



'Habitat-associated soundscape' hypothesis tested on several coral reefs within a lagoon (Bora-Bora Island, French Polynesia)

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Abstract

Coral reefs encompass different habitats that have their own living communities. The present study aimed to test the hypothesis that these different kinds of habitats were characterized by specific soundscapes. Within the lagoon of Bora-Bora, acoustic recordings and visual surveys of substrate type and fish communities were conducted on four reef sites belonging to the three main geomorphological habitats (fringing reef, channel reef, barrier reef) from February to April 2021. Two acoustic parameters were measured for each site and month, during the day and at night: the peak frequency (F_{peak} , in Hz) and the corresponding power spectral density (PSD_{peak} , in $\text{dB re } 1 \mu\text{Pa}^2 \text{ Hz}^{-1}$). Our results showed that each geomorphological unit could be characterized by these two parameters and therefore had a specific acoustic signature. Moreover, our study showed that a higher living coral cover was significantly positively correlated with F_{peak} in the low-frequency band (50–2000 Hz) during day-time. Although biodiversity indices based on visual surveys did not differ significantly, fish communities and soundscapes were significantly different between sites. Overall, our study underlines the importance of passive acoustics in coral reef monitoring as soundscapes are habitat specific.

Keywords Coral reefs · Biophony · Passive acoustic monitoring · Remote sensing · Fish sounds

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Introduction

In the context of the current global environmental changes, being able to monitor biodiversity in endangered ecosystems such as coral reefs is a necessary challenge for ecologists and conservationists (Barnosky et al. 2011; Wilkinson et al. 2013; Lecchini et al. 2021a). Several methods of biodiversity evaluation such as trawling, visual observations and counting, or camera trapping have been used over the past decades (Jackson et al. 2014; Moritz et al. 2018). Unfortunately, they often only consider the most noticeable species and are often time-consuming, invasive, and limited to accessible sites (Zenone et al. 2017). Moreover, numerous ecosystems, notably coral reefs, are complex three-dimensional habitats with many cryptic invertebrate or fish species (Plaisance et al. 2011; Galzin et al. 2016; Lammers and Munger 2016), which can be overlooked by traditional visual surveys. In recent years, the use of sounds produced by animals, *i.e.*, Passive Acoustic Monitoring (PAM) (Sueur and Farina 2015; Sugai et al. 2019), has provided new and complementary insights into the monitoring of biodiversity patterns within dense and complex ecosystems both in

terrestrial (Obrist et al. 2010; Blumstein et al. 2011), and more recently, marine environments (Bertucci et al. 2016, 2020a; Di Iorio et al. 2018; Bolgan and Parmentier 2020; Bolgan et al. 2020; Pieretti and Danovaro 2020; Raick et al. 2021, 2023; Havlik et al. 2022).

In coral reefs, many sympatric fish species produce sounds in various social contexts, such as during agonistic interactions with competitors, as well as during courtship and spawning (Fish and Mowbray 1970; Tricas and Boyle 2014). Worldwide, 27% of the 179 fish families that live on tropical coral reefs are currently considered as vocal (Lobel et al. 2010). Recently, Parmentier and collaborators (2021) estimated that approximately half of the fish families (32 of 66) found on Moorea Island (French Polynesia) may produce sounds. This high diversity of vocal fishes is reflected by an important sonic diversity, which constitutes a key part of the biophony (Pijanowski et al. 2011; Bertucci et al. 2020b). The biophony also encompasses sounds generated by many other marine animals such as crustaceans, molluscs, or echinoderms (Cato 1978; Radford et al. 2008; Staaterman 2016; Coquereau et al. 2016). In addition to the biophony, sounds produced by geological/meteorological events (*i.e.*, the geophony) and sounds produced by human activities (*i.e.*, the anthropophony) are part of soundscapes (Wenz 1962; Kinda 2013; Buscaino et al. 2016; Ferrier-Pagès et al. 2021). The Acoustic Habitat Hypothesis states that the habitats that sound-dependent species choose have unique acoustic characteristics, based on their functional needs and their ability to produce and detect sounds (Mullet et al. 2017). One of its basic foundations is the hypothesis of “habitat-associated soundscapes”. Bertucci and collaborators (2015) showed that different neighbouring habitats of Moorea’s reef (French Polynesia) had different intensities in their power-spectra within the 20–5000 Hz frequency bandwidth. These variations in sound levels could be linked either to the density and diversity of fish and invertebrate species (Nedelec et al. 2015; Bertucci et al. 2016; Pieretti et al. 2017; Wilson et al. 2020), or to physical environmental properties such as the type of substrate, structural habitat complexity, or health status of the reef (Lammers et al. 2008; Kennedy et al. 2010). Despite these recent studies, detailed knowledge about the links between marine biodiversity and acoustic features are still scarce. It is particularly important because underwater soundscapes are strongly impacted by noise pollution generated by human activities (Duarte et al. 2021; Ferrier-Pagès et al. 2021).

Bora-Bora is one of the most famous international travel destinations and is considered as the tourism showcase of the French Polynesian territory (Blondy 2016; Lecchini et al. 2021a). In 2020/2021, the COVID-19 pandemic led to drastic restrictions on human activities worldwide, and tourism was one of the most impacted economic sectors (Utkarsh and Sigala 2021). All tourism activities ceased in French

Polynesia during multiple lockdowns due to social and travel restrictions (Lecchini et al. 2021b). The present study aimed at taking advantage of the absence of tourism activities on Bora-Bora from February to April 2021 to test the hypothesis of “habitat-associated soundscapes” with different kinds of reefs within the lagoon and to explore a possible link between marine biodiversity and soundscapes in coral reefs.

Methods

Study sites

The study was conducted in the lagoon of Bora-Bora (French Polynesia) from February to April 2021, during the warm season. Bora-Bora is a 20 km² tropical volcanic island circled by a 70 km² barrier reef (Lepresle et al. 2016). Four reef sites were selected on the three main geomorphological habitats (from the coast to the ocean: fringing reef, channel reef, barrier reef) in the South part of Bora-Bora’s lagoon (Bertucci et al. 2020b; Lecchini et al. 2021a). Two sites were chosen on the barrier reef: BR1 (16°32′47.904″ S, 151°47′9.312″ W) and BR2 (16°31′46.956″ S, 151°47′19.823″ W) (between 1 and 2 m depth). One site was located on the fringing reef (FR1—between 1 and 3 m depth) (16°32′11.543″ S, 151°43′30.575″ W) and one in the channel (C1—between 1 and 5 m depth) (16°30′7.416″ S, 151°46′5.448″ W) (Fig. 1).

