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LOCAL SONIC ACTIVITY REVEALS POTENTIAL PARTITIONING IN A CORAL REEF FISH COMMUNITY

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ABSTRACT

How vocal organisms share acoustic space has primarily received attention in terrestrial environments. Comparable studies in marine environments, however, remain rare. By recording sounds on a coral reef in French Polynesia for 48 h and 24 h, this study provides first insights on how different sound types are distributed within the acoustic space and may create acoustic niches optimizing acoustic communication within a highly diverse community containing numerous soniferous fish species. Day-time was dominated by two to six sound types, while recordings performed at night revealed a more diverse vocal community made of up to nineteen sound types. Calling activity was distributed over time allowing each sound type to dominate the soundscape sequentially. Additionally, differences in the acoustic features of sounds occurring during the same period were observed. Such partitioning in time and acoustic spaces would reduce potential overlaps of sounds produced by vocal species living in sympatry in coral reefs.

Introduction

Acoustic space is a limited niche parameter; thus, co-occurring species can reduce competition if they use this space in different ways (Hastings and Širović 2015). The acoustic niche hypothesis (ANH) predicts that signals produced by species vocalizing within a community should not overlap, requiring a partitioning in the temporal and spectral domains (Krause 1993) to increase chances for the intended conspecific recipients to hear a signal among all competing biotic and abiotic sounds (Stone 2000; Krause 2002; Ruppé et al. 2015). A major challenge encountered by vocal organisms is to efficiently insert their signals in the general background noise while avoiding any potential costly overlaps with other signals (Grafe 1996). Occupying different periods of time and different frequency bands would then be an effective way for heterospecifics to avoid acoustic competition (Krause 1993). However, contrasting studies suggest that acoustic competition may instead lead to signal convergence between species vocalizing at the same time with similar acoustic features (Planqué and Slabbekoorn 2008; Tobias et al. 2014). To further increase signal distinctiveness and opportunities for correct signal discrimination, some species of frogs, birds and mammals increase the duration of their signals or their calling rate to increase the probability of being detected (Miller 1982; Brumm et al. 2004).

In fishes, the use of passive recording methods detected a clear temporal partitioning between diurnal and nocturnal vocal communities (defined as groups of species producing sounds) living in a deep rocky reef (Ruppé et al. 2015; Farina and James 2016). While the different sounds produced diurnally were found to often overlap in their pulse periods and dominant frequencies, overlap was rarely found between sounds recorded nocturnally (Ruppé et al. 2015). This increased level of call distinctiveness has been linked to a greater need to be distinguished during night hours since reduced visual cues increase the importance of sound communication. Partitioning of the vocal activity may also respond to a high density of callers, creating competition for communication space (Ruppé et al. 2015). Among the most biologically diverse ecosystems worldwide, coral reefs provide an excellent system to explore acoustic partitioning strategies in fish. The high taxonomic diversity of coral reefs, associated to a high number of soniferous fish species (e.g. Parmentier et al. 2011, 2016, 2017, 2019), should constitute a strong pressure on the vocalization strategies of fishes. Indeed, acoustic behaviours are prominent in these biodiversity hotspots. Sympatric populations of hundreds of fish species produce sounds during agonistic interactions with competitors, in response to predators or threats, and during courtship and spawning (Fine et al. 1977; Myrberg 1981; Allen and Werner 2002; Bellwood and Wainwright 2002; Amorim 2006). Coral reefs may then be considered as acoustic hotspots, and called "choral reefs" as proposed by Lobel and colleagues (Lobel et al. 2010; Lobel 2013). On a Hawaiian reef, for example, a study documented 85 sounds types produced by 45 of the 96 resident species (Tricas and Boyle 2014). Agonistic sounds produced during competitive interactions over food, space, or nests, were identified for damselfishes (Pomacentridae), surgeonfishes (Acanthu- ridae), butterflyfishes (Chaetodontidae), and triggerfishes (Balistidae). Reproductive sounds associated with courtship, spawning, or nest defence were produced by damselfishes, surgeonfishes, butterflyfishes, goatfishes (Mullidae), parrotfishes (Scaridae), wrasses (Labridae) and Moorish idols (Zanclidae).

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The majority of the work on acoustic partitioning has been conducted in terrestrial environments on focal taxa such as insects (e.g. Schmidt and Römer 2011; Schmidt et al. 2013; Schmidt and Balakrishnan 2015), amphibians (e.g. Sinsch et al. 2012; Bignotte-Giró and López-Iborra 2018; Lima et al. 2019), birds (e.g. Naugler and Ratcliffe 1994; Brumm 2006; Luther 2009) and marine mammals (e.g. Mossbridge and Thomas 1999). Significantly less is known regarding fish (Ruppé et al. 2015).

In recent years, passive acoustic monitoring has allowed the continuous non-invasive monitoring of marine environments (Luczkovich et al. 2008; Bertucci et al. 2016, 2017), but how different fish species share a habitat's available acoustic space and how a vocal community can avoid cacophony remain mostly unexplored in the majority of fish acoustic studies (e.g. Mullet et al. 2017). While former studies often focused on individual species vocal activity, current recording capacity allows for a more collective approach of the marine biophony. Biotic sounds can now provide valuable information not only on the presence and identity of sound producers but also on how they interact within a community (Rountree et al. 2006; Luczkovich et al. 2008). Here, we explored the sonic activity of a French Polynesian coral reef to appreciate the local diversity of sound types, categorize these sounds, study how they were distributed on a daily basis, and whether their acoustic features differed. We hypothesize that different sound types should be detected at specific moments of the day and sound types that may cooccur should present differences in their acoustic features to optimize the calling strategies of vocal species within the community, as predicted by the ANH.

