# Fish sounds of photic and mesophotic coral reefs: variation with depth and type of island

Xavier Raick[1,2], Lucia Di Iorio[3,2], David Lecchini[4,5], Cédric Gervaise[2], Laetitia Hédouin[4,5], Under The Pole Consortium[6], Gonzalo Pérez-Rosales[4], Héloïse Rouzé[4,7], Frédéric Bertucci[1,4] & Éric Parmentier[1]

[1] Laboratory of Functional and Evolutionary Morphology, Freshwater and Oceanic Science Unit of Research, B6c allée du 6 août, University of Liège, 4000 Liège, Belgium

[2] Chorus Institute, 5 rue Gallice, 38100 Grenoble, France

[3] Université de Perpignan Via Domitia, CNRS, CEFREM UMR 5110, 52 avenue Paul Alduy, 66860 Perpignan, France

[4] PSL University, EPHE-UPVD-CNRS, USR 3278 CRIOBE, BP 1013 98729 Papetoai, Moorea, French Polynesia

[5] Laboratoire d'Excellence "CORAIL", 58 avenue Paul Alduy, 66860 Perpignan, France

[6] Under the Pole Expeditions, 1 Rue des Senneurs, 29900, Concarneau, France. Members: G. Bardout, J. Fauchet, A. Ferucci, F. Gazzola, G. Lagarrigue, J. Leblond, E. Marivint, A. Mittau, N. Mollon, N. Paulme, E. Périé-Bardout, R. Pete, S. Pujolle and G. Siu.

[7] Marine Laboratory, University of Guam, 96923, Mangilao, GU, USA

Correspondence and requests for materials should be addressed to xavier.raick@uliege.be and lucia.diiorio@chorusacoustics.com

**Orcid:** 0000-0002-1977-0289

**Phone:** +32 4 366 51 33

## Abstract

Mesophotic Coral Ecosystems remain largely unexplored. The aim of this study was to determine how the acoustic fish biodiversity varied depending on the depth and the type of island in six Polynesian islands. The link between benthic cover and fish sound diversity was established. In most islands, acoustic fish α-diversity decreased between 20 and 60 m but not between 60 and 120 m. Fish sound types community composition was more driven by depth, likely due to benthic coral cover differences, than by the type of island. These results show fish sounds exhibit a bathymetric stratification and can reflect different habitat features. It opens perspectives in the monitoring of mesophotic coral ecosystems using passive acoustics.

**Keywords:** soundscape, French Polynesia, passive acoustic monitoring, mesophotic coral ecosystems, biophony

## 1. INTRODUCTION

Coral reefs are one of the biggest biodiversity hotspots on Earth. However, species richness and diversity are not homogeneous in coral reefs as they vary depending on the depth (Pyle et al. 2016) and the type of island, i.e. coral atolls (also named low islands) or high islands (volcanic island surrounded by a barrier reef) (Donaldson 2002).

Light-dependent coral reefs can be divided into shallow-water coral reefs (between the surface and 30/40 m) and Mesophotic Coral Ecosystems (MCEs) (Kahng et al. 2016) that extend from 30/40 m to/over 150 m (Hinderstein et al. 2010; Pyle et al. 2016; Baldwin et al. 2018). The lower limit is defined as the maximum depth at which there is sufficient sunlight to support photosynthesis and, consequently, the growth of zooxanthellate hermatypic corals (Bongaerts et al. 2010; Rouzé et al. 2021). Contrarily to shallow-water coral reefs, the ecology and population dynamics of MCEs remains largely unknown because they are not easily accessible to humans (Pyle et al. 2016). MCEs are, however, thought to serve as refuges for different reef species and could contribute to the recovery of photic reefs (Bongaerts et al. 2010; Van Oppen et al. 2011). Depth gradients in coral reefs are described for fish assemblages. Upper (30 to 60 m) mesophotic fish communities share similarities with shallow-water (surface to 30 m) coral reef communities (Wagner et al. 2014; Kahng et al. 2016), while the lower mesophotic zone (between 60 and 150 m) has unique fish assemblages (Kahng et al. 2016; Pinheiro et al. 2016). The faunal shift between the upper and lower MCEs fauna is generally found between 60 and 90 m (Pinheiro et al. 2016; Pyle et al. 2016; Baldwin et al. 2018).

Differences in coral cover and fish assemblages have also been reported in relation to the type of island (Donaldson 2002). In Polynesian atolls, the barrier reef appears to be divided into an upper slope made of a succession of spurs and grooves followed by a sloping terrace, and a lower slope which is more steeply inclined (Pichon 2019). In high islands, the profile is more variable because of more recent volcanic formations (Pichon 2019). Generally, it is divided into three parts: (1) the upper slope (until 30 m) containing spurs, grooves, terraces, buttresses; (2) a less inclined slope (between 30 and 70 m) of variable nature (predominantly hard bottom coral substrate or a sandy plain); and (3) a steep slope or drop off with a higher inclination (bellow 70 m) (Pichon 2019). The substrate is important since most fish species between 30 and 70 m are found where hard substrates are dominant, while the central sandy part of the slope has low fish diversity and abundance (Vigliola 1993; Vigliola et al. 1996).

French Polynesia extends over 5 million km$^2$ (Rancher and Rougerie 1994; Rougerie et al. 1997) and is divided into five archipelagos: Austral, Gambier, Marquesas, Society and Tuamotu Islands. Some islands are coral atolls, like all the islands in the Tuamotu Archipelago (Purkis et al. 2017), while most islands from other archipelagos are high islands (Pichon 2019). The majority of the Polynesian coral reef research is focused on the shallow part of the islands of the Society Archipelago and regions of the Tuamotu Archipelago (Purkis et al. 2017; Pichon 2019). Like in other parts of the world, little is known about MCEs. This is particularly true below 80 m (Pichon 2019), where descriptions are generally limited to bottom relief. Only sparse information is available on the fish communities at these depths. Reefs are often named "choral reefs" because their shallow parts are known to be acoustic hotspots (Lobel et al. 2010; Tricas and Boyle 2014; Bertucci et al. 2020). Many fish species from the photic reef are known to be vocal (Fish and Mowbray 1970; Tricas and Boyle 2014; Raick et al. 2018; Parmentier et al. 2021), and there are indications that deeper habitats (75 to 90 m) also host vocal fish species (Bertucci et al. 2017). Therefore, passive acoustics could be used as a proxy to investigate fish communities (Tricas and Boyle 2014; Carriço et al. 2019; Desiderà et al. 2019) in deeper reefs. However, despite being a useful tool to study the diversity of fish assemblages, there is little knowledge on the association between acoustic diversity with depth, the type of island or benthic cover features in coral reefs.

The aim of this study is to describe the acoustic fish biodiversity from the photic reef to the MCE in six Polynesian locations, i.e., three atolls (Rangiroa, Raroia and Tikehau) and three high islands (Bora Bora, Mangareva and Moorea), to determine if and how the acoustic fish biodiversity varies depending on the depth (20, 60 and 120 m), the type of island, and how this is related to habitat features.