The substrate composition of each site was described by setting up three transect lines (25 m long). The substrate type (living coral, dead coral, sand, and macro-algae) were reported every meter using the point intercept transect method (Loya 1978). FR1 had the highest living coral cover (mean ± SD: 67 ± 7%). The highest percentage of dead coral was observed on C1 (61 ± 21%). The four sites also differed in terms of sand cover, with 27 ± 10% of sand on BR1 and less than 7% on the other sites. Lastly, macro-algae were observed on the barrier reef sites only (BR1: 7 ± 4% and BR2: 8 ± 1%) (Table 1).

Acoustic recordings

Autonomous SNAP acoustic recorders (Loggerhead Instruments; Sarasota, FL, USA; <https://www.loggerhead.com/snap>) equipped with HTI-96-Min hydrophones (sensitivity of 169.9 dB and 170.1 dB re 1 V for a sound pressure of 1 µPa; flat frequency response from 2 Hz to 30 kHz) were used to record the soundscapes at each study site. Acoustic recorders were positioned at 2 m depth and always at the same location for each temporal replicate to reduce variability. Three temporal replicates were realized per site (February, March, and April) over the two days following the new moon to standardize recording conditions (Galzin 1987;

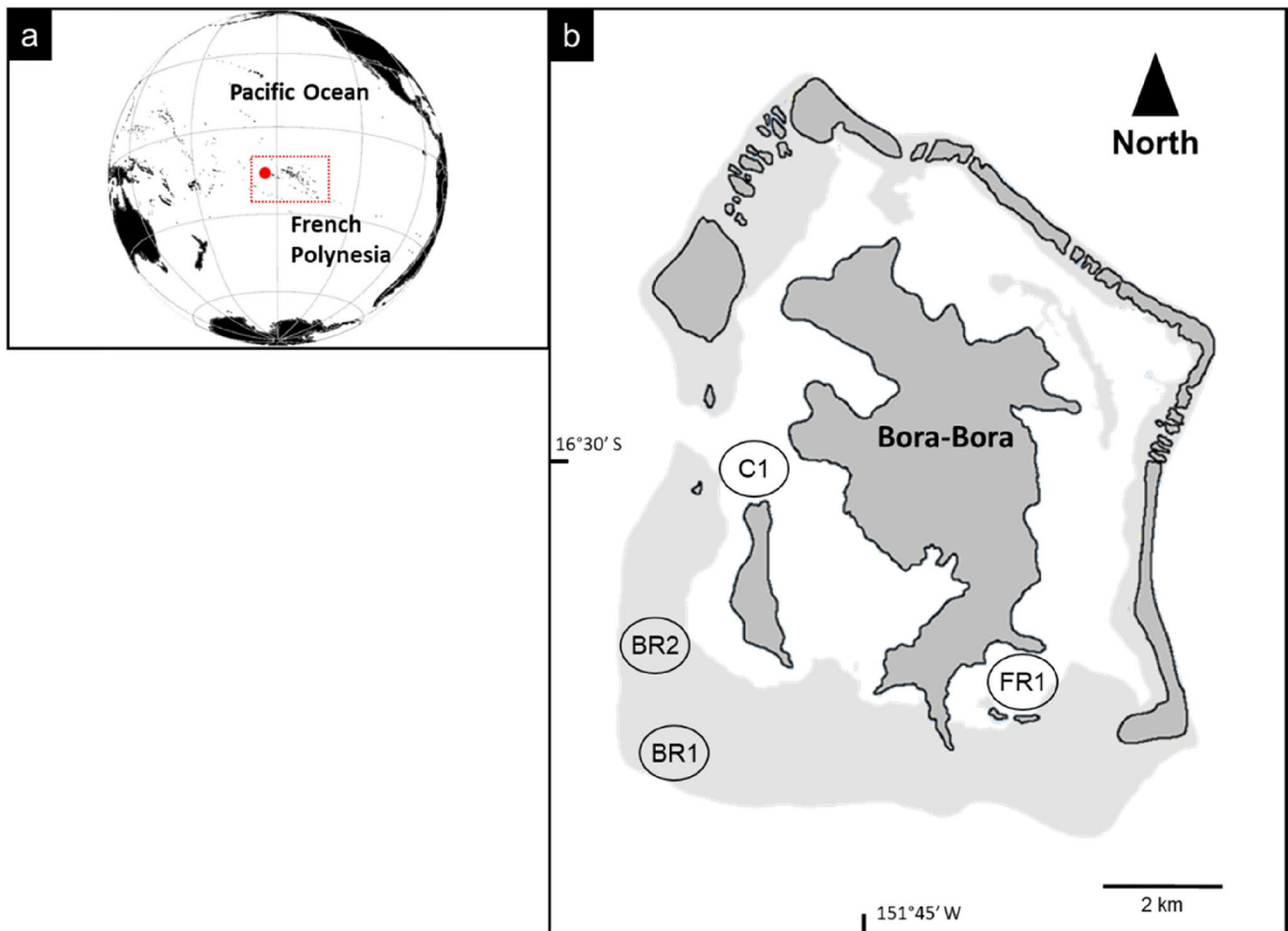


Fig. 1 a Map of the Pacific Ocean showing the location of French Polynesia (red square) and Bora-Bora (red dot), and b map of Bora-Bora showing the 4 study sites. FR1 on the fringing reef, BR1 and BR2 on the barrier reef, and C1 in the channel. The study was conducted during a period of COVID-19-related social restrictions from

mid-February to mid-May 2021. There were no international tourists on Bora-Bora and boat traffic was low in the lagoon due to reduced local tourism activities. The maps were drawn by the authors using PhotoFiltre 7 software (version 7.1.2—www.photofiltre.com). Dark grey represents land areas, light grey represents reef areas

Table 1 Proportion (%) of substrate cover (living coral, dead coral, sand, and macro-algae) of the four reef sites inside the lagoon of Bora-Bora

	% Living coral	% Dead coral	% Sand	% Macro-algae
FR1	67 ± 7	31 ± 7	2 ± 2	0
BR1	31 ± 2	35 ± 16	27 ± 10	7 ± 4
BR2	32 ± 3	56 ± 16	4 ± 3	8 ± 1
C1	32 ± 3	61 ± 21	7 ± 4	0

FR1: the fringing reef, BR1 and BR2: the barrier reef, and C1: channel. Values are mean ± SD

Lecchini and Galzin 2005). Recordings were conducted during 24 h with a duty cycle of 1 min of recording every 10 min at a sampling rate of 44.1 kHz (16-bit resolution).