Materials and methods

DATA COLLECTION

Two passive acoustic recording sessions were conducted on the north coast of Moorea Island (French Polynesia—17° 28'S, 149° 53'W) in March and April 2015. All recordings were conducted on the fore reef at a depth of 20 m within the bounds of the Tiahura marine protected area.

An autonomous underwater long-term acoustic recorder Remora-ST (Loggerhead Instruments, Sarasota, FL, USA) was deployed from 04-Mar-2015 to 06-Mar-2015 and from 6-Apr-2015 to 7-Apr-2015, for 48 h and 24 h, respectively. A study performed at the same period showed no variations in the acoustic characteristics of the local soundscape nor modifications of the local ichthyologic community during this one-month period (Bertucci et al. 2016). The recorder was connected to a HTI96-min hydrophone (sensitivity: - 211 dB re 1 V for a sound pressure of 1 µPa, flat frequency response 2 Hz to 30 kHz; High Tech Inc, Long Beach, MS, USA) and was scheduled to record sounds for 5 min every hour at a sampling rate of 48 kHz (16-bit resolution), with a + 33 dB gain. The recorder was attached to a block of lead positioned on the sea floor.

To assess local species diversity and abundance, visual surveys of benthic habitat and fish communities were conducted prior to acoustic recorder deployment in the area of recording. Three 20 m transect lines were placed parallel to the shore and 2.5 m apart (see Galzin et al. 2016 for details).

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DATA PROCESSING

Recordings were down sampled at a rate of 6 kHz using Avi- soft-SASLab Pro-5.2.10 software and a 20 Hz high-pass filter was applied to eliminate very low frequencies, thus providing an analysis range from 20 Hz to 3 kHz, corresponding to the frequency range in which most fish species are known to vocalize and hear (Lobel et al. 2010; Tavolga et al. 2012). Acoustical analyses were conducted by visually and aurally inspecting the oscillograms (representation of the amplitude of a sound as a function of time) and spectrograms (representation of the frequency composition as a function of time; Fast Fourier Transform FFT, 128 points, Hamming window, 75% overlap) over a 30 s time window. Night-time recordings were characterized by a higher ambient noise than day-time recordings, particularly due to the increased activity of invertebrates (Bertucci et al. 2016), but day-time recordings still experienced high ambient noise likely due to transient boat noise. This day-time and night-time ambient noise, however, never prevented the detection of biological sounds with good signal-to-noise ratio in the 20 Hz-3 kHz frequency band. Each distinct biological sound was tagged using the insert label function of Avisoft software and was attributed a sound type based on its a priori features. Sound types could refer to the likely sound-producing family (e.g. Pomacentridae or Balistidae) based on the existing literature, or be based on a descriptive or onomatopoeic name (e.g. growl, pulse train, boom). Recordings were examined blindly by two observers who regularly cross-checked their sound tagging to produce a consistent final transcript of sound types.

DATA ANALYSIS

The number of sounds and the number of sound types detected over 24 h were calculated for eight 3 h-periods (starting with the 10:00-12:00 period), which allows for separating critical calling periods (i.e. dawn, day, dusk and night-time). The normality and homogeneity of the variances were respectively tested by means of Shapiro-Wilk tests ($N = 8$, $W = 0.97$, $P = 0.06\text{-}0.12$) and Bartlett's tests ($N = 8$, $\chi^2_7 = 6.18\text{-}9.31$, $P = 0.23\text{-}0.52$). Kruskal-Wallis tests were used to compare differences in the number of detected sounds and sound types between the 3 h-periods. Dunn's post-hoc tests for multiple pairwise comparisons were then performed should a significant difference be found.

Sound types were isolated and their median numbers were reported. Sound types with a median number under five times per 5-min interval per hour were not considered in the analysis. These sounds may be produced by organisms with a decreased vocal activity at the time of the recordings and which are thus less dependent on present acoustic partitioning. Their low occurrence also often result in a low number of sounds for subsequent analysis. The daily pattern of sound production was reported for each sound type by comparing their relative contribution (%) to the total number of sounds detected per hour. Temporal partitioning was determined for each sound type using a Kruskal-Wallis test to compare vocal activity between the 8 different 3 h-periods. Dunn's post-hoc tests were then performed should significant differences be identified.

Acoustic analysis was conducted on $N = 10\text{-}16$ sounds from the 11 most prominent sound types, i.e. which consistently showed a good signal-to-noise ratio allowing sounds to be analysed. The following acoustic characteristics were measured from oscillograms: the total duration of sounds (ms), the number of pulses within a sound, the period of pulses (peak-to-peak interval, ms) and the pulse duration (ms). The dominant frequency (Hz) was measured from logarithmic power spectra (Electronic Supplementary Material 1). The normality of all acoustic features was tested by means of Shapiro-Wilk tests ($N = 11$, $W = 0.39$-091, all $P < 10^{-3}$). Kruskal-Wallis tests were therefore used to compare acoustic features of co-occurring sound types. Dunn's post-hoc tests for multiple pairwise comparisons were then performed should a significant difference be found.

All analysis were two-sided and carried out in R 3.4.2 (R Core Team) at $\alpha = 0.05$.

Results

DIVERSITY OF SOUNDS

Visual surveys revealed the presence of 83 different fish species and 1966 observed individuals, among which 55 vocal species representing 1599 individuals (Table 1). Living coral covered 43 ± 4% of the substratum (full data available on https://observatoire.criobe.pf).