## 2. MATERIAL AND METHODS

### 2.1. Sampling

Data sampling was conducted between March 2018 and April 2019 in six Polynesian islands from three archipelagos: Society Islands, Gambier Islands and Tuamotu Islands (Fig. 1A, Table SP1). Three islands were high islands (Bora Bora, Moorea and Mangareva) and three were atolls (Rangiroa, Raroia and Tikehau) (Fig. 1B, Table SP1). The sampling was realized by deep divers from Under the Pole Expeditions (Concarneau, France). At each island, three different depths were sampled simultaneously on the external slope of the reef, one in the photic reef (20 m) and two in the mesophotic reef (60 m and 120 m) (except at Mangareva, where only 20 m and 60 m depths were sampled).

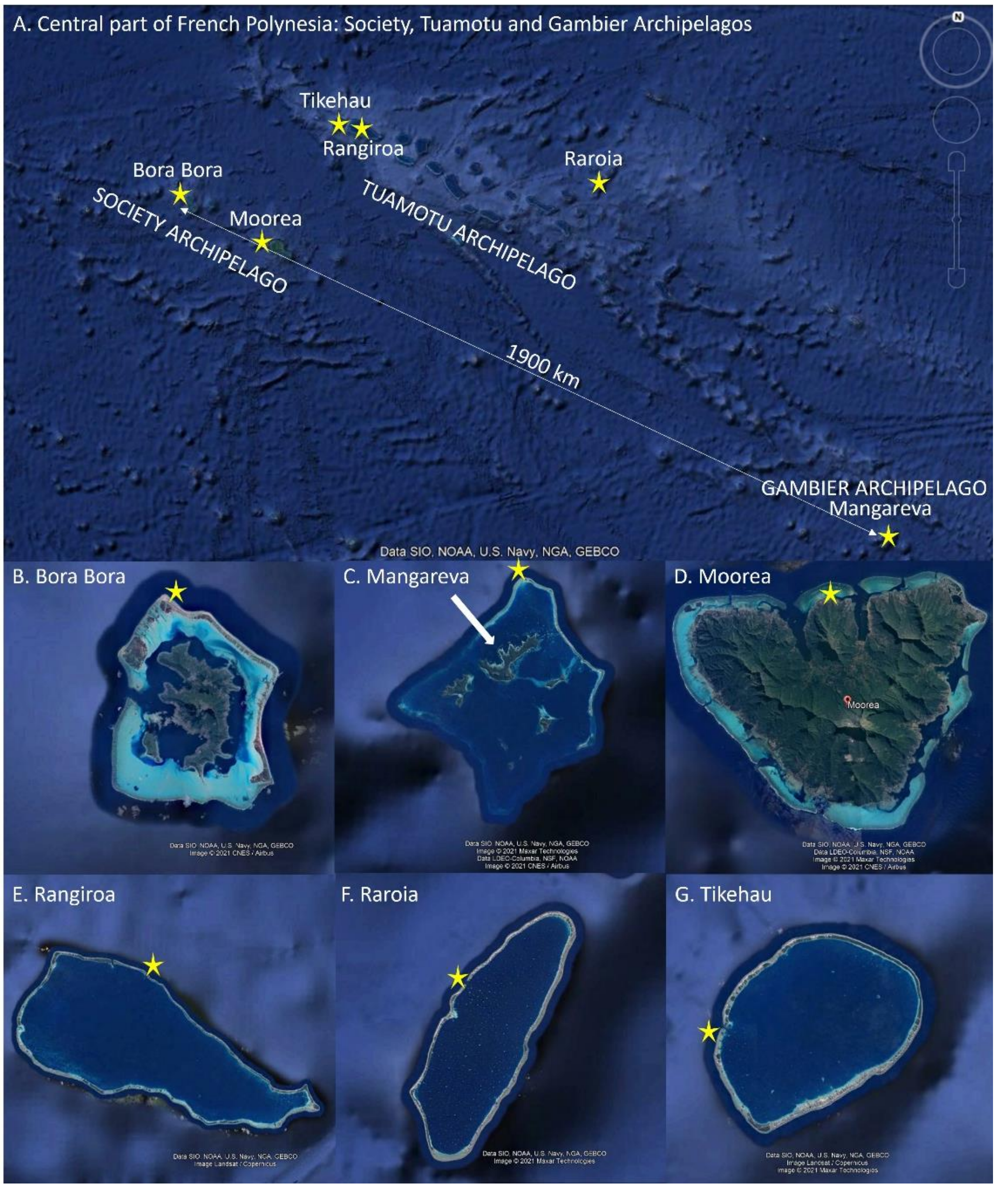

**Fig. 1 Location of sampling sites A** Central part of French Polynesia: Society, Tuamotu and Gambier Archipelagos. **B** Bora Bora, **C** Gambier Archipelago with Mangareva in the centre, **D** Moorea (these three islands are high islands), **E** Rangiroa, **F** Raroia and **G** Tikehau (these three islands are atolls). Yellow stars indicate sampling sites. Images from SIO, NOAA, U.S. Navy, NGA, GEBCO 2021 Maxar Technologies Data LDEO-Columbia NSF, NOAA 2021 CNES / Airbus

At each depth, an autonomous underwater long-term acoustic recorder SNAP (Loggerhead Instruments; Sarasota, FL, USA) connected to a HTI96 hydrophone (sensitivities: −170.5, −170.2 and −169.7 dB re 1 V for a sound pressure of 1 µPa, flat frequency response from 2 Hz to 30 kHz) was deployed during 72 h. The recorders were attached vertically to the pole of a 4 kg weighted tripod structure (60 cm high) placed on the sea bottom. All the recorders were scheduled to record sounds for 1 minute every 10 minutes at a sampling rate of 44.1 kHz (16-bit resolution), with a + 2.05 dB gain.

In addition, for each island, a total of 90 photo-quadrats (i.e., 30 quadrats per depth) 0.75 x 0.75 $m^2$ were realized during each deployment (Fig. SP1) and used to characterize the benthic cover. The benthic cover was divided in 16 categories: (1) sand, (2) dead coral, (3) rubble, (4) consolidate substrate, (5) scleractinians, (6) black coral and gorgonians, (7) hydroids, (8) Anthoathecatae, (9) encrusting sponges, (10) non encrusting sponges, (11) turf, (12) calcifying algae, (13) fleshy algae, (14) macroalgae including *Halimeda* algae, (15) encrusting algae and (16) other sessile invertebrates. Values of the quadrats (percent cover) of each of these categories were averaged to obtain mean values for each depth and each island. Finally, temperature was sampled with a MIDAS CTD (Valeport; Totnes, UK) between the surface and 130 m at all the islands except for Mangareva. The thermocline was generally between 60 and 120 m (Fig. SP2).