The variability of the speed of sound propagation due to sea-water temperature (T) and salinity (S) was neglected

due to their limited variations during the warm season on Bora-Bora ($T = 28 \pm 1 \text{ }^\circ\text{C}$, $S = 36.1 \pm 0.2$; mean ± SD, from February to April, data from SNO Corail—<http://www.criobe.pf/>). In the case of bad weather conditions (wind speed > 20 knots or wave period > 10 s) during the initially scheduled 24 h of recording, the acoustic recorders were left in place for an additional day to avoid meteorological bias.

Soundscapes analyses were performed using PAM Guide (Merchant et al. 2015) in R version 4.1.1 (R Core Team 2021). Recordings were subsampled at 20 kHz. Soundscapes were divided in two frequency bands: a high-frequency band, between 2 and 10 kHz, and a low-frequency band, between 50 Hz and 2 kHz (Raick et al. 2021). The high-frequency band is known to be dominated by invertebrate sonic activities (Hildebrand 2009; Coquereau et al. 2016; Raick et al. 2021), and the low-frequency band is known

to be dominated by fish sounds (Lobel et al. 2010; Tavolga et al. 2012; Raick et al. 2021, 2023).

A different size of the Fast Fourier Transform (FFT) was used for each frequency band: FFT = 64 points for the high-frequency band, and FFT = 256 points for the low-frequency band (Raick et al. 2021). For both bands, a Hamming window with an overlap of 50% was used. This filter is defined by good frequency resolution, reduced spectral leakage, and acceptable noise performance (Bojkovic et al. 2017). Both frequency bands were studied during the day-time (05:30 a.m.–05:25 p.m.) and night-time (05:30 p.m.–05:25 a.m.) in order to separate the sounds produced by diurnal and nocturnal communities (Galzin 1987; Bertucci et al. 2015, 2020b; Raick et al. 2021).

The median (50th percentile) Power Spectral Density (PSD, in dB re $1 \mu\text{Pa}^2 \text{Hz}^{-1}$) of each temporal replicate (one per month) was calculated for both frequency bands and for both time periods (day and night). PAM Guide was used to generate PSD value. Graphics were produced with Python version 3.8.3 (Van Rossum and Drake 1995). On PSD plots, the peak frequency (F_{peak} , in kHz) and the corresponding power spectral density amplitude (PSD_{peak} , in dB re $1 \mu\text{Pa}^2 \text{Hz}^{-1}$) were displayed for each site and temporal replicate.

Fish records

All fish, except Blenniidae, Carapidae, Gobiidae, and Tripterygiidae that were too cryptic to be observed (Siu et al. 2017), were recorded to the species level by visual surveys along the three transects (25 m long and 4 m wide, i.e., 100 m^2 per transect) on each site during the morning (08:00 a.m.–11:00 a.m.) over the two days following the new moon (Lecchini and Galzin 2005; Nakamura et al. 2009). These fish surveys were performed before the start of the audio recordings. As sonic benthic invertebrates are mainly cryptic, they were not counted. Three parameters were extracted from the surveys on each site to describe fish communities (Table 2): fish density (number of individuals per 100 m^2 , D), species richness (total number of species per 100 m^2 , SR), and the Shannon–Wiener index of fish diversity (H-index). Based on the list of vocal fish species of French Polynesia (Parmentier et al. 2021), three additional parameters were calculated: density of vocal fish species (D_{vocal}), species richness of vocal fish species (SR_{vocal}), and H-index of vocal fish species (H_{vocal}).

Statistical analysis

All statistical analyses were conducted using R version 4.1.1 (R Core Team 2021) at a significance level of $\alpha = 0.05$. Acoustic and fish parameters did not meet normality and homoscedasticity assumptions (Shapiro–Wilk’s tests, $W = 0.87–0.98$, all $P < 0.001$). Non-parametric tests

were therefore used. Moreover, for both acoustic parameters (F_{peak} and PSD_{peak}), no significant differences between the three sampling months were found (Kruskal–Wallis tests, $\chi^2 < 2.81$, $P > 0.24$ —Table 3). February, March, and April were hence considered as replicates in the following statistical analyses. Every one-minute recording containing the sound of a motorboat were removed from the dataset after listening to audio files using VLC Media player (version 3.0.16). Similar statistical results were obtained in both the complete dataset and the dataset with near boats passages removed (Mann–Whitney U test, $V = 38$ and $V = 58$, $P = 0.38$ and $P = 0.75$ respectively). Thereafter, the analysis focused on the complete data set.

To analyze the acoustic parameters (F_{peak} and PSD_{peak}) either between the four sites or between day- and night-time, Kruskal–Wallis tests were used, followed by Dunn’s *post-hoc* tests. To compare fish community parameters (D, SR, H-index, D_{vocal} , SR_{vocal} , and H_{vocal} -index) between the four sites, Kruskal–Wallis tests were used, followed by Dunn’s *post-hoc* tests. A canonical correspondence analysis (CCA) was conducted to test the influence of benthic cover on vocal fish community composition (Ter Braak 1987; Di Iorio et al. 2021; Raick et al. 2023). The CCA was used to find the best dispersion of fish species and to relate them to combinations of environmental variables (i.e., benthic cover features) (Ter Braak 1987). A “forward stepwise variable selection” model-building process (which gradually adds significant variables based on the Akaike information criterion) was used to determine which variables are most relevant for the model (Chambers and Hastie 2017). The relevant variables were thus added to the ordination plot to study their relationships to fish community composition (function *ordi-ellipse*, *vegan* package with a 95% confidence interval). The CCA was conducted only on vocal fish species parameters (D_{vocal} , SR_{vocal} , and H_{vocal} -index) since they were strongly auto-correlated with all fish species parameters (D, SR, and H-index) (Spearman’s correlation, respectively: $\rho = [0.94, 0.80, 0.80]$, $P = [0.051, 0.33, 0.33]$).