Table 1. List of the fish species observed at the recording site

Species	Number	Species	Number
Acanthurus nigricauda	3	*Labroides bicolor*	4
Acanthurus nigrofuscus	9	*Labroides dimidiatus*	3
Acanthurus olivaceus	1	*Labroides rubrolabiatus*	5
Acanthurus pyroferus	1	***Lepidozygus tapeinosoma***	150
Acanthurus thompsoni	14	*Macropharyngodon meleagris*	3
Anampses Caeruleopunctatus	1	***Melichthys niger***	1
Aphareus furca	3	***Melichthys vidua***	8
Balistapus undulatus	6	***Myripristis kuntee***	1
Canthigaster amboinensis	1	*Naso lituratus*	7
Caracanthus maculatus	14	*Nemateleotris magnifica*	4
Centropyge bispinosa	5	*Neocirrhites armatus*	29
Centropyge flavissima	29	*Odonus niger*	8
Centropyge loriculus	25	*Paracirrhites arcatus*	64
Cephalopholis argus	8	*Paracirrhites forsteri*	1
Cephalopholis urodeta	10	***Parupeneus insularis***	1
Chaetodon ornatissimus	5	***Parupeneus multifasciatus***	7
Chaetodon pelewensis	22	*Plagiotremus tapeinosoma*	10
Chaetodon quadrimaculatus	4	***Plectroglyphidodon johnstonianus***	41
Chaetodon reticulatus	4	***Plectroglyphidodon lacrymatus***	5
Chaetodon unimaculatus	6	***Pomachromis fuscidorsalis***	15
Cheilinus oxycephalus	3	***Pseudanthias mooreanus***	8
Chlorurus sordidus	14	***Pseudanthias olivaceus***	30
Chromis acares	510	*Pseudocheilinus hexataenia*	22
Chromis agilis	5	*Pseudocheilinus octotaenia*	2

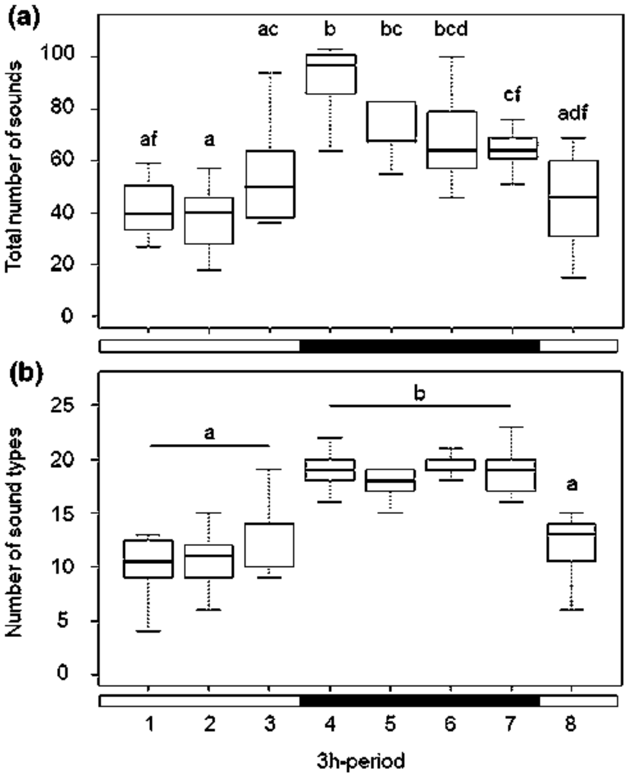
Chromis iomelas	60
Chromis margaritifer	85
Chromis vanderbilti	380
Chromis xanthura	2
Cirrhilabrus exquisitus	7
Cirrhilabrus scottorum	29
Cirripectes variolosus	2
Coris gaimard	1
Ctenochaetus binotatus	4
Ctenochaetus flavicauda	5
Ctenochaetus striatus	10
Dascyllus trimaculatus	6
Epibulus insidiator	1
Forcipiger flavissimus	1
Gomphosus varius	10
Halichoeres claudia	13
Halichoeres hortulanus	3
Hemigymnus fasciatus	1
Pseudocheilinus tetrataenia	13
Ptereleotris evides	1
Sargocentron caudimaculatum	2
Sargocentron microstoma	6
Scarus altipinnis	5
Scarus frenatus	2
Scarus ghobban	1
Scarus globiceps	4
Scarus oviceps	5
Scarus psittacus	10
Stegastes fasciolatus	23
Stethojulis bandanensis	8
Sufflamen bursa	3
Thalassoma lutescens	1
Thalassoma quinquevittatum	24
Zebrasoma scopas	4
Zebrasoma veliferum	2

Bold names indicate vocal species and species belonging to a vocal genus

A total of 4278 sounds were detected. Sounds were categorized into 22 main sound types, each composed of 12-459 sounds. There were significant increases in the number of sounds (Kruskal-Wallis test, $\chi^2_7 = 38.94$, $P < 10^{-3}$) and in the number of sound types (Kruskal-Wallis test, $\chi^2_7 = 50.69$, $P < 0.01$) detected at dusk, i.e. between periods 3 and 4 (16:00-21:00) (Fig. 1). Total number of sounds peaked at period 4 (19:00-21:00) and gradually decreased throughout the night (Fig. 1a). However, the number of sound types remained significantly higher throughout the night before decreasing at dawn (period 8, 07:00-09:00) and remain relatively low throughout the day (Fig. 1b).

