with each resource class was calculated and values above 50% are represented as spheres on the graph. Each color corresponds to a different sound type. (B) Schematical representation of the spectrograms of the 13 most abundant sound types with the corresponding color code (FFT = 256, sampling frequency = 4 kHz). In the spectrograms, the hotter the color, the more intense the sounds are (no calibration was performed on Raven).

Unlike AS, PS exhibited similar frequency spectrum usage at both depths, except for PS16. At 120 m, PS16 had higher peak frequencies more prominently (Fig. A.3 and Fig. 7). PS primarily differentiated based on their pulse period (Axis III), regardless of depth (Fig. A.3 and Fig. 7). Concerning FM, CS1 sound type was temporally distinct from the other two FM sound types which had more similar acoustic activity and pulse periods (Axis I and Axis III, respectively). However, this temporal resource competition was offset at the frequency level. Specifically, the DS2 sound type distinguished itself from the other two FM sound types by a different frequency spectrum exploitation.

3.2.2. Comparison of the width of the realized acoustic niches

The realized acoustic niche breadth, and therefore the ‘specialization’ of the sound types, varied by sound type and depth. The 13 sound types occupy distinct realized acoustic niches. The overall realized acoustic niche breadth of the AS4 type was narrower than that of the other two AS sound types (AS5 and AS1), which had more similar overall realized acoustic niche breadths (Table 3). This was due to AS4 having a narrower realized temporal niche than AS1 and AS5 at both depths (Table 3). However, a comparison of the two depths revealed that the realized niche breadths for frequency resources decreased with depth for all AS sound types (Table 3). AS occupy fewer resource classes and exhibit frequency-based specialization at depth.

Table 3 Width of the realized acoustic niches for each sound type. $NB_{temp}*$ = standardized niche breadth for the temporal axis; $NB_{freq}*$ = standardized niche breadth for the frequency axis; $NB_{pp}*$ = standardized niche breadth for the pulse period axis; and $NB_{tot}*$ = overall standardized niche breadth.

	NBtemp*		**NBfreq***		**NBpp***		**NBtot***	
	60 m	**120 m**	**60 m**	**120 m**	**60 m**	**120 m**	**60 m**	**120 m**
AS4	0.14	0.12	0.21	0.16	0.12	0.11	0.17	0.15
AS5	0.30	0.30	0.41	0.29	0.11	0.09	0.26	0.23
AS1	0.58	0.56	0.18	0.14	0.12	0.14	0.30	0.30
PS3	0.64	0.44	0.11	0.13	0.10	0.07	0.30	0.22
PS17	0.72	0.65	0.13	0.15	0.17	0.17	0.37	0.33
PS16	0.63	0.50	0.22	0.40	0.20	0.27	0.36	0.40
PS18	0.67	0.58	0.07	0.11	0.15	0.15	0.33	0.30
FPT1	0.77	0.71	0.12	0.22	0.17	0.12	0.38	0.36
FPT2	0.73	0.54	0.13	0.10	0.19	0.25	0.37	0.33
FPT4	0.60	0.68	0.16	0.18	0.08	0.08	0.29	0.34
DS2	0.13	0.30	0.38	0.35	0.15	0.16	0.22	0.28
US1	0.33	0.37	0.11	0.09	0.10	0.14	0.20	0.23
CS1	0.27	0.34	0.13	0.12	0.13	0.11	0.20	0.22
Community level	0.40	0.32	0.31	0.43	0.41	0.40	0.38	0.40

The overall realized acoustic niche breadths were similar for most PS types at both depths (Table 3). However, two out of the seven PS sound types exhibited different realized acoustic niche breadths along specific axes at certain depths. PS3 is a distinctive PS type. Its overall realized acoustic niche breadth at 120 m was narrower than the average width of all PS types ($NB_{tot}*$ = 0.22 vs 0.33 ± 0.06). This trend was less evident at 60 m ($NB_{tot}*$ = 0.30 vs 0.34 ± 0.036). Furthermore, its realized acoustic niche breadth along the temporal axis at 120 m was narrower compared to 60 m (Fig. 8, Table 3). This suggests that the PS3 type is more ‘specialized’ and exhibits more focused acoustic activity at 120 m compared to 60 m, where its activity is more spread out over time (Fig. 7).