## 2.2. Fish sounds selection

The audio files were subsampled at 4 kHz in order to focus on the low-frequency (0 – 2 kHz) part of the sound files, because fish are known to vocalize in this frequency band (Cato 1978; Raick et al. 2021). Because sunset is the time of the day with the highest acoustic activity of Polynesian coral reef fishes (Raick et al. 2021) and sound type identification is time-consuming, inspection of the files was focused on the hours of civil sunsets only (measured at Faanui, Papeete and Rikitea; https://www.sunrise-and-sunset.com/fr/). Files from three consecutive days were therefore visually and aurally inspected between 05:00 PM and 07:00 PM using RavenPro Sound Analysis Software 1.5 (Cornell Lab of Ornithology; Ithaca, NY, USA).

Fish sounds were classified into categories (referred to as sound types) with a dichotomous key (see *Supplementary Sound Identification Key*) based on qualitative and quantitative acoustic properties (Desiderà et al. 2019). A sound type is defined as a category that contains sounds that share similar acoustic features. On the one hand, a sound type is likely usually produced by one species and/or contain sounds from multiple, sometimes closely related species. On the other hand, different sound types could also be produced by the same species (Bertucci et al. 2015; Raick 2015; Mélotte et al. 2019; Parmentier et al. 2019).

### 2.3. Fish sounds description

A detailed description of ten sounds with a good signal-to-noise ratio allowing sounds to be characterized was realized for each sound type. Measurements were conducted on oscillograms and power spectra with Avisoft SAS Lab Pro (Avisoft Bioacoustics; Glienicke/Nordbahn, Germany). For each sound, the following features were manually measured: total duration of the sound (ms), peak frequency (Hz), number of pulses and pulse period (ms); (pseudo-) harmonic interval (if applicable, Hz), i.e., the frequency range between two consecutive harmonics or pseudo-harmonics (i.e., a harmonic of the amplitude-modulated function); frequency interquartile interval (Hz); or presence of several peaks in the power spectra (if applicable). In addition, the 90% frequency bandwidth (BW, in Hz) was measured on the spectrograms on RavenPro Sound Analysis Software as the difference between the 5% and 95% frequency of the signal selection. For each sound type, the mean value and the standard deviation (SD) of the features were calculated.

### 2.4. Influence of depth and island type on sound abundance

To assess differences in fish sound abundance related to depth, the relative abundance (%) and the number of fish sounds (sounds per hour) of each sound types were compared between the three depths (20 m, 60 m and 120 m) and the six islands. Normality and homoscedasticity were tested with Shapiro–Wilk and Bartlett tests. Kruskal–Wallis tests (KW) with Dunn's *post-hoc* tests with a Benjamini–Hochberg correction were used to compare BW of three sound types between the three studied depths. All statistics were realized using the R software version 3.6.1. (R Core Team 2019) and the significance level was $\alpha = 0.05$.

## 2.5. Shannon acoustic diversity

The Shannon index of acoustic α-diversity was determined based on the established sound type repertoire for each depth of each island. Three temporal replicates for each recording position were used (sunset of day 1, day 2 and day 3) (library *vegan*, function *Shannon*). Then, the overlap of α-diversity was determined between the three depths and between the three pairs of depths to investigate acoustic similarities between depth ranges. The overlap is a measurement based on a ratio of α-diversity over γ-diversity (Jost 2007).

To test whether the Shannon acoustic diversity differs between depths and the types of islands, an analysis of variance was performed (function *aov*). Depth (20, 60 or 120 m) and the type of island (atoll or high island) were set as factors nested within seasons (i.e., the period of sampling: March/April or September/October, Table SP1). Diagnostic plots were used to verify assumptions. Because temperature data was not available for all the islands, the effect of temperature could not be tested, but it was discussed, as it is known to influence fish assemblage composition (Alvarez et al. 2021).

Finally, to test the influence of benthic cover features on Shannon acoustic diversity, a linear model was used. Only influencing benthic cover variables were included in the model and chosen using a forward stepwise method based on the AIC (Chambers 1992).

## 2.6. Acoustic community composition

Acoustic community composition was compared using Bray–Curtis distance matrices (function *vegdist*) that quantify the dissimilarity between two sites based on counts of each sound type at each site (Bray and Curtis 1957). For all the tests, a log-standardization was used to reduce the influence of abundant sound types. The dispersion was calculated (function *betadisper*) and permutation based-tests of multivariate homogeneity of group variances were implemented on the results.

### *Similarity of acoustic communities*

The similarities in acoustic fish community composition between depths (20, 60 and 120 m) and types of islands (atolls vs. high islands) were tested using analyses of similarities (function *anosim*, number of permutations: 999). Significant differences between groups were tested based on the Bray-Curtis dissimilarity matrices. The *anosim* statistic R, i.e., the metric quantifying similarities between groups, was determined by examining the mean ranks of the dissimilarities both between groups ($r_B$) and within groups ($r_W$) and was calculated as $R = (r_B - r_W)\ divisor^{-1}$ with *divisor* calculated to obtain R in the interval [−1, 1]. Positive R values indicate more similarity within groups, null values indicate random grouping, and negative R values indicate more similarity between than within groups (Warton et al. 2012).

### *Influence of depth and island type on the acoustic community composition*

To test whether the acoustic community composition differs with depth and the type of island, permutational multivariate analyses of variance (PerMANOVA) based on the calculated distance matrices were carried out (function *adonis*) (Anderson 2017). Depth (20, 60 or 120 m) and type of island (atoll or high island) were set as factors, islands (Bora Bora, Mangareva, Moorea, Rangiroa, Raroia or Tikehau) were set as random factor nested within season. A permutation-based test was used to test the multivariate homogeneity of group variances (Table SP8). Finally, Nonmetric Multidimensional Scaling (NMDS) was performed (function *metaMDS*) to represent acoustic communities in relation to the type of island and depth.

### *Influence of benthic cover on the acoustic community composition*

A canonical correspondence analysis (CCA) was conducted to test the influence of benthic cover features on acoustic community composition (function *cca*). The CCA was used to find the best dispersion of sound types, and to relate them to combinations of benthic cover features (ter Braak 1986). A model-building process was used to reduce the number of explanatory variables and select the most effective CCA model. A forward stepwise variable selection method was applied, which gradually adds significant variables based on the Akaike information criterion (AIC) to help determine which are most relevant for the model (Chambers 1992). Grouping variables (depth and type of island) were added to the ordination plot to see their relationships to acoustic community composition and coral cover variables (function *ordiellipse, vegan* package with a 95% confidence interval). All statistics were realized using the R software version 3.6.1. (R Core Team, 2019).

## 3. RESULTS

A total of 17,574 fish sounds were detected during sunsets at all depths and at all islands (Table SP4). Among the defined sound types, only those with at least ten selections were kept for the analyses. Consequently, 45 different fish sound types were used, representing 92% of all the identified sounds.