Lastly, to analyze a possible link between marine biodiversity and acoustic diversity, Spearman correlation tests (with Holm’s correction) were conducted between the acoustic parameters (F_{peak} and PSD_{peak}), the substrate composition (% of living coral, dead coral, sand, and macroalgae), and vocal fish species parameters (D_{vocal} , SR_{vocal} , and H_{vocal} -index) during the day-time in the low-frequency band. For night-time in the low-frequency band and during day- or night-time in the high-frequency band, correlations were only tested between acoustic parameters and the substrate composition because of the lack of invertebrate counts and the difficulty to conduct night surveys and to link observations with vocal fish species parameters).

Table 2 Names and abbreviations of vocal fish species considered to calculate the three parameters

Fish name	Abbreviation	Fish name	Abbreviation
<i>Abudefduf septemfasciatus</i>	Asep	<i>Dascyllus flavicaudus</i>	Df
<i>Abudefduf sexfasciatus</i>	Asex	<i>Diodon histrix</i>	Dh
<i>Acanthurus blochii</i>	Ab	<i>Epinephelus merra</i>	Em
<i>Acanthurus guttatus</i>	Ag	<i>Forcipiger longirostris</i>	Fl
<i>Acanthurus lineatus</i>	Al	<i>Gomphosus varius</i>	Gv
<i>Acanthurus nigricans</i>	Ans	<i>Heniochus chrysostomus</i>	Hc
<i>Acanthurus nigricauda</i>	Ana	<i>Lutjanus fulvus</i>	Lf
<i>Acanthurus triostegus</i>	At	<i>Mulloidichthys flavolineatus</i>	Mf
<i>Agrilinus sordidus</i>	Asor	<i>Mulloidichthys vanicolensis</i>	Mv
<i>Balistapus undulatus</i>	Bu	<i>Myripristis adusta</i>	Ma
<i>Caranx melampygus</i>	Cme	<i>Myripristis pralina</i>	Mp
<i>Centropyge bispinosa</i>	Cbis	<i>Neoniphon sammara</i>	Ns
<i>Centropyge flavissima</i>	Cf	<i>Ostracion cubicus</i>	Oc
<i>Cephalopholis argus</i>	Car	<i>Ostracion meleagris</i>	Om
<i>Chaetodon lunula</i>	Clu	<i>Parupeneus barberinus</i>	Pb
<i>Chaetodon auriga</i>	Cau	<i>Parupeneus multifasciatus</i>	Pmu
<i>Chaetodon bennetti</i>	Cben	<i>Pomacentrus pavo</i>	Pp
<i>Chaetodon citrinellus</i>	Cc	<i>Rhinecanthus aculeatus</i>	Ra
<i>Chaetodon ephippium</i>	Ce	<i>Sargocentron microstoma</i>	Sm
<i>Chaetodon ornatissimus</i>	Co	<i>Sargocentron spiniferum</i>	Ssi
<i>Chaetodon pelewensis</i>	Cp	<i>Scarus altipinnis</i>	Sa
<i>Chaetodon reticulatus</i>	Cr	<i>Scarus oviceps</i>	So
<i>Chaetodon trifasciatus</i>	Cti	<i>Scarus psittacus</i>	Sp
<i>Chaetodon ulietensis</i>	Cul	<i>Scarus schlegeli</i>	Sch
<i>Chaetodon unimaculatus</i>	Cun	<i>Scarus sordidus</i>	Sco
<i>Chaetodon vagabundus</i>	Cva	<i>Stegastes nigricans</i>	Sn
<i>Chromis iomelas</i>	Cio	<i>Sufflamen bursa</i>	Sbu
<i>Chromis viridis</i>	Cvi	<i>Thalassoma amblycephalum</i>	Ta
<i>Chrysiptera glauca</i>	Cgl	<i>Thalassoma hardwicke</i>	Th
<i>Chrysiptera leucopoma</i>	Cle	<i>Thalassoma lutescens</i>	Tl
<i>Coris aygula</i>	Cay	<i>Thalassoma purpurum</i>	Tp
<i>Ctenochaetus binotatus</i>	Cbin	<i>Zanclus cornutus</i>	Zc
<i>Ctenochaetus striatus</i>	Cst	<i>Zebraosoma scopas</i>	Zs
<i>Dascyllus aruanus</i>	Da	<i>Zebraosoma veliferum</i>	Zv

Table 3 Comparisons of the three temporal replicates (months) for each site (FR1:fringing reef, BR1 and BR2:barrier reef, and C1:channel reef) for the peak frequency (F_{peak}) and the power spectral density (PSD_{peak}) with Kruskal–Wallis tests

Kruskal–Wallis tests	Variable	χ^2	Df	P
FR1	Power spectral density	1.37	2	0.50
	Peak frequency	2.1	2	0.34
BR1	Power spectral density	0.14	2	0.93
	Peak frequency	1.4	2	0.49
BR2	Power spectral density	2.24	2	0.32
	Peak frequency	2.81	2	0.24
C1	Power spectral density	1.97	2	0.37
	Peak frequency	0.91	2	0.63

Df degrees of freedom

Results

Biophony in the high-frequency band (2–10 kHz)

During day-time (Fig. 2a), three of the four studied sites (BR1, BR2, and C1) had a similar median F_{peak} , between 5.1 and 6.2 kHz, while FR1 had a significantly lower F_{peak} centred at 3.7 kHz (Kruskal–Wallis test, $\chi^2_3 = 13.3$, $P = 0.003$ —Online Resource 1; see Dunn *post-hoc* tests' results in Online Resource 2). During night-time, F_{peak} displayed a similar pattern than during day-time (Fig. 2b). BR1, BR2, and C1 had an F_{peak} between 5.3 and 6.3 kHz, while FR1 had a significantly lower F_{peak} , centred at 3.7 kHz (Kruskal–Wallis test, $\chi^2_3 = 10.1$, $P = 0.01$).