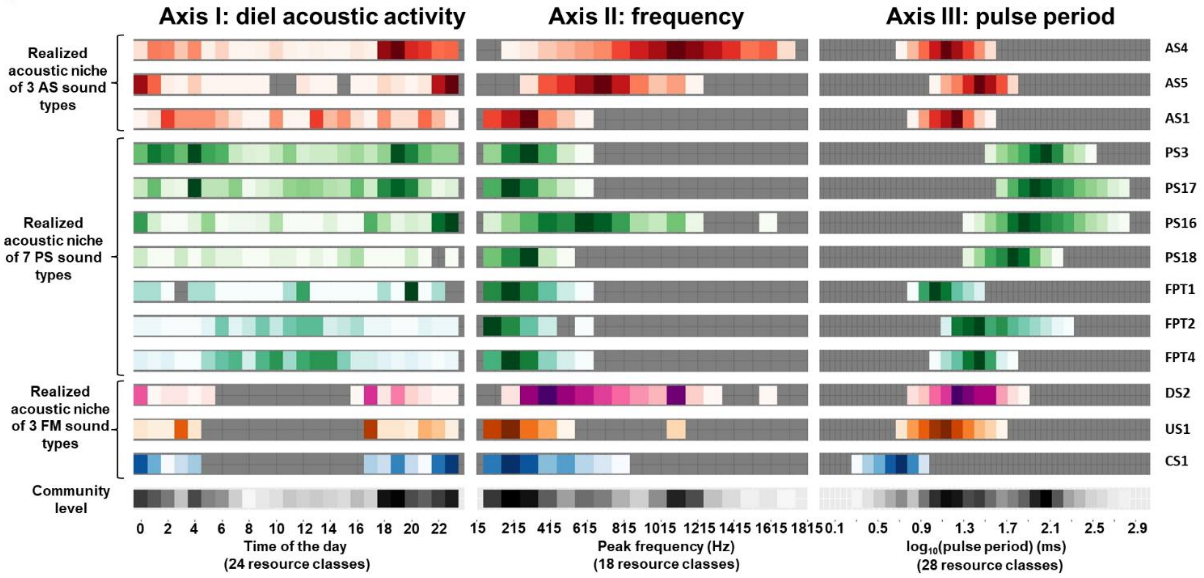

Figure 7. Realized acoustic niche analysis of the 13 most abundant sound types and the entire community level at 120 m depth. Each panel represents an axis of the realized acoustic niche (axis I: diel acoustic activity, 24 resource classes; axis II: frequency, 18 resource classes; axis III: pulse period, 18 resource classes). Data for each axis were organized in a resource matrix, where each row represented a sound type and each column a resource class. For each sound type and resource axis, the number of sounds associated with each resource class was calculated and is presented with a color scale as a relative percentage (where the darker the color, the higher the percentage). The range of acoustic resources utilized by the entire acoustic community was calculated from the sum of all sounds present in each resource class for each of the three axes.