### 3.1. Fish sounds description

According to Desiderà et al. (2019), fish sounds could be divided into two main categories: frequency-modulated signals (FM) and pulse series (PS) *lato sensu*, i.e., series of at least three short broadband transient pulses. Polynesian PS sounds were divided into two sub-categories: PS *stricto sensu*, sounds with distinguishable pulses and without (pseudo-)harmonics, and arched sounds (AS), i.e., sounds with ultra-short pulse periods that appear as (pseudo-)harmonics in the spectrographic representation (Fig. 2). The AS sound type category comprises ultra-fast pulse series (UFPS) and long tonal non-frequency modulated calls (LT) described by Desiderà et al. (2019).

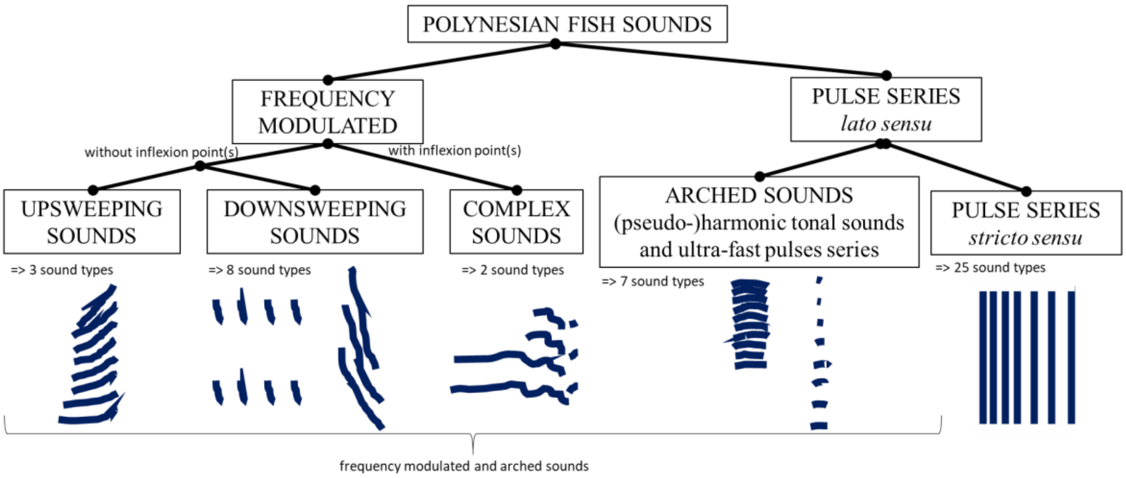

**Fig. 2 Dichotomous classification of Polynesian fish sounds with graphical illustrations of a few sound types.**

The most abundant sound type (42% of the total number of sounds) was an arched sound referred to as AS4 sound that shares similarities with the ultra-fast pulse series, also known as *kwa* sound recorded in the Mediterranean Sea (Di Iorio et al. 2018). The AS4 sound type was a pulse train of 183 ± 7 ms (mean ± standard deviation) duration, characterized by 12 ± 1 pulses and a pulse period of 15 ± 1 ms. In the spectrograms, they appeared as pseudo-harmonic arched sounds. In the power-spectra, mean pseudo-harmonic interval (HI) was around 68 ± 4 Hz with an interquartile interval of 393 ± 20 Hz. Their waveforms were characterized by a peak frequency of 847 ± 148 Hz modulated in amplitude by a periodic envelope with $HI^{-1}$ oscillations (Fig. SP3M).

Frequency-modulated (FM) sounds were divided in downsweeping (DS), upsweeping (US) and complex sweeps (CS), i.e., with more than one frequency modulation (mix of downsweeps and upsweeps). When considering the total occurrence, the most abundant sound type of each sub-category was, respectively, the DS1, US1 and CS1. CS1 was a long complex frequency modulated sound also referred to as whoot because of its high similarity with the "*whoot*" described by Bertucci et al. (2020). The main features of each type of FM sound are detailed in the supplementary Table SP3, as well as in oscillograms and power spectra in the Fig. SP3.

US1 sounds were harmonic upsweeping sounds of 335 ± 80 ms duration, characterized by a waveform with 32 ± 6 pulses and a pulse period of 11 ± 0.2 ms. The peak frequency was 225 ± 49 Hz and corresponded to the fundamental frequency or to the first harmonic. The mean harmonic-interval was 94 ± 2 Hz (Fig. SP3J). CS1 were pulse trains of 940 ± 174 ms duration, characterized by 168 ± 66 peaks and a peak period of 5 ± 0.3 ms. Their waveform was characterized by two consecutive parts (first part: 756 ± 291 ms with 150 ± 65 peaks of 5 ± 0.5 ms; second part: 84 ± 9 ms with 18 ± 2 peaks of 5 ± 0.3 ms). Their power-spectra presented a complex harmonic structure with two peaks around 200 Hz (one at 190 ± 6 Hz and one at 227 ± 9 Hz) and two peaks around 400 Hz (one at 363 ± 11 Hz and one at 423 ± 35 Hz) with a mean harmonic-interval of 183 ± 19 Hz (Fig. SP3T).

The PS *stricto sensu* category comprised at least 25 different sound types. Seven sound types were characterised by an average pulse period between 19 and 40 ms. These seven sound types can be group in the *Fast Pulse Train* (FPT) category described by Desiderà et al. (2019). One sound type was a slow pulse series (pulse period: 822 ± 289 ms, SPS). The 17 others sound types had intermediate pulse period values. Sounds lasted from 86 ± 45 ms (for FPT5) to 5.68 ± 7.71 s (for PS6). The main features (duration, number of peaks, peak frequency and period) of each type of PS sound are detailed in Table SP2, whereas the oscillograms and power spectrum of each sound are presented in Fig. SP2.

### 3.2. Influence of depth and island type on sound abundance

Acoustic fish community composition differed between depths (Fig. SP4). PS sounds dominated at 20 m while AS and FM sounds were more abundant at 120 m. However, the number of some sound types (e.g., AS4, US1 and CS1) increased with depth while the opposite was observed for other sound types (e.g., FPT4, FPT5, PS16, PS17, DS1 and DS4) (Fig. 3, Fig. SP6). The ten most abundant sound types represented 78% of the overall sound type abundance (Fig. 3, Table SP4). They were found in all islands. The abundance of six of them (DS1, DS4, FPT4, FPT5, PS16 and PS17) decreased with depth, while it increased for three other sound types (AS4, US1 and CS1) (Fig. SP5, Table SP5). Among the sounds that "decreased with depth", the most abundant ones at 20 m were short pulse series and fast pulse trains (see Table SP2): PS16, FPT5, PS17 and FPT4 sound types (Fig. 3). Among the sounds that "increased with depth", the most abundant ones at 120 m were the AS4 (= *kwa*-like sound), the US1 and the CS1(= whoot) sound types (Fig. 3, Fig. SP6). At all depths, the most abundant sound type in atolls was the AS4 (average occurrence between 22 to 78%, Fig. SP6). In high islands, the most abundant sounds were AS4, FPT5, PS16 and PS17 sound types (Table SP4b, Fig. SP6). Noticeably, the number of AS4 sounds increased with depth ($n = 229$ per hour at 20 m, $n = 684$ per hour at 60 m, and $n = 1077$ per hour at 120 m, Fig. 3, Fig. SP5, Fig. SP6, Table SP5), so did their signal-to-noise ratio, and their bandwidth (BW = 350, 402 & 478 Hz; KW: $\chi^2 = 374$, df = 2, $P < 0.0001$; Dunn: Z = 18, 11 & −10, all $P < 0.0001$) suggesting they are mainly produced in the deep part of the reef. At Moorea, Rangiroa, Raroia and Tikehau, the number of AS4 sounds was higher at 120 m while it was higher at 60 m at Bora Bora (Table SP5). At Bora Bora, Moorea, Rangiroa and Raroia, the bandwidth of AS4 was greater at 120 m than at other depths ranges (KW: $\chi^2$ = 18, 111, 89, 171, df = 2, all $P < 0.001$; Dunn: Z = 2, 4, 4, 10, 8, 7, 13, 6, $P = 0.02$, $< 0.001$, $< 0.001$, all others $P < 0.0001$) while at Tikehau, the bandwidth was higher at 60 m compared to the other depths (KW: $\chi^2 = 148$, df = 2, $P < 0.0001$; Dunn: Z = −2 and −12, $P = 0.02$ and $< 0.0001$).