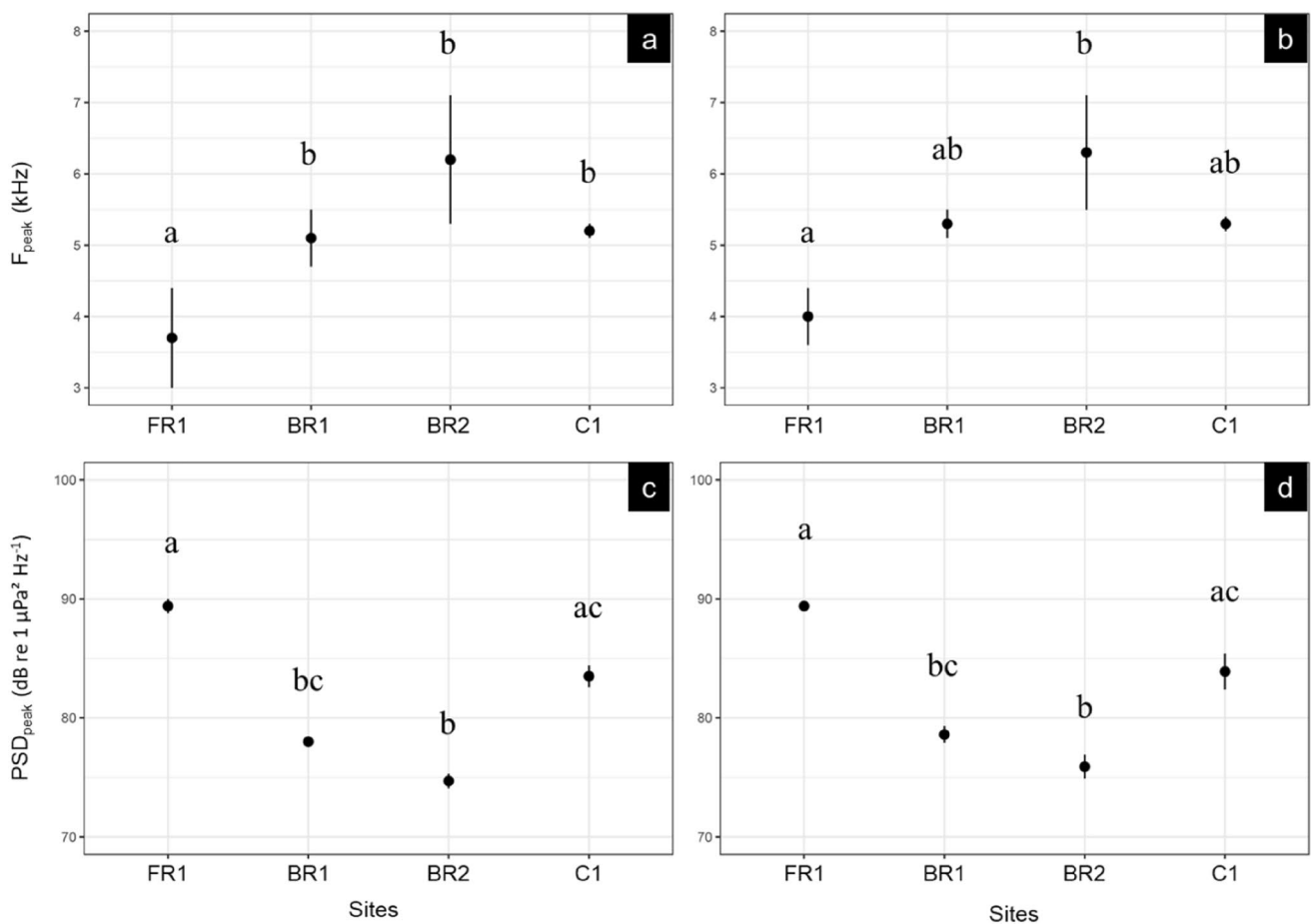


Fig. 2 Acoustic parameters (F_{peak} and PSD_{peak}) for the high-frequency band (2–10 kHz) for each site. F_{peak} (a, b) and PSD_{peak} (c, d). Panels a and c are for day-time. Panels b and d are for night-time. Values are means of the three temporal replicates \pm standard deviation. Different

letters indicate significant differences at $P < 0.05$, provided by Dunn's post hoc tests. Sites with similar letters are not significantly different. Sites with different letters are significantly different

During day-time, the median PSD level (PSD_{peak}) of FR1 was significantly higher than that of BR1 and BR2 (Fig. 2c, Kruskal–Wallis test, $\chi^2_3 = 21.6$, $P < 0.001$ —Online Resource 1; see Dunn *post-hoc* tests' results in Online Resource 2). BR2 had the lowest PSD_{peak} (74.7 ± 0.6 dB re $1 \mu Pa^2 Hz^{-1}$). C1 had a significantly higher PSD_{peak} than BR2 (83.5 ± 0.9 dB re $1 \mu Pa^2 Hz^{-1}$). During night-time (Fig. 2d), FR1 had the highest PSD_{peak} (89.4 ± 0.1 dB re $1 \mu Pa^2 Hz^{-1}$), and BR2 the lowest (75.9 ± 1.0 dB re $1 \mu Pa^2 Hz^{-1}$) (Kruskal–Wallis test, $\chi^2_3 = 18.9$, $P < 0.001$).

The four sites showed no significant differences between day-time and night-time for F_{peak} or PSD_{peak} (Online Resource 1—Kruskal–Wallis test, $\chi^2_{12} < 92$, $P \geq 0.24$). Lastly, when looking together PSD_{peak} and F_{peak} values during day-time and night-time, FR1 and BR2 were the most different sites. FR1 had the highest PSD_{peak} and the lowest F_{peak} , while BR2 had the lowest PSD_{peak} and the highest F_{peak} . The two barrier sites (BR1 and BR2) were the most similar habitats (Fig. 2).

Biophony in the low-frequency band (50–2000 Hz)

During day-time (Fig. 3a), BR1, BR2, and C1 had a similar F_{peak} , between 230 and 260 Hz, while FR1 had a significantly higher F_{peak} centred at 350 Hz (Kruskal–Wallis test, $\chi^2_3 = 19.5$, $P < 0.001$ —Online Resource 1; see Dunn *post-hoc* tests' results in Online Resource 2). During night-time (Fig. 3b), BR1 and BR2 had a similar F_{peak} (259 ± 1 Hz and 261 ± 24 Hz respectively), while C1 had the lowest F_{peak} (168 ± 5.0 Hz), and FR1 the highest (314 ± 37 Hz) (Kruskal–Wallis test, $\chi^2_3 = 18.2$, $P < 0.001$).