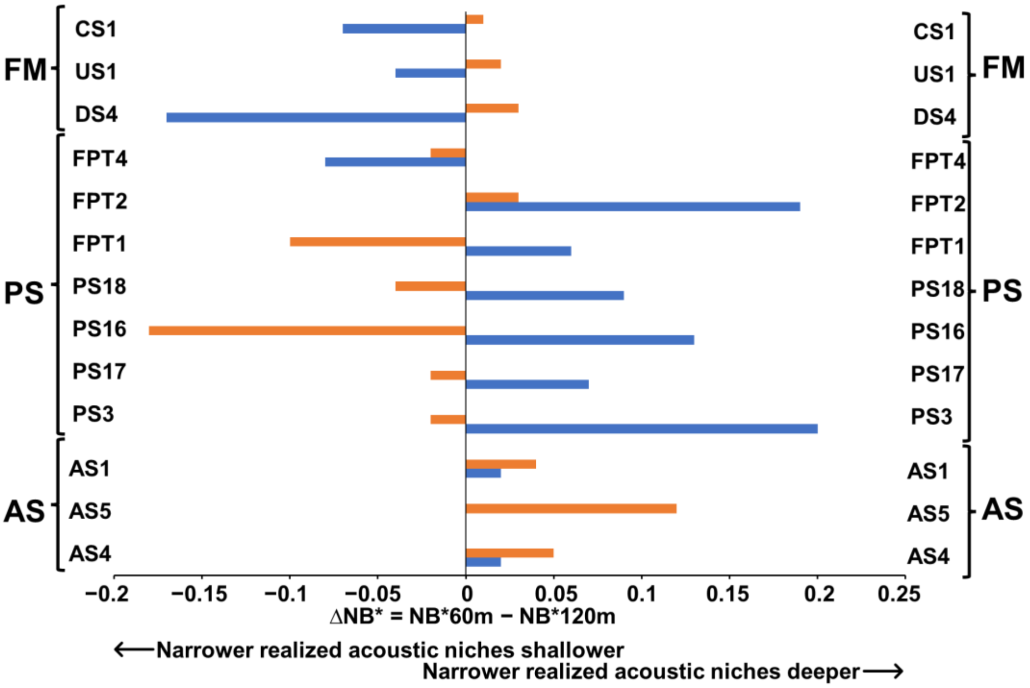

Figure 8. Differences in the widths of the realized acoustic niches for the 13 most abundant sound types between 60 and 120 m. Delta in the width of the diel realized acoustic niche (ΔNB^*_{temp}) in blue and frequency realized acoustic niche (ΔNB^*_{freq}) in orange. ΔNB* = NB*60m − NB*120m.

CS1, US1, and DS2 exhibited similar overall realized acoustic niche breadths at each depth. However, the values differed between the two depths. At 120 m, the realized temporal niche breadth values were all higher than at 60 m ($NB_{temp}*_{60m} = 0.24 \pm 0.10$, $NB_{temp}*_{120m} = 0.36 \pm 0.021$). This is related to the fact that acoustic activity of FM sound types was more prominent at 120 m than at 60 m.

Overall, FM sound types (CS1, US1, and DS2) had realized temporal niche widths that increased with depth (Fig. 8). It could be interpreted as the temporal window of vocalization widening due to individuals vocalizing beyond the mean vocalization period. On the other hand, most PS (FPT2, FPT1, PS18, PS16, PS17, and PS3) had their realized temporal niche breadths decreasing with depth. The realized temporal niche breadths of AS (AS1, AS5, and AS4) decreased slightly. Concerning the frequency axis, the contrary was observed: the realized niche breadths of FM and AS, whose abundance increased with depth, decreased with depth and the ones of most PS, whose abundance decreased with depth increased. This suggests that the more individuals are vocalizing, the more there is need to restrict the frequency range to avoid overlap. With depth, the specialization of FM and AS sound types appears accentuated on the frequency axis, while the specialization of PS sound types is more pronounced along the diel axis.

When examining the realized acoustic niches at the community level, clear differences in temporal and frequency axes were observed between the two depths (Fig. 7 and Fig. A.3). Specifically, the realized temporal niche breadth at 120 m was narrower than at 60 m ($NB_{temp}*_{120m} = 0.32$ vs $NB_{temp}*_{60m} = 0.40$), while the realized frequency niche breadth at 120 m is wider than at 60 m ($NB_{freq}*_{120m} = 0.43$ vs $NB_{temp}*_{60m} = 0.31$). This indicates that at greater depths, acoustic activity was more concentrated during specific time periods, particularly during the night, and the frequency spectrum was more broadly utilized, particularly at higher frequencies (Fig. 6).

4. DISCUSSION

4.1. The effect of depth and diel cycle on acoustic communities

The analysis of the selected sound types revealed diverse trends in their distribution. This includes the identification of sound types that are predominantly detected during the day or at night. Notably, the periods of sunset and sunrise emerge as critical time periods when specific sound types are produced, highlighting the importance of these transitional times in the daily rhythm of sound emission as highlighted in previous literature (Parmentier et al. 2010, 2016, Mooney et al. 2016, Suthers & Fay 2016, Rountree et al. 2018, Rowell et al. 2019, 2020). Within these sounds, the most abundant sound type in Tuamotu MCEs, AS4, is particularly interesting since it shares acoustic characteristics with the ‘kwa’ sound type recorded in the Mediterranean Sea (Di Iorio et al. 2018), such as the presence of pseudo-harmonics, similar pulse periods duration, and similar nychthemeral cycle (Raick et al. 2023c). The ‘kwa’ in the

Mediterranean Sea was originally attributed to fish of the genus *Scorpaena* (Scorpaenidae) (Bolgan et al. 2019). Consequently, the AS4 sound type detected in French Polynesian MCEs could plausibly be produced by one or more species of Scorpaenidae that inhabit this region (Raick et al. 2025). Phylogenetic conservatism, and related morphological constraints, could explain why a similar niche is occupied in the two different environments.