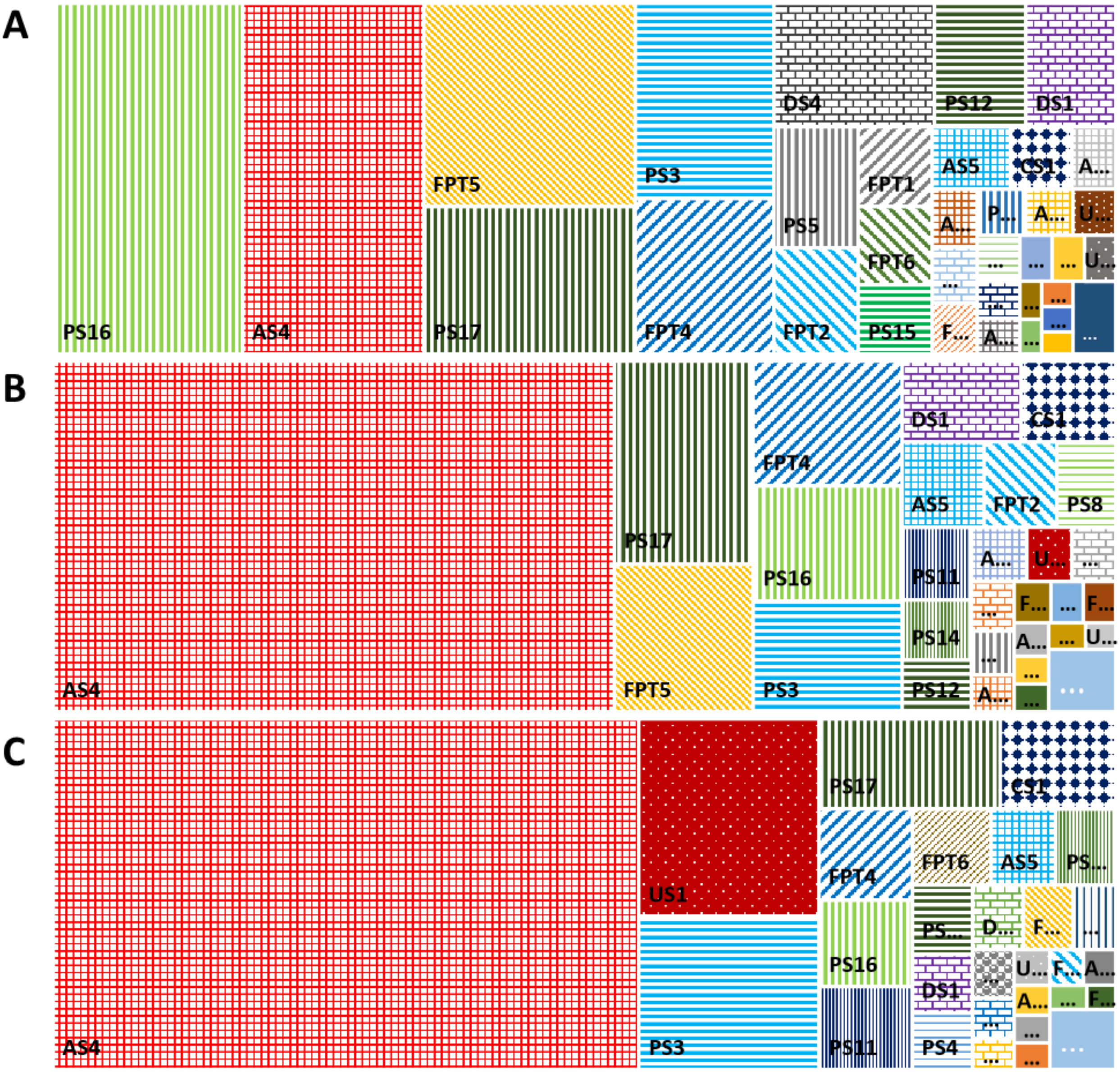

**Fig. 3 Treemaps of the number of sound types per depth: A** 20 m, **B** 60 m and **C** 120 m. Stripes = FM, diagonal stripes = FPT, dots = US, bricks = DS, checkerboard = CS sound types.

Similar patterns were observed for other FM sounds. For example, the number of US1 increased with depth (n = 7 per hour at 20 m, n = 9 per hour at 60 m and n = 187 per hour at 120 m, Fig. 3). This was also the case for CS1 sounds (n = 9 per hour at 20 m, n = 23 per hour at 60 m and n = 54 per hour at 120 m). Moorea was the only island where the number of CS1 was higher at 60 m than at 120 m (73 vs. 15 per hour). The bandwidth of CS1 increased with depth (BW = 229, 379 and 418 Hz at 20, 60 and 120 m respectively; KW: $\chi^2 = 30$, df = 2, $P < 0.0001$; Dunn: Z = 5, 3, −3, all $P < 0.01$).

### 3.3. Shannon acoustic diversity

The highest Shannon acoustic diversity was found at 20 m at Moorea (Shannon: 2.77 ± 0.02, median ± 0.5 IQR, Table SP6), while the lowest value was observed at 60 m at Rangiroa (Shannon: 0.99 ± 0.05). For all the islands except for Mangareva, the Shannon acoustic diversity decreased between 20 and 60 m (Fig. 4). Between 60 and 120 m, either it increased again (e.g., Rangiroa), decreased (e.g., Tikehau) or showed no differences (e.g., Moorea) (Table SP6, Table SP7).