During day-time (Fig. 3c), the PSD_{peak} of FR1 was significantly higher than in BR2, which had the lowest PSD_{peak} (101.6 ± 0.6 dB re $1 \mu Pa^2 Hz^{-1}$, and 95.9 ± 0.4 dB re $1 \mu Pa^2 Hz^{-1}$ respectively—Kruskal–Wallis test, $\chi^2_3 = 14.8$, $P < 0.001$). C1 and BR1 had a similar PSD_{peak} centred at 99.5 dB re $1 \mu Pa^2 Hz^{-1}$ (100 ± 0.8 dB re $1 \mu Pa^2 Hz^{-1}$, and 98.6 ± 1.3 dB re $1 \mu Pa^2 Hz^{-1}$ respectively). During night-time (Fig. 3d), PSD_{peak} had inter-site patterns

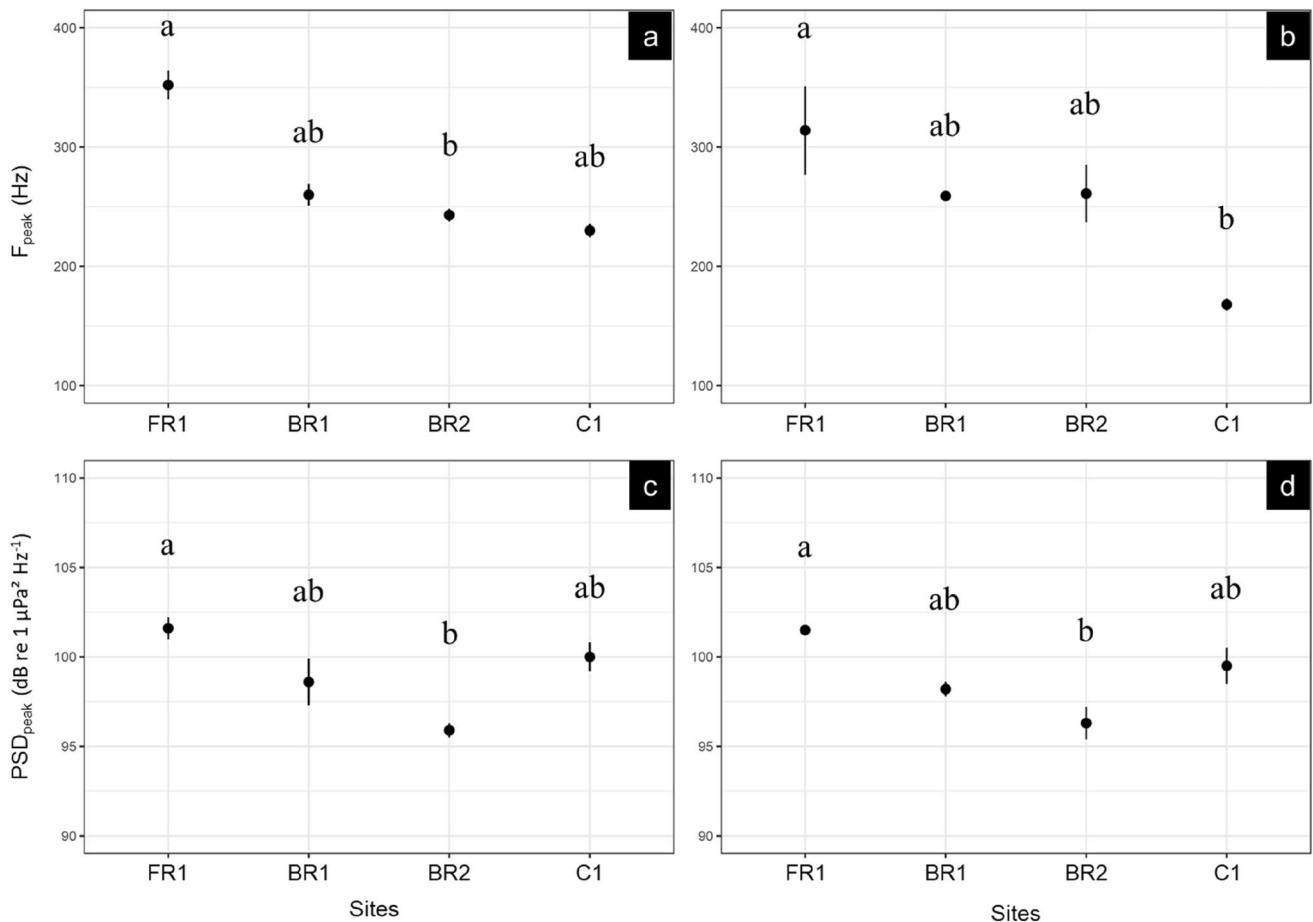


Fig. 3 Acoustic parameters (F_{peak} and PSD_{peak}) for the low-frequency band (50–2000 Hz) for each site. F_{peak} (a, b) and PSD_{peak} (b, d). Panels a and c are for day-time. Panels b and d are for night-time. Values are means of the three temporal replicates \pm standard deviation. Dif-

ferent letters indicate significant differences at $P < 0.05$, provided by Dunn's post hoc tests. Sites with similar letters are not significantly different. Sites with different letters are significantly different

similar to day-time ones (Kruskal–Wallis test, $\chi^2_3 = 20.1$, $P < 0.001$). FR1 PSD_{peak} was significantly higher than BR2 (101.5 ± 0.1 dB re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$, and 96.3 ± 0.9 dB re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$ respectively), which had the lowest PSD_{peak} (Fig. 3b). Similarly, C1 and BR1 had a similar PSD_{peak} centred at 99 dB (99.5 ± 1.0 dB re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$, and 98.2 ± 0.4 dB re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$ respectively).

The four sites showed no significant differences between day-time and night-time for F_{peak} or PSD_{peak} (Online Resource 1—Kruskal–Wallis test, $\chi^2_{12} < 95$, $P > 0.19$). Lastly, when looking together PSD_{peak} and F_{peak} values during day-time and night-time, FR1 had the highest values of PSD_{peak} and F_{peak} during the day- and night-time. C1 had the lowest F_{peak} while BR2 had the lowest PSD_{peak} . The two barrier sites (BR1 and BR2) were the most similar habitats (Fig. 3).