The conducted GAMs provided a deeper insight into the temporal partitioning of the entire acoustic community of MCEs. The temporal segregation can serve as a primary mean for fish to minimize competition for frequency resources (Krause 1993). However, the observed differences in acoustic activity (both temporal and spectral) may also reflect species vertical movements that may also have an impact on the competition driving partitioning.

The division of the acoustic community into a diurnal and a nocturnal community aligns with observations made in other marine environments (Ruppé et al. 2015, Bertucci et al. 2020). However, beyond this general result, our study demonstrates that the nocturnal community itself can further be subdivided into two sub-communities. Having more detailed data on the temporal changes in light percentage in these specific deep reefs would provide a better understanding of the exact moment when the peaks of different calls diverge.

FM sound types reached their maximum abundance around the middle of the night. The predominance of FM sound types in decreased light conditions may be related to the need to produce sufficiently distinctive signals. Incorporating frequency modulations could serve as a method to enhance the stereotypical nature and the distinctiveness of the fish call. Moreover, the propagation of frequency modulated signals seems to be less affected by noise. This may be due to the fact that in an FM signal, information is transmitted by varying the frequency, not the amplitude, and noise primarily affects amplitude. Producing short FM sounds may be more energy-efficient than maintaining long-duration sounds or complex temporal patterns. Ethologically, several examples exist of fish producing FM during reproduction (Lobel 1992, Amorim & Vasconcelos 2008), an behavior often happening at night since this period allows to minimize predation risk during spawning (Wilson et al. 2014). Frequency modulated sound types were also more prevalent in deeper waters (e.g., CS1) likely for similar reasons. In the absence of light, sounds cannot be complemented by visual stimuli (Parmentier et al. 2010, Ruppé et al. 2015). Sounds could therefore possess more distinctive characteristics to facilitate effective communication. This suggests that a single factor (light intensity) acting in two different ways (depth and diel cycle) may have a similar effect on the acoustic community. As a result, it seems that, within the framework of the Acoustic Adaptation Hypothesis (AAH), FM sounds may represent an acoustic adaptation to reduced light intensity conditions.

The results not only highlight the presence of nychthemeral cycles, but also revealed a depth-related difference. While it was known that fewer PS sound types are present at greater depths during specific periods, such as sunset (Raick et al. 2023c), this study demonstrates that as depth increases, more FM sounds are detected at night and fewer during the day, a pattern not observed with PS sounds.

4.2. Realized acoustic niches

All sound types exhibited distinct realized acoustic niches. AS sound types and FM sound types mainly differentiated along the temporal and the frequency axes, while PS sound types primarily differentiated based on their pulse period. At 113 m depth, it has previously been observed that fish sounds are temporally and frequentially partitioned while a significant difference in pulse period was not highlighted (Ruppé et al. 2015). In other taxa, another axis can encompass other acoustic features such as sound duration. In South America, the red howler monkey vocalizes both during the day and night, but the vocalizations are generally longer at night than during the day (Drubbel & Folia Primatologica 1993). In addition to these axes, differences could occur in the modulated character of the sound. In marine mammals, sound modulation has also been demonstrated as an adaptation to exploit a new acoustic niche by killer whales when leopard seals (another predator vocalizing at the same frequencies) were acoustically present during a part of the year (Mossbridge & Thomas 1999). In our analysis, we observed that the studied FM sound types were predominantly present at deeper depths. Furthermore, these sound types exhibited larger realized acoustic niches at these depths. This observation suggests that differentiation based on FM modulation could serve as an additional niche assessment criterion, constituting an additional axis of differentiation not used in previous studies dealing with acoustic fish ecology. This distinction supplements the differences already noted across the other three axes. Contrary to the studied FM sound types, the realized niche breadths for frequency resources seemed to decrease with depth for all the three studied AS sound types: they exhibit frequency-based specialization at depth. The overall realized acoustic niche breadths were similar for most PS sound types but some particular PS had temporal niche breadth narrower with depth. This indicates that, at greater depths, PS sounds are emitted more frequently during specific time periods, whereas other sound types are emitted at more precise frequencies, increasing the soundscape partitioning. In the variations associated with depth, it cannot be ruled out that factors other than those related to competition for acoustic space may also influence acoustic parameters. For instance, species-specific depth preferences.