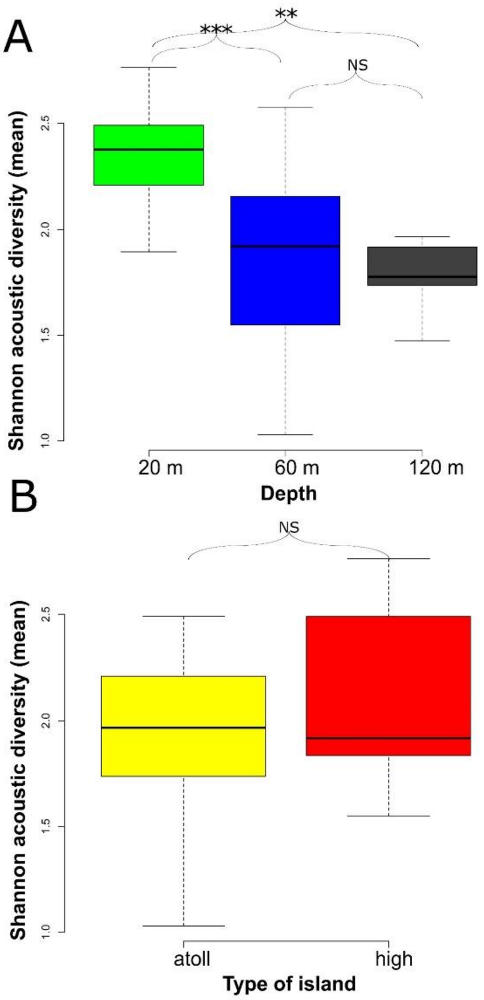

**Fig. 4 Boxplot of the Shannon acoustic diversity depending of (A) depth (20, 60 or 120 m) and (B) the type of island (atoll vs. high island).** Boxes represent the median ± interquartile range (IQR) and lines represent Q1 – 1.5 IQR and Q3 + 1.5 IQR. *** $P < 0.0001$, ** $0.0001 < P < 0.001$, NS = not significant (Analysis of variance, Table SP7)

The overlap of α-diversity was higher between 60 and 120 m (74%) than between 20 and 60 m or between 20 and 120 m (60% in both cases, Table SP7), indicating stronger similarities between mesophotic environments. The overlap of α-diversity between the two types of islands (atolls and high islands) was 62%. Atolls generally showed a higher within island-type overlap than high islands (75% vs 46%).

The Shannon acoustic diversity differed with depth (analysis of variance, F = 8.59, $P$ = 0.00068, Table SP7). The Shannon acoustic diversity differed between 20 and 60 m (Tukey test, $P$ = 0.00079) but not between 60 m and 120 m ($P$ = 0.82). All the benthic cover variables influenced the Shannon acoustic diversity (Table SP7).

### 3.4. Fish sound types community composition

*Similarity of acoustic communities*

The similarity statistic R indicated a higher similarity within sites when comparing 20 and 60 m (R = 0.30, $P$ < 0.001) than when comparing 60 and 120 m (R = 0.17, $P$ = 0.004). Atolls and high islands showed higher similarities in acoustic community composition than depths (R = 0.29 and 0.26, $P$ = 0.015 and 0.001, respectively).

*Influence of depth and island type on the acoustic community composition*

Permutational multivariate analyses of variance (PerMANOVA) on acoustic β-diversity revealed that depth had the strongest effect on acoustic community composition (df = 5, Sum Sq = 1.58, Mean Sq = 0.32, F = 4.79, $R^2$ = 0.32, $P$ = 0.001) (Fig. 5). To a lesser extent, the type of island had also an effect (df = 2, Sum Sq = 0.59, Mean Sq = 0.29, F = 4.46, $R^2$ = 0.12, $P$ = 0.002) (Fig 5, Table SP9). Some sound types, such as the pulse sequence PS1 and the downsweeping sound DS8, appeared to be strongly associated with deep reefs as they were only recorded at 120 m. Other sound types, including the complex sound CS2 (Fig. SP3, Table SP3) were only found at 20 m, or in the case of PS7 only at 20 and 60 m. Some sounds, such as the fast pulse train FPT7 were only found in atolls while others, such as the upsweeping sound US3 were only recorded at high islands. In addition, when visualizing acoustic community composition, atolls appeared clearly separated from high islands at 20 m (Fig. SP7), suggesting island-type differences in the shallow part of the coral reefs.

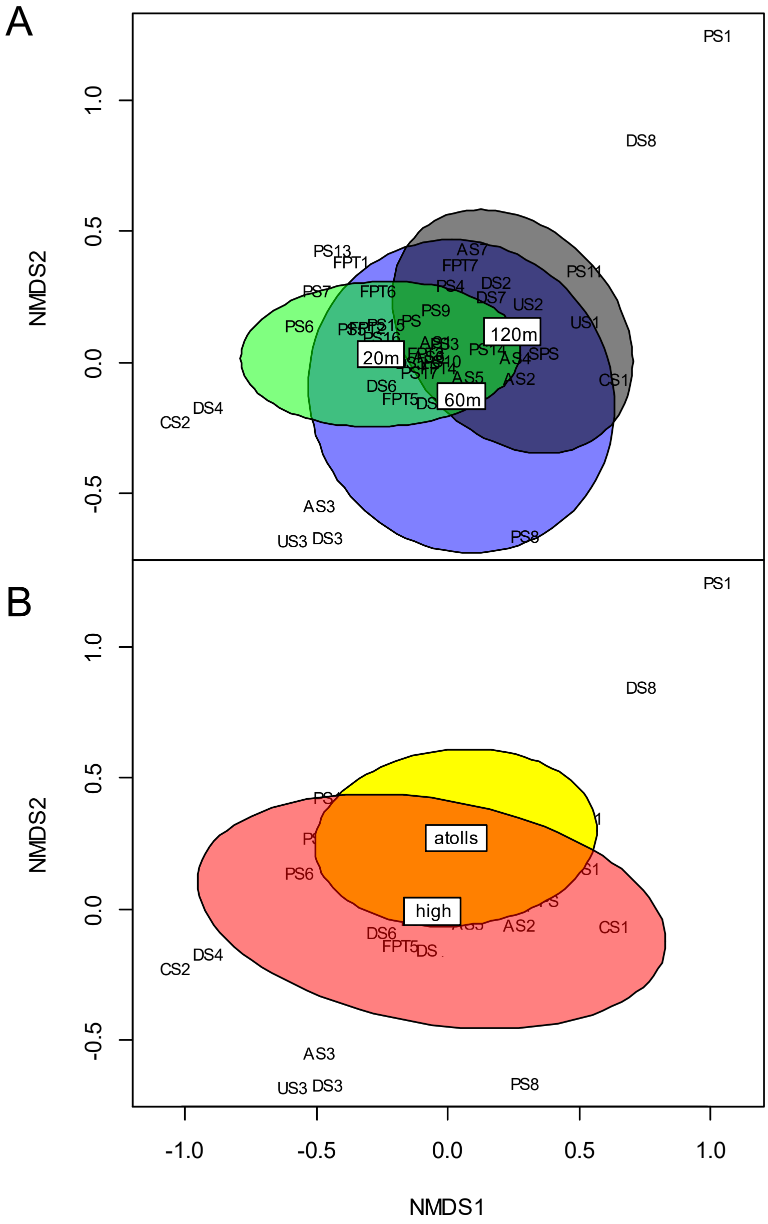

**Fig. 4 Effect of (A) depth and (B) type of island on acoustic fish communities assessed on sound types (c.f. Tables SP2 and SP3 for sound type abbreviations) represented in two-dimensional "Nonmetric Multidimensional Scaling" ordination plot of centroids based on Bray-Curtis distance.** Groupings are presented with ellipses (95% confidence around the centroid).