Vocal fish communities & link between acoustic and ecological parameters

The fish communities varied significantly among the four sites in terms of H-index for all fish (Kruskal–Wallis test, $\chi^2_3 = 14.5$, $P = 0.002$) and H-index for vocal fish species (Kruskal–Wallis test, $\chi^2_3 = 9.6$, $P = 0.02$) (Table 4, Online Resource 1). Thus, FR1 had the lowest H-index and H_{vocal} -index. The highest H-index was found on BR1 and the highest H_{vocal} -index was found on BR2. In contrast, the species richness (SR) and density (D) of all species and of vocal fish species did not significantly vary among the four sites (Kruskal–Wallis tests, $\chi^2_3 = 0.78$ – 6.62 , all $P > 0.05$ —Table 3, Online Resource 1).

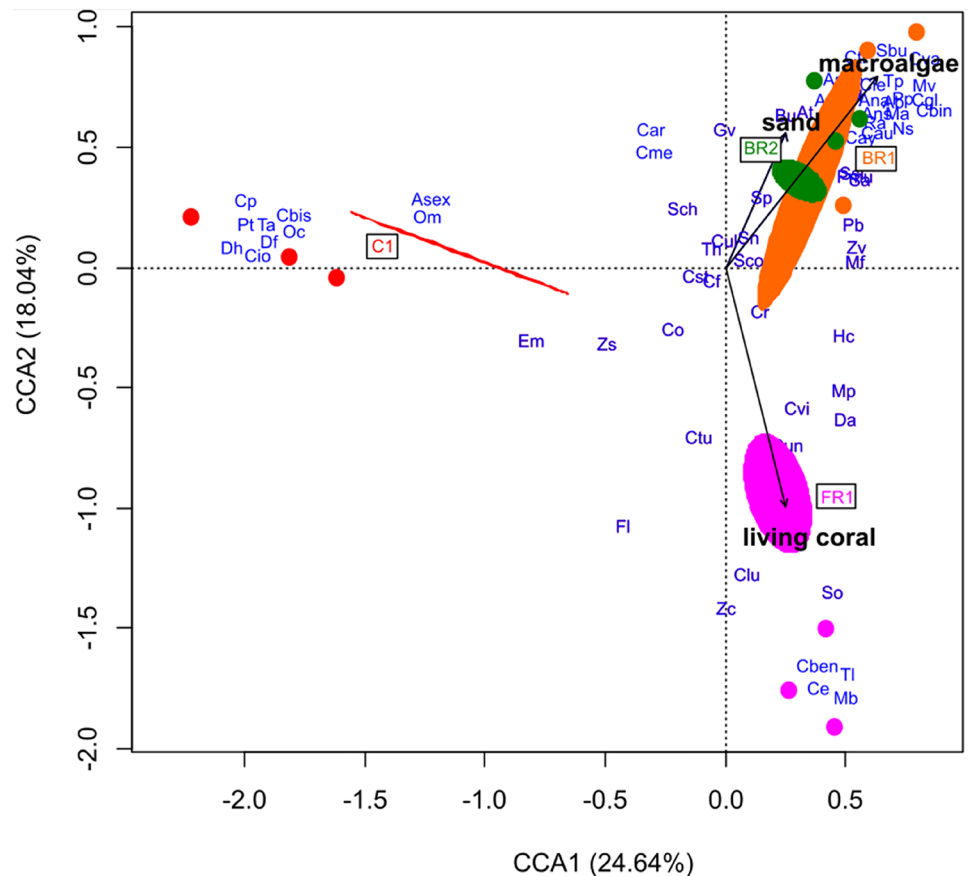
The CCA indicated that the vocal fish community composition was mainly influenced by the percentages

Table 4 Species richness (SR and SR_{vocal}), density (D and D_{vocal}), and H-index (H and H_{vocal}) of all fish and of vocal fish species of the four study sites

	All fish			Vocal fish species		
	SR	D	H	SR_{vocal}	D_{vocal}	H_{vocal}
FR1	28 ± 19	288 ± 223	2.02 ± 0.29	26 ± 17	281 ± 213	1.98 ± 0.27
BR1	29 ± 7	258 ± 132	2.62 ± 0.22	23 ± 6	239 ± 124	2.32 ± 0.15
BR2	39 ± 20	320 ± 219	2.53 ± 0.27	31 ± 14	281 ± 179	2.34 ± 0.23
C1	22 ± 10	226 ± 133	2.35 ± 0.18	20 ± 10	214 ± 121	2.20 ± 0.20

Values are means of the three temporal replicates ± standard deviation

Fig. 4 Canonical Correspondence Analysis (CCA) ordination plots of the vocal fish community composition. The analysis is based on Bray–Curtis dissimilarities of relative abundance of the 64 vocal fish species present at the four sites (C1 in red, BR1 in orange, BR2 in green and FR1 in pink, and three temporal replicates per site: colour points). Black arrows show the influence of benthic cover features. Ellipses are 95% confidence intervals for each site. For the correspondence between the abbreviations and the list of species, see Table 2



of macro-algae, living coral, and sand (Fig. 4). Among the 64 vocal species observed, 31 were specific to one site, but nine of the ten most abundant vocal species were present in all four sites (but with some different abundances according to the sites). Thus, FR1 was mainly characterized by a high percentage of living coral (fish species specific to this site: *Chaetodon bennetti*, *Chaetodon ephippium*, *Myripristis pralinia*, and *Thalassoma lutescens*). BR1 and BR2 were mainly characterized by the highest proportion of sand and macro-algae (fish species specific to these two sites: *Ctenochaetus binotatus*, *Mulloidichthys vanicolensis*, *Neoniphon samara*, and *Sufflamen bursa*). Those three sites had positive CCA1 scores (i.e., were located on the right side of the axis). C1 had

negative CCA1 scores (i.e., were located on the left side of the axis), with few site-specific species (*Centropyge bispinosa*, *Chaetodon pelewensis*, *Chromis iomelas*, and *Dascyllus flavicaudus*).

Lastly, the possible link between marine biodiversity and soundscapes was analyzed. Spearman correlation tests showed that only the percentage of living coral (LC) was positively correlated with the peak frequency (F_{peak}) during day-time and in the low-frequency band ($\rho = 0.91$; $P = 0.001$ —Table 5). No significant correlation between any acoustic and any environmental parameters were detected at night in the low-frequency band and during the day- or night-time in the high-frequency band (see Online Resource 3).