Detected sound types could be divided into three groups according to their detection times (Fig. 2). Group 1 consisted of four sound types detected continuously over 24 h with no marked peak period during day or night, and representing between 10 and 45% of the total number of sound detected (Fig. 2, grey sound types). During day-time (07:00-18:00), a second group of two sound types (group 2) added to group 1 (Fig. 2, yellow-orange sound types). These two groups dominated the soundscape, representing all together between 75% at 06:00 and 100% at 10:00 of the total number of sounds detected. At dusk, group 2 was substituted by group 3 which was more diverse and made of 14 sound types (Fig. 2, blue and purple sound types). During the night (19:00-06:00), groups 1 and 3 accounted for 95% to 100% of the detected sounds (Fig. 2). Some sound types belonging to group 3 were recorded occasionally during day-time although in a very low proportion. In addition to these three groups, two minority sound types were detected. A "buzz-like" sound type was detected during day- and night-times but not continuously unlike other sound types from group 1, and it never accounted for more than 6% of the total number of detected sounds (Fig. 2, light blue sound type). A "knocking" sound type appeared to be detected from 09:00 to 15:00 during day-time and from 00:00 to 04:00 during night-time (Fig. 2, light green sound type). Like the "buzz-like" sound type, it never exceeded 6% of the total number of detected sounds.

Figure 1a. Total number of sounds and **Figure 1b.** number of sound types detected for each 3 h-period (N = 24). Period 1: 10:00-12:00, Period 2: 13:00-15:00, Period 3: 16:00-18:00, Period 4: 19:00-21:00, Period 5: 22:00-00:00, Period 6: 01:00-03:00, Period 7: 04:0006:00, Period 8: 07:00-09:00. White horizontal bars below x-axis represent day-time, black horizontal bar represents night-time. Boxes are the first and third quartiles, thick horizontal bars are the median and whiskers correspond to the range (min-max) of the distributions. Different letters show significant differences for P < 0.05, provided by Dunn's post hoc tests. Time periods with similar letters are not significantly different, time periods with different letters are significantly different.



TEMPORAL PARTITIONING OF SOUND TYPES

The 11 most dominant sound types, which displayed consistently high signal-to-noise ratio, were considered for acoustical analysis (Fig. 3, Table 2). The daily pattern of these sound types revealed successive periods at which the different sound types were predominantly detected.

Day-time was dominated by the two sound types of group 2, which are sounds typically attributed to Balistidae (Type 1) and Pomacentridae (Type 2) (Fig. 3a). Type 1 (Kruskal Wallis test: $\chi^2_7 = 30.45$, $P < 10^{-3}$) showed a significantly higher number of sounds from 10:00 to 18:00 (periods 1 to 3) than from 19:00 to 03:00 (periods 4-6) (Dunn's post-hoc tests: Z=2.79-3.43, P = 0.02-0.045). On the contrary, Type 2 appeared more homogenously detected and a significant difference (Kruskal-Wallis test: $\chi^2_7 = 23.11$, P = 0.0016) was found only between period 2 (13:00-15:00) and period 4 (19:00-21:00) with more sounds detected during day-time (Dunn's post-hoc test: Z = 3.42, P = 0.017). Another sound type, likely produced by fishes of the family Holocentridae, and belonging to group 1, was detected during night and day (Fig. 3b) with a significantly higher number of sounds detected during period 3

(16:00-18:00) than during period 6 (01:00-03:00) (Kruskal-Wallis test: $\chi^2_7 = 15.69$, $P = 0.028$; Dunn's post-hoc test: $Z = 3.35$, $P = 0.022$).

Up to 19 sound types were detected during night-time and were distributed across the different 3 h-periods. Periods 4, 5 and 6 (19:00-03:00) in particular were characterized by a succession of specific combinations of dominating sounds types, including series of booming, pulsed and knocking sounds (Fig. 3c-e). Period 4 was dominated by sound type 4 that was exclusively detected during this 3 h-period (Kruskal-Wallis test: $\chi^2_7 = 40.67$, $P < 10^{-3}$; Dunn's post-hoc tests: $Z = 4.09$-4.87, all $P < 10^{-3}$). Type 5 and Type 6 also showed significantly higher number of sounds during period 4 than during day-time (periods 1-3) (Type 5: Kruskal-Wallis test: $\chi^2_7 = 20.85$, P = 0.004; Dunn's post-hoc tests: Z = 2.69-3.19, P = 0.03-0.045; Type 6: Kruskal-Wallis test: $\chi^2_7 = 14.59$, P = 0.042; Dunn's post- hoc tests: Z=2.14-2.74, P = 0.03-0.045). The same pattern was observed for Type 7 (Kruskal-Wallis test: χ^2_7 = 28.01, P = 0.0002) during the subsequent 3 h-period (period 5: 22:00-00:00) (Dunn's post-hoc tests: Z = 3.05-3.89, P = 0.003-0.045) and for Type 9 during period 6 (01:00-03:00) (Kruskal Wallis test: χ^2_7 = 29.61, P = 0.0001; Dunn's post-hoc tests: Z = 3.04-3.54, P = 0.01-0.045). Finally, sound type 11, consisting of a fast series of pulses, appeared to be produced during the whole night with a peak during period 7 (04:00-06:00) (Fig. 3f) with significantly more sounds detected than during day-time (periods 1-3) (Kruskal-Wallis test: χ^2_7 = 28.89, P = 0.0001; Dunn's post- hoc tests: Z = 3.35-3.61, P = 0.008-0.02).

No significant differences were found between 3 h-peri- ods for sound types 8 and 10 (Kruskal-Wallis tests: χ 27 = 8.53-2.85, P = 0.29-0.89).