### *Influence of benthic cover on the acoustic community composition*

The Canonical Correspondence Analysis (CCA) indicated that the acoustic community composition, based on sound types, was influenced by depth and the type of island. Inspection of the CCA ordination plot allows the association of sound types to benthic cover features (Fig. 5, Table SP10, Table SP11). Positive CCA1 values are mainly explained by non-encrusting sponges, sand, and to a lesser extent by black coral / gorgonians and hydroids (CCA1 scores: 0.75, 0.62, 0.38 and 0.32, respectively). Negative CCA1 values are mainly explained by macroalgae, scleractinians and dead coral (−0.80, −0.68 and −0.57 respectively). The benthic cover explains part of the difference between islands.

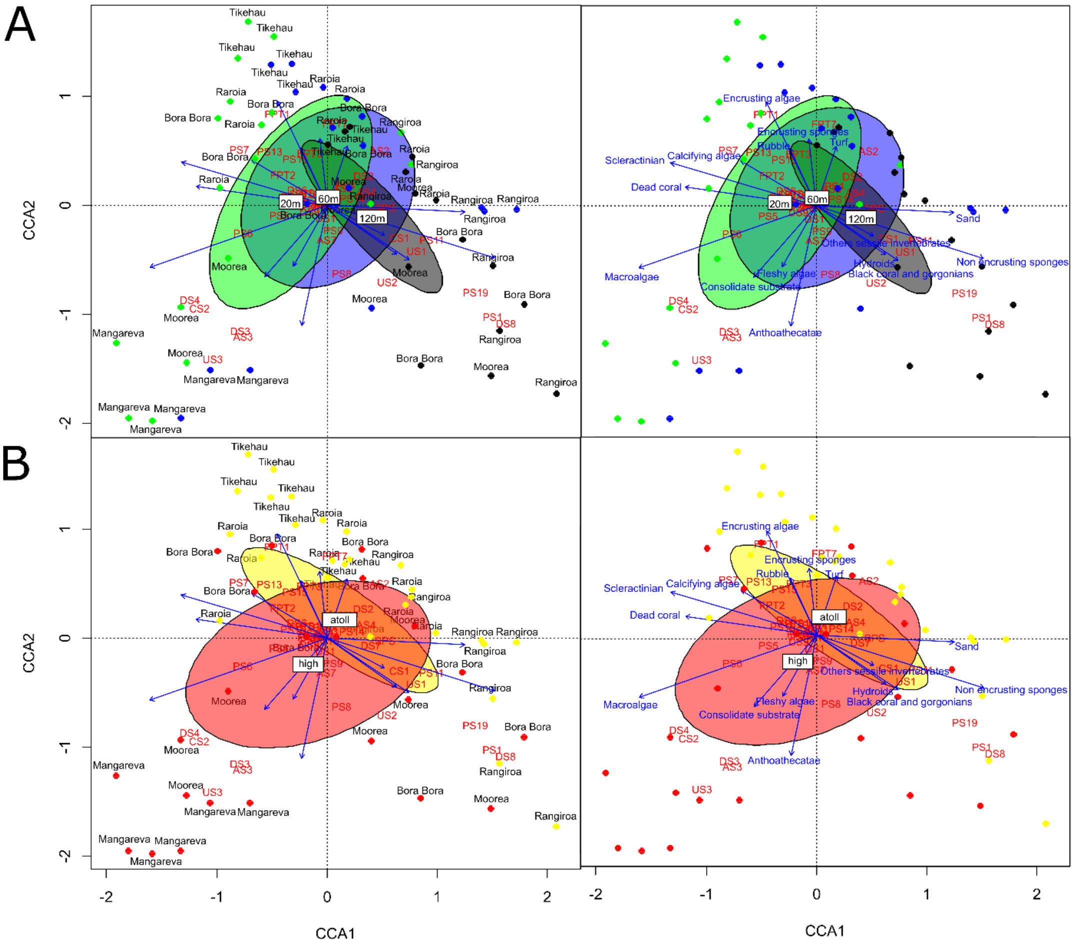

**Fig. 5 Canonical correspondence analysis ordination plots of the acoustic fish community composition based on Bray−Curtis dissimilarities of relative abundance of N = 45 sound types (in red) at (A) three depths (green: 20 m, blue: 60 m, black: 120 m) and (B) for two types of islands (yellow: atolls, red: high islands).** Blue arrows show the influence of benthic cover features. Ellipses are 95% confidence interval. For better visualisation figures have been split in two pannels with islands labels on the left and benthic cover labels on the right.

At 20 m, the most present benthic cover is scleractinians for all the islands (between 32% and 56%; except for Rangiroa, with more consolidate substrate: 35% vs 11%). Despite a domination by scleractinians, a variability is observed at 20 m between the different islands (Fig. 6). In Tikehau reef (atoll), turf accounts for more than 28%, while rubble account for more than 20% in Bora Bora and Rangiroa. In Moorea (high island), when comparing with sounds, the presence of CS2 in the photic reef seems to be associated with the presence of consolidate substrate, fleshy algae and macroalgae, while PS7 seems to be rather linked to the presence of scleractinians, calcifying and encrusting algae (Fig. 6). At 60 m benthic cover composition was highly variable. Some islands are dominated by scleractinians (e.g., Mangareva and Tikehau), others by consolidate substrate (e.g., Moorea and Raroia) and sand dominates the reef of Rangiroa. This is also visible in the CCA ordination plot, where the reef of Rangiroa at 60 m is located within deeper reefs (Fig. 6). This greater variability in the benthic cover could explain why 60 m appears to be a transition depth for acoustic fish communities. Finally, at 120 m, the most present benthic cover is sediment substrate and sand for all the islands. However, differences exist. For example, at 120 m in Bora Bora, there is 59% to 100% more black coral compared to the other islands.

## 4. DISCUSSION

Polynesian underwater soundscapes were rich, even at depth, with at least 45 non-occasional fish sound types recorded during sunset. It is worth mentioning the fish sound type diversity reported here is only part of the complex biophony found in the low-frequency part of the soundscape (i.e., below 2 kHz) in coral reefs, that can also comprise vocalizations from other taxa such as whales (Lammers et al. 2003) or tonal rumble sounds of mantis shrimps (Patek and Caldwell 2006; Patek et al. 2009).