Table 5 Matrix of Spearman correlation tests between acoustic and ecological data during the day-time in the low-frequency band

	F_{peak}	PSD_{peak}	SR_{vocal}	D_{vocal}	H_{vocal}
LC	$r=0.57$ $P=0.002$	$r=0.31$ $P=0.21$	$r=0.05$ $P=0.96$	$r=0.20$ $P=0.99$	$r=-0.58$ $P=0.1$
DC	$r=-0.51$ $P=0.41$	$r=-0.52$ $P=0.09$	$r=0.02$ $P=0.88$	$r=-0.16$ $P=0.76$	$r=0.20$ $P=0.44$
S	$r=-0.18$ $P=0.68$	$r=0$ $P=0.98$	$r=0.05$ $P=0.73$	$r=0.05$ $P=0.71$	$r=0.45$ $P=0.28$
Ma	$r=-0.18$ $P=0.79$	$r=-0.34$ $P=0.3$	$r=0.43$ $P=0.29$	$r=0.48$ $P=0.35$	$r=0.55$ $P=0.09$

r corresponds to the correlation value, and P to the P-value. Only the percentage of living coral (LC) was significantly and positively correlated with the peak frequency (F_{peak}). Significant values are in bold
DC dead coral, *S* sand, *Ma* macro-algae

Discussion

In coral reefs, several studies have found a spatial variation in reef sounds, suggesting that habitat-associated soundscapes can provide essential information about the quality of a habitat (Kennedy et al. 2010; Staaterman et al. 2013; Bertucci et al. 2015) and its animal communities (Nedelec et al. 2015; Bertucci et al. 2020b; Raick et al. 2023). On Bora-Bora, we showed that three main morphological units (barrier reef, fringing reef and channel) differed in terms of two acoustic features: the peak frequency (F_{peak}) and the corresponding power spectral density (PSD_{peak}). In particular, we showed that a higher living coral cover was significantly positively correlated with F_{peak} in the low-frequency band during day-time. Several studies (Nedelec et al. 2015; Raick et al. 2023) provided evidence that variations in the soundscape features of coral reefs in French Polynesia could be linked with habitat and their corresponding vocal communities. Other studies showed that a reef with a higher living coral cover is often associated to higher sound pressure levels (Tricas and Boyle 2014; Bertucci et al. 2016) since healthy coral communities can shelter more species than damaged coral reefs. Therefore, changes in species assemblage associated with different states of habitat degradation or anthropogenic pressures could be detected by means of acoustics, i.e., through altered acoustic activity of organisms, acoustic diversity or changes in some spectral characteristics. Significant differences in the high-frequency parameters are likely due to different invertebrate communities and/or in their abundance (Hildebrand 2009; Raick et al. 2021). Yet, there is still an important lack of knowledge about the sounds produced by marine invertebrate species compared to fish, despite that their signals dominate underwater soundscape of many coastal habitats (Staaterman 2016). Their low interference with anthropogenic noise would however make them very good candidates

for detecting environmental changes (Staaterman et al. 2014; Staaterman 2016). To date, snapping shrimps (Johnson et al. 1947; Knowlton and Moulton 1963; Chitre et al. 2012), sea urchins (Radford et al. 2008), lobsters (Meyer-Rochow and Penrose 1976; Patek 2001; Buscaino et al. 2011) and crabs (Salmon 1967; Salmon and Hyatt 1983), for example, are already known to contribute to the soundscapes of many temperate, subtropical and tropical coastal habitats. Similarly, despite fish communities and soundscapes in the low-frequency range were significantly different, biodiversity indices based on visual surveys did not differ significantly (with the exception of the H-index in the fringing reef). This suggests that the acoustic environment is influenced by the activity of some vocal species and not by the totality of species present. A prerequisite for future studies on the ecology of marine organisms and underwater soundscapes is therefore the specific identification of soniferous species and the characterisation of the sounds generated by these animals. The nocturnal fish biophony needs to be better understood. Indeed, diurnal vocalizations, mainly attributed to Pomacentridae, can be more accurately characterised thanks to visual confirmations (Tricas and Boyle 2014; Raick et al. 2021, 2023). At night, visual observations are more difficult and the use of light would alter fish behaviours. Moreover, complementary non-invasive methods, such as environmental DNA could be used in future surveys to provide more precise evaluation of biodiversity.

The variations in acoustic characteristics were not significant between the three temporal replicates (monthly from February to April 2021), making PAM efficient to study local biophony through time. Our study provides information about ambient reef sounds that are habitat-specific in the absence of a strong human activity (due to COVID-19 sanitary restrictions). This will therefore constitute a baseline for future monitoring studies on the effects of the presence or absence of tourists on coral reefs. It is now well accepted that anthropogenic noise is an emerging pollutant and threat for subaquatic environments. An increasing number of studies show that higher noise levels in marine environments linked to human activities are impacting animals and their ecosystems in complex ways through acute and chronic stresses (Duarte et al. 2021; Ferrier-Pagès et al. 2021). Many aspects such as effects on population dynamics, and on cumulative impacts with other stressors are still insufficiently understood.

Nevertheless, while acoustic recorders can now be deployed for long periods, in places that are not easily accessible, making sounds an almost continuous proxy of biodiversity, advances in sound detection and soundscape description are needed for long-term acoustic monitoring to keep pace with current environmental changes and associated biodiversity loss. Two recent studies (Pieretti and Danovaro 2020; Dimoff et al. 2021) suggested that the

extensive use of acoustic monitoring is hampered by the lack of algorithms enabling the discrimination of different sound sources (e.g., geophysical, anthropogenic, and biological). In this perspective, the use of artificial intelligence to develop automatic learning and classification models based on sound libraries is very promising and would be greatly needed in order to speed up data processing (Ross et al. 2018; Bergler et al. 2022). Hopefully, such improvement will strengthen the relevance of acoustic tools in national and international regulatory frameworks.

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Author contribution LM, XR, and DL designed the monitoring protocol. LM, EG, TM, VS, EB, and DL collected the data. LM, XR and FB analysed the data and prepared the figures. LM, XR and FB wrote the manuscript. EP and DL reviewed and edited the different version of the manuscript. All authors reviewed the final version of the manuscript.

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Declarations

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