ACOUSTIC PARTITIONING OF CO-OCCURRING SOUND TYPES

Acoustical analysis revealed that all co-occurring sound types were significantly different in at least one of their measured characteristics.

Total duration of sounds (Kruskal-Wallis test: χ 210 = 101.02, $P < 10^{-3}$) differed significantly between Type 1 and Type 2, which co-occurred during day-time (Dunn's post-hoc test: Z = 4.22, P = 0.001). These 2 sound types were also significantly different in their dominant frequency (Kruskal-Wallis test: χ210 = 113.03, $P < 10^{-3}$) with Type 2 showing a higher dominant frequency (Dunn's post-hoc test: Z = 3.08, P = 0.045).

The number of pulses (Kruskal-Wallis test: χ210 = 99.74, $P < 10^{-3}$) was significantly higher in Type 4 than in co-occurring Type 5 and Type 6 during 3 h-period 4 (19:00-21:00) (Dunn's post-hoc tests: Type 4 vs. Type 5, Z = 5.95, P < 10 3; Type 4 vs. Type 6, Z = 5.71, $P < 10^{-3}$). Type 4, Type 5 and Type 6 also differed in their period of pulses (Kruskal-Wallis test: χ210 = 120.56, P < 10^{-3}) and pulse duration (Kruskal-Wallis test: χ210 = 124.71, $P < 10^{-3}$). Type 4 showed a significantly shorter period (Dunn's post- hoc tests: Type 4 vs. Type 5, Z=6.81, $P < 10^{-3}$; Type 4 vs. Type 6, Z = 5.95, $P < 10^{-3}$) and shorter pulse duration than Type 5 and Type 6 (Dunn's post-hoc tests: Type 4 vs. Type 5, Z=7.31, $P < 10^{-3}$; Type 4 vs. Type 6, Z=3.76, P = 0.006). While sounds of Type 5 and Type 6 did not differ in their number of pulses (Dunn's post-hoc test, Z = 0.19, P = 1), period of pulses (Dunn's post-hoc test, Z = 0.34, P = 1) and pulse duration (Dunn's post-hoc test, Z = 2.88, P = 0.12), they significantly differed in their dominant frequency (Dunn's post-hoc test: Z=4.31, $P = 0.0007$) with sounds of Type 5 having a lower dominant frequency. Dominant frequencies of Type 5 and Type 6 sounds did not differ from the one of Type 4 sounds (Dunn's post-hoc tests: $Z = 1.88$-2.76, $P = 0.17$-1).

Similarly, period of pulses (Dunn's post-hoc test: $Z = 5.31$, $P < 10^{-3}$) and pulse duration (Dunn's post-hoc test: $Z = 3.75$, $P = 0.006$) allowed differentiation of sounds of Type 7 and Type 8, co-occurring mostly during 3 h-period 5 (22:00-00:00), with Type 7 displaying a shorter period and shorter pulses than Type 8. Type 8 also showed a lower dominant frequency than Type 7 (Dunn's post-hoc test: Z=5.86, $P < 10^{-3}$).

Dominant frequency was the only feature differentiating sounds of Type 9 and Type 10 during the 3 h-period 6 (Dunn's post-hoc test: Z=4.54, $P = 0.0002$) with sounds of Type 10 showing lower frequencies than Type 9.

Figure 2. Relative contribution (average %) of the different sound types in the total number of sounds detected for each hour (N = 72). Each sound type is represented by a different colour. Greys: group 1 = sound types detected continuously during day- and night-times; Yellow-orange: group 2 = sound types detected mainly during day-time; Blues-purples: group 3 = sound types detected mainly during night-time; Light blue: "buzz-like" sound type; Light green: "knocking" sound type. White horizontal bars below x-axis represent day-time, black horizontal bar represents nighttime.

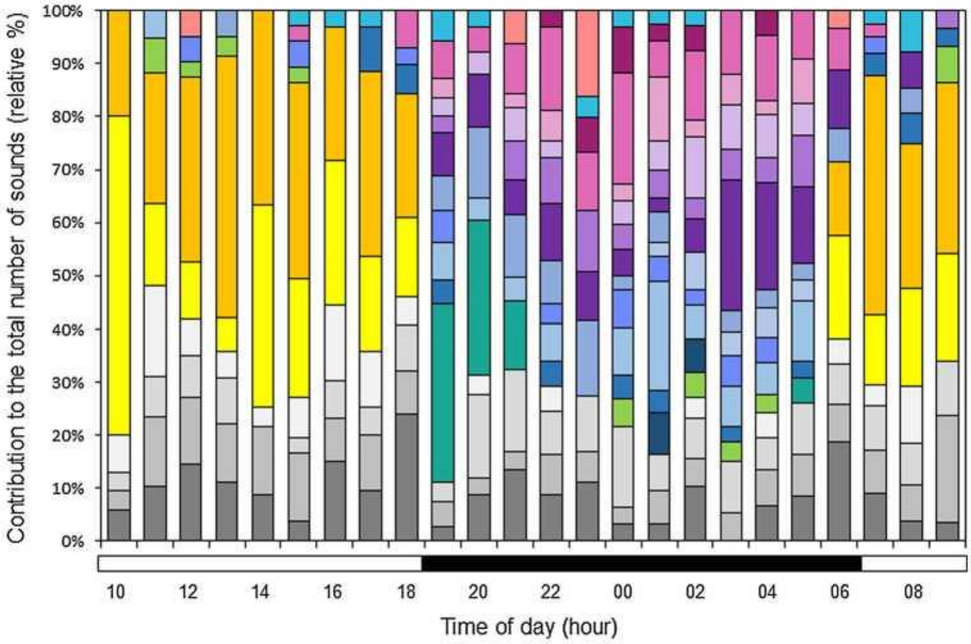


Figure 3. Presentation of the consecutive peak periods of the 11 most commonly detected sound type over 24 h and their oscillograms. The succession of the different peak periods, during which a significant increase in the number of sounds was found, is highlighted by dashed lines. Period 1: 10:00-12:00, Period 2: 13:00-15:00, Period 3: 16:00-18:00, Period 4: 19:00-21:00, Period 5: 22:00-00:00, Period 6: 01:00-03:00, Period 7: 04:00-06:00, Period 8: 07:00-09:00. White horizontal bars below x -axis represent day-time, black horizontal bar represents night-time. Colours are preserved with Fig. 2

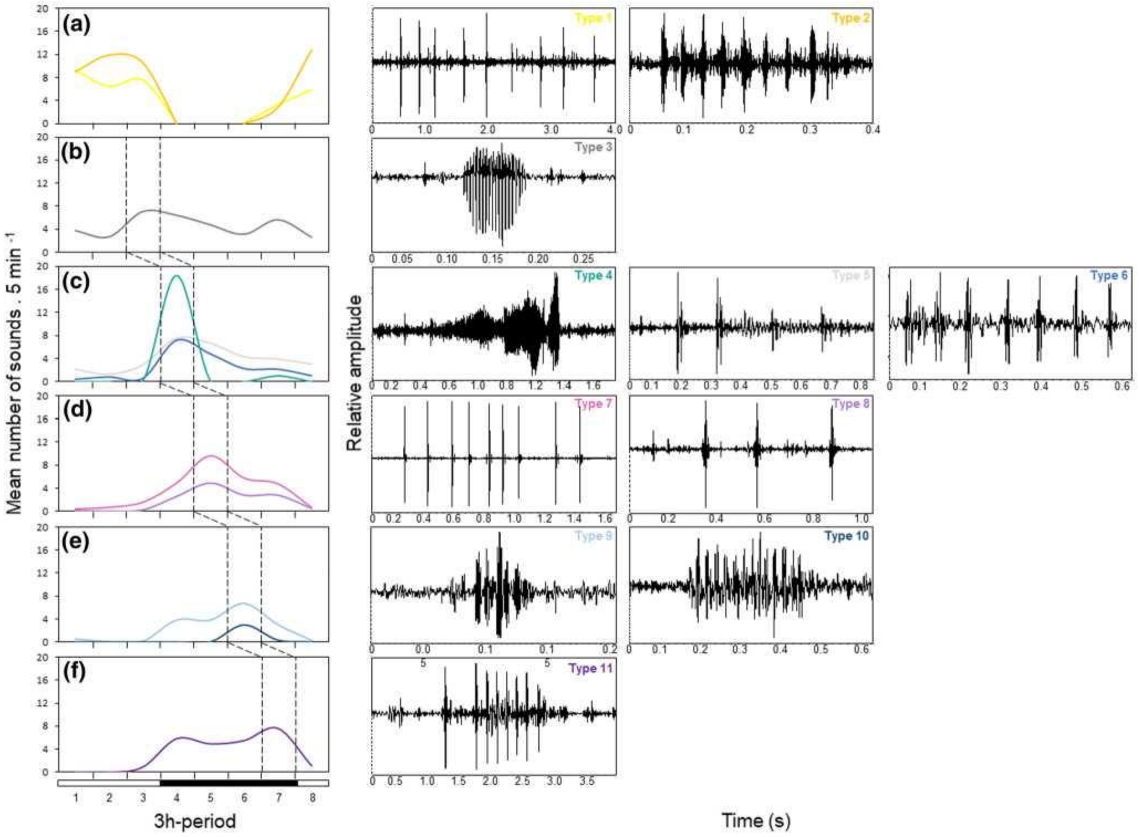


Table 2. Acoustic characteristics of the 11 most prominent sound types

Sound type	*N*	Description	Duration (ms)	Number of pulses	Pulse period (ms)	Pulse duration (ms)	Dominant frequency (Hz)
1	15	Balistidae	1435±1161	5 ± 3	313 ± 134	31 ± 8	305 ± 191
2	15	Pomacentridae	168 ± 80	5 ± 2	36 ± 6	18 ± 5	594 ± 83
3	12	Holocentridae	40 ± 19	11 ± 4	4 ± 0.6	3 ± 1	552 ± 38
4	16	"Whoot"	776±200	155 ± 40	3 ± 1	2 ± 1	216 ± 26
5	13	Boom series	782±636	4 ± 3	215 ± 113	58 ± 22	146 ± 33
6	10	Pulse series	634±407	4 ± 1	211 ± 83	18 ± 10	379±103
7	10	Knock series	1027±1147	6 ± 4	214 ± 155	9 ± 1	530 ± 83
8	10	Slow boom series	1292±956	3 ± 2	426 ± 101	41 ± 13	139 ± 35
9	13	Creaks	173 ± 82	9 ± 2	22 ± 14	10 ± 4	498±165
10	11	Growl	217 ± 84	17 ± 5	12 ± 9	2 ± 1	172 ± 67
11	11	Fast pulse series	406 ± 172	6 ± 2	69 ± 25	23 ± 8	223 ± 85

Values are mean ± SD

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Discussion

By focusing on the patterns of sound production in a coral reef of Moorea Island, the present study allowed for detection of a large diversity of sound types and highlighted how they may be organized to avoid a cacophony. While day-time was dominated by two to six different sound types, recordings performed at night revealed a more diverse vocal community made of up to nineteen sound types (nine of which were exclusively recorded between dusk and dawn). While sounds of different types were detected throughout the entire night, with a relatively large overlap in their detection periods, peaks in their detection rate were not synchronous and each sound type dominated the soundscape successively. In addition, co-occurring sound types showed differences in at least one acoustic feature preventing misidentification.

Over the last years, sound production has been investigated in a large number of coral reef fishes in French Polynesia (Parmentier et al. 2011, 2016, 2017). Based on their acoustic characteristics and their time of occurrence, sounds dominating day-time in the present study may be attributed to Balistidae (Type 1) (Parmentier et al. 2017) and Pomacen- tridae (Type 2) (Parmentier et al. 2016). Several species of these two families are commonly observed around Moorea Island (Siu et al. 2017). These two co-occurring sound types significantly differed in their total duration and dominant frequency. Sound Type 3 was attributed to Holocentridae (Parmentier et al. 2011) which is also common on French Polynesian reefs (Siu et al. 2017). While this latter sound type was regularly detected over 24 h, it significantly peaked at the end of the day and decreased throughout the night. The source of the long frequency modulated sounds described as "whoots" (Type 4) could not be identified as it had not been recorded before in Moorea. This long and tonal-like sound differed from the two other sound types detected during period 4 (Type 5 and Type 6) by a higher number of shorter pulses with a shorter period. The latter two sound types were both series of pulses and were only differentiated by their dominant frequencies. The low frequency booming sound (Type 5) produced in series or in single ways matches the common characteristics of Serranidae sounds (Bertucci et al. 2015; Jublier et al. 2020), also very common in Polynesian reefs (Siu et al. 2017). Type 6, like sound types 7-11, could not be attributed to a potential producer and further investigations are needed. Even though no temporal differences were found between time periods for sounds of Type 8, it significantly differed from its co-occurring sounds type (Type 7) in all acoustic features but number of pulses. Likewise, sounds of Type 10 were uniformly detected but differed from sounds of Type 11 in their dominant frequencies when the highest detection rate of both sounds were observed. Overall, the present results show that the local vocal activity was not uniform in time with sound types dominating the soundscape during specific periods of the day and with significant differences in the acoustic features of co-occurring sound types. This permits optimization of calling strategies within the community, which might therefore support the acoustic niche hypothesis (Krause 1993), allowing vocal species to communicate efficiently in such a diverse ecosystem.

The patterns of sound production described in this study are from one single site on Moorea Island, and thus have to be considered as snapshots that need to be complemented. The pool of reported sound types are only a fraction of a larger acoustic community. Additionally, not all detected sound types were considered in the analysis as some were omitted because they were too rare to make analyse, and it is likely that other sound types might not have been detected at all due to a low signal-to-noise ratio. These undocumented additional sources may significantly add to the complexity of a reef's score.

Furthermore, this study focused only on daily pattern but further analysis of recordings performed over longer periods of time may reveal more detailed diel patterns and seasonal patterns in the vocal activity of vocal fish communities, as is the case in terrestrial groups (e.g. Shieh et al. 2015; Vokurková et al. 2018). Temporal partitioning may therefore happen at larger time scales. Recently, Jublier et al. (2020) presented the phenological patterns of six types of sounds at different temporal scales, from hourly, to daily, to lunar cycles occurring from 04-Jun-2017 to 12-Jun-2017, and from 06-Jul-2017 to 12-Jul-2017 during the reproduction aggregation of several species of coral reef fishes in the atoll of Fakarava (French Polynesia). Similarly, investigations over longer periods of time revealed seasonal partitioning between seven different fish choruses lasting from days to weeks. Over an 18-month recording period in Western Australia, Parsons et al. (2016) described clear diel patterns occurring successively between December and April (early spring and late summer). However, source species could only be proposed for two of these choruses. One chorus corresponded to the vocal activity of family Terapontidae, another was composed of sounds from families Holocentridae, Priacanthidae and Apogonidae. Moreover, such long term survey was based on the analysis of long term spectrograms and failed to detect similar diel and seasonal dynamics of shorter isolated pulsed sounds, which were not creating choruses. More exhaustive sampling and analysis are needed, over longer period of time, to have a more dynamic and exhaustive representation of the vocal activity of coral reefs. In particular, investigations should be conducted to identify the different vocal species calling at night to more precisely define the acoustic communities, species vocal repertoire and how species share the acoustic space.

Reports of partitioning in fishes are growing (Parsons et al. 2016; Staaterman et al. 2013; Hastings and Širović 2015; Ruppé et al. 2015), and therefore constitute further evidences for the acoustic niche hypothesis. At the specific level, for example, calls of neighbouring toadfish Opsa- nus beta do not overlap with each other as individuals can increase their call rate and change their call duration when they vocalize in a chorus (Thorson and Fine 2002). In the western Atlantic, the sounds of two species, the black drum (Pogonias cromis) and a toadfish (Opsanus sp.), dominate the soundscape (Rice et al. 2017). Black drums produce pulsed sounds in the 75-200 Hz frequency band, while the toadfish sounds have a dominant frequency of 200 Hz but with a shorter pulse period making their sounds almost continuous (Rice et al. 2017). Black drum chorus could also be overlapped by the chorus of the red drum (Sciaenops ocellatus). However, if S. ocellatus sounds present a similar pulse period, they cover a wider frequency band (up to 1000 Hz) (Rice et al. 2017). The present study highlighted that different temporal features of sounds could also allow co-occurring signals not to overlap. This might be particularly important in fishes where most sounds occupy a narrow (20 Hz-3 kHz) frequency band (Lobel et al. 2010; Tavolga et al. 2012) with limited frequency modulations unlike terrestrial animals. Considering the commonly pulsatile nature of sounds in fishes, adjustment of the temporal features of their signals appear as a suitable strategy to efficiently insert them in the general background noise.

Finally, spatial partitioning has also been reported in insects (e.g. Schmidt and Balakrishnan 2015; Römer 2020). Species could move apart in both horizontal (being limited by the availability of suitable habitats) and vertical spaces (constrained by the canopy height). The same may apply to the ichthyologic vocal communities of coral reefs. Coral reef fish species have highly specialized habitat requirements. Some species are typically found in sandy patches while some other will use different types of coral as shelters, which will lead to different species assemblages (Bacchet et al. 2006; Bertucci et al. 2017) and hence potentially to different contiguous acoustic communities in terms of types, richness and complexity of their sounds. Future investigations using hydrophone arrays might help reveal how different species spatially segregate and whether the resulting communities are acoustically isolated from each other or not.

Acoustic communities in fishes and how vocal activities are structured remain clearly underexplored (Tricas and Boyle 2014; Ruppé et al. 2015; Mouy et al. 2018; Carriço et al. 2019). In accordance with the ecological niche concept (Chase and Leibold 2003), results of the present study suggest that the existing taxonomic diversity of soniferous fishes in a coral reef is related to their ability to share the acoustic space. As a consequence, various species may coexist in the same environment with low overlaps of their acoustic signals. Competition for acoustic space may have numerous implications in the evolution of acoustic signals and intraspecific communication in underwater environments. However, this partitioning might be impaired in perturbed environments, and may be affected by current changes causing modifications of communities (e.g. loss of biodiversity, invasive species), shifts in acoustic phenology and potential modifications of signal parameters linked to increases in water temperature, acidity and most importantly noise (Sueur et al. 2019). Long term monitoring of acoustic communities may then appear particularly valuable to track changes in biodiversity and ecosystems functioning.

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COMPLIANCE WITH ETHICAL STANDARDS

Conflict of interest All authors declare they have no conflict of interest.

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

References

Allen G, Werner T (2002) Coral reef fish assessment in the ‘coral triangle’ of southeastern Asia. Environ Biol Fish 65:202-214

Amorim MCP (2006) Diversity in sound production in fish. In: Ladich F, Collin SP, Moller P, Kapoor BG (eds) Communication in fishes. Science Publishers, Enfield, pp 71-105

Bacchet P, Zysman T, Lefèvre Y (2006) Guide des poissons de Tahiti et ses îles, 4th edn. Au vent des îles éditions, Tahiti

Bellwood DR, Wainwright PC (2002) The history and biogeography of fishes on coral reefs. In: Sale PF (ed) Coral reef fishes. Dynamics and diversity in a complex ecosystem. Academic Press, San Diego, pp 5-32

Bertucci F, Lejeune P, Payrot J, Parmentier E (2015) Sound production by dusky grouper Epinephelus marginatus at spawning aggregation sites. J Fish Biol 87:400-421

Bertucci F, Parmentier E, Lecellier G, Hawkins AD, Lecchini D (2016) Acoustic indices provide information on the status of coral reefs: an example from Moorea Island in the South Pacific. Sci Rep 6:33326

Bertucci F, Parmentier E, Berthe C, Besson M, Aubin T, Hawkins AD, Lecchini D (2017) Snapshot recording provide a first description of the acoustic signatures of deeper habitats adjacent to coral reefs of Moorea. PeerJ 5:e4019

Bignotte-Giró I, López-Iborra GM (2018) Acoustic niche partitioning in five Cuban frogs of the genus Eleutherodactylus. Amphibia Reptilia 40(1):1-11

Brumm H (2006) Signalling through acoustic windows: nightingales avoid interspecific competition by short-term adjustment of song timing. J Comp Physiol A 192(12):1279-1285

Brumm H, Voss K, Köllmer I, Todt D (2004) Acoustic communication in noise: regulation of call characteristics in a New World monkey. J Exp Biol 207(3):443-448

Carriço R, Silva MA, Menezes GM, Fonseca PJ, Amorim MCP (2019) Characterization of the acoustic community of vocal fishes in the Azores. Peer J 7:e7772

Chase JM, Leibold MA (2003) Ecological niche: linking classical and contemporary approaches. The University of Chicago Press, Chicago

Farina A, James P (2016) The acoustic communities: definition, description and ecological role. Biosystems 147:11-20

Fine ML, Winn HE, Olla BL (1977) Communication in fishes. In: Sebeok TA (ed) How animals communicate. Indiana University Press, Bloomington, pp 472-518

Galzin R, Lecchini D, Lison de Loma T, Moritz C, Parravicini V, Siu G (2016) Long term monitoring of coral and fish assemblages (1983-2014) in Tiahura reefs, Moorea, French Polynesia. Cybium 40:31-41

Grafe T (1996) The function of call alternation in the African reed frog (Hyperolius marmoratus): Precise call timing prevents auditory masking. Behav Ecol Sociobiol 38:149-158

Hastings PA, Širović A (2015) Soundscapes offer unique opportunities for studies of fish communities. Proc Natl Acad Sci 112(19):5866-5867

Jublier N, Bertucci F, Kéver L, Colleye O, Ballesta L, Nemeth RS, Lecchini D, Rhodes KL, Parmentier E (2020) Passive monitoring of phenological acoustic patterns reveals the sound of the camouflage grouper, Epinephelus polyphekadion. Aquat Conserv Mar Freshw Ecosyst 30(1):42-52

Krause BL (1993) The niche hypothesis: a