In French Polynesia, the acoustic fish community of the deep part of the reefs and the shallow part of the atolls was dominated by a single fish sound: the AS4 that shows high similarities with the */kwa/* sound, suspected to be produced by nocturnal benthic Mediterranean *Scorpaena* spp. (Di Iorio et al. 2018; Bolgan et al. 2019). Although AS4 and AS5 sounds share similar features, they differ in terms of peak frequency. These two sound types could therefore be produced by two different species of Scorpaenidae, a group well represented in French Polynesia, with 37 to 39 sp. (Siu et al. 2017). Among the other sound types, PS10 is composed of a long succession of low-frequency pulses and it shares similarities with sounds from temperate Ophidiidae (Parmentier et al. 2010a), and may thus be emitted by fish of this family known to inhabit coral reefs (Parmentier et al. 2021). FPT2 is a long fast pulse train that presents similarities with Cottidae sounds (Müller 1857). FPT5 sounds could be attributed to Pomacentridae recorded in coral reefs (Mann and Lobel 1995; Parmentier et al. 2009, 2010b), while FPT6 shares similarities with the “Pomacentridae” sound type described previously in Moorea (Bertucci et al. 2020). Finally, AS1 was a low-frequency (i.e., below 700 Hz) long tonal call that was similar to Serranidae sounds (e.g., *Epinephelus adscensionis*) (Fish and Mowbray 1970). This family is very diverse in French Polynesia, with at least 68 to 69 species (Siu et al. 2017). Other sound types like the US1 and the CS1, two abundant sounds at 120 m could not be attributed to a clade. CS1 seems to correspond to the *whoot* previously recorded at Moorea (Bertucci et al. 2020).

Acoustic fish diversity and calls composition showed a depth dependence. Both FM and PS sounds were recorded at all the depths, but PS *stricto sensu* were more abundant at 20 m where they constituted 67% of all the sounds vs. only 27% at 120 m. The soundscape was dominated by AS sounds at 120 m (57% of all the sounds at 120 m but only 21% at 20 m). However, US and CS sound types were, respectively, 9.79x and 1.96x more abundant at 120 m than at 20 m. In a study conducted in South Africa, frequency of sounds made during daytime overlap, whereas there was a clear distinction between nocturnal sounds (Ruppé et al. 2015) suggesting that diurnal fishes living in the photic zone would mainly use sounds to support visual behaviours such as courtship rituals, aggressive attitudes, or colour pattern changes. At night, in the dark, or in an environment with more colour absorption (like MCEs), vision is progressively substituted by other senses like hearing. In this context, it becomes more important for their vocal inhabitants to produce more stereotyped sounds. Bertucci et al. (2017) reported a higher sound level in the photic reef compared to the mesophotic reef in Moorea Island. Similar observations were made for all the studied reefs. However, the acoustic diversity reported in this study was not necessarily lower in deeper environments. MCEs showed distinct acoustic communities with sound types strongly associated or only found in this deeper ecosystem (e.g., US1 and CS1) (Fig. 5 and 6). This is in accordance with the hypothesis suggesting that the sonic environment in the mesophotic zone is not composed of sounds propagated from the upper part of the reef (Bertucci et al. 2017). This is also in line with depth gradients found in temperate acoustic communities (Di Iorio et al. 2021). This study also indicates that acoustic fish communities, from the surface to 120 m, are divided into two parts with a buffer zone around 60 m. This buffer zone seems to coincide with a zone showing a higher fish species richness on the drop-off (Bertucci et al. 2017). In addition, another explanation of this division is likely related to temperature and more precisely to the presence of one to several thermoclines, known to influence fish assemblage composition (Alvarez et al. 2021). Finally, depth-dependent differences in acoustic fish communities are also related to changes in the benthic cover composition (Di Iorio et al. 2021). Different studies have demonstrated the existence of a positive relationship between acoustic metrics and coral cover in shallow reefs (Kaplan et al. 2015; Nedelec et al. 2015; Bertucci et al. 2016). In this study, deep sites were characterised by an increase in the percentage of sponges, sand, black corals and gorgonians, and a decrease in the percentage of macroalgae and scleractinians. The transition zone in the upper part of MCEs is acoustically closer to the deep part of the MCEs than to the photic part of the reefs, showing a greater overlap between MCEs. However, the level of dissimilarities of acoustic fish communities appeared different within the two MCEs depths: a small dissimilarity was found at 120 m while the highest one was observed at 60 m (Fig. 5A and 6A), indicating a higher variability at 60 m than 120 m. This could be explained by the highest diversity of benthic cover composition at 60 m and by the transition from one assemblage of coral species to another one. For example, around 60 to 70 m at Tikehau a shift occurs from *Pachyseris speciosa* assemblages by assemblages dominated by *Leptoseris* and *Echinophyllia* species (Faure and Laboute 1984; Pichon 2019). In addition, within a single island the reef at 60 m can be dominated by a monospecific coral cover (e.g., 70 to 80% of *Pachyseris speciosa* at Moorea) or by sedimentary deposits.

In addition to differences linked to the depth and related benthic cover, part of the acoustic variability can also be explained by the type of island (Fig. 5B and 6B). Dissimilarities are higher in high islands than in atolls. Atolls are known to exhibit less habitat diversity compared to high islands with greater habitat diversity (Donaldson 2002). Moreover, reefs with similar degrees of habitat diversity, are known to have similar fish fauna (Donaldson 1996; Kulbicki 1996), and shifts in habitat structure are reflected in changes in the diversity of the fish fauna (Anderson et al 1981). Another potential explanation for the similarity results between island types may be because three of the studied atolls belong to Tuamotu Archipelago, while the three studied high islands do not belong to the same archipelago (Bora Bora and Moorea are part of the Society Archipelago whereas Mangareva belongs to Gambier Archipelago). However, acoustic fish communities of Moorea’s photic reef appeared to be closely related to the ones at Mangareva, suggesting that differences are rather explained by the type of island than the archipelago. Moreover, the acoustic composition of the photic reef of Bora Bora shared more similarities with the one of atolls like Raroia and Tikehau. Bora Bora’s peculiarity could be linked to the fact that this island has an intermediate status between an atoll and a high island. Indeed, this island is sometimes called an almost-atoll due to its large lagoon (Rougerie et al. 1997).

This study suggests that acoustic fish community composition and diversity reflects habitat characteristics and can be indicative of subtle differences in vertical gradients, buffer zones and benthic cover. The occurrence of abundant and specific sound types of the MCEs makes acoustic monitoring of fish assemblages a promising tool to follow temporal changes in MCEs.

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## Author contributions

XR analysed and interpreted the acoustic data under the supervision of LDI and EP. XR wrote the first version of the manuscript. XR, EP and LDI wrote the final version of the manuscript with inputs from GPR and FB. LDI conceived the analyses. DL and LH helped with funding acquisition. CG provided algorithms. UTP performed the sampling. GPR and HR provided data from cover quadrats analyses under the supervision of LH. FB prepared the acoustic equipment for the sampling and stored the data.

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