When all three axes (time, frequency, and pulse period) are considered together and if caution is exercised when extrapolating from sound types to species (a point discussed in the next paragraph), it becomes apparent that each sound type tends to occupy a distinct acoustic niche, which is consistent with species actively partitioning the soundscapes, i.e., forming the foundation of the ANH. The ANH is a concept that has started to be explored in fish (Ruppé et al. 2015, Bertucci et al. 2020, Bolgan et al. 2022), but it has been studied for a longer time in other zoological groups, particularly mammals (Mossbridge & Thomas 1999), birds (Chitnis et al. 2020), and amphibians (Duellman & Pyles 1983, Sinsch et al. 2012, Allen-Ankins & Schwarzkopf 2021). However, the results are not equivalent across taxa and environments.

While in tropical birds, partitioning has primarily been observed at the temporal level (Hart et al. 2021), frequency partitioning has been shown in frogs (Villanueva-Rivera 2014). In anurans, differentiation of niches involves not only frequency but also frequency modulation (Lima et al. 2019).

The coexistence of soniferous species within a habitat inherently involves the occupation of different acoustic niches, with each species potentially utilizing the same range of resources differently. This coexistence can lead to competition for resources, which may result in specialization. In this study, we assumed that each sound type corresponded to a species (Desiderà et al. 2019, Di Iorio et al. 2021, Raick et al. 2023c). The results from this study focused on acoustic niches, not on ecological niches. Caution is needed when extrapolating from ones to the others. For example, the minimization of the competition for different resources within the soundscape assumes that these sound types are produced by different species. However, it is known that the same species could produce different kinds of sounds (Dos Santos et al. 2000, Amorim et al. 2008, Amorim & Vasconcelos 2008, Parmentier et al. 2010, 2022, Kéver et al. 2014, Raick 2015) and that some sound types could encompass sounds produced by several closely-related species (Raick et al. 2017, Di Iorio et al. 2018), potentially emitting sounds at different frequencies. This is because, when a fish species emits different types of sounds, they may often share the same fundamental/peak frequency (Desiderà et al. 2019). It is important to avoid at best classifying distinct sounds from the same species as separate units, as this could artificially create a diel distinction by reflecting patterns of different sound types, rather than truly indicating differentiation in the acoustic niche. Once the difference between acoustic and ecological niches is kept in mind and depth differences are explored at the level of the whole community, it is observed that the realized temporal niche breadth is narrower with depth, while the realized frequency niche breadth is wider with depth. This could indicates that at greater depths, acoustic activity becomes more focused during specific time periods, particularly during the night, and there is a broader exploitation of the frequency spectrum, particularly at higher frequencies (Fig. 6).

In ecology, there is an assumption that low abundances and narrow niches (i.e., specialization) are positively correlated (Hanski & Koskela 1978, Polechová & Storch 2008). This correlation may also extend to acoustic niches (Bolgan et al. 2022). However, at least one example can be found with *Ophidion rochei* in the Mediterranean Sea and contradicts this assumption for fish (Bolgan et al. 2022), suggesting that different levels of sonic system plasticity may be linked to various strategies for sharing the acoustic space (Bolgan et al. 2022). To gain a more comprehensive understanding of community dynamics, it is essential to consider ecological context, such as species hearing capabilities, along with phylogenetic niche conservatism (Sugai et al. 2021) and morpho-allometric constraints. To better understand the link between the acoustic separation we observe and the evolutionary adaptation behind it, it will be helpful to identify the species producing the sounds.

Overall, this study showed that acoustic characteristics and community dynamics of fish sounds in MCEs varied significantly with both depth and diel cycles, two factors related to light reduction, deepening our understanding of MCEs' dynamics.

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Author contributions

Conceptualization, X.R.; methodology, X.R.; software, X.R.; validation, X.R., L.D.I., and É.P.; formal analysis, X.R. and J.C.; investigation, X.R. and J.C.; resources, U.T.P. and F.B.; data curation, X.R.; writing—original draft preparation, X.R. and J.C.; writing—review and editing, X.R., L.D.I., F.B., É.P., D.L., and J.C.; visualization, X.R. and J.C.; supervision, X.R.; project administration, X.R.; funding acquisition, D.L. and U.T.P.

Conflict of interest

The authors declare no conflict of interest.

Data availability statement

Additional information is provided in the Supplementary Information, including a dichotomous key and marine sounds below 2 kHz from French Polynesia. The latter two items are also openly accessible via Zenodo at https://zenodo.org/records/10592329 and https://zenodo.org/records/12570714. All acoustic files used in this study are available at https://zenodo.org/records/11960305. The data are provided at a sampling rate of 44.1 kHz and were subsampled to 4 kHz for this study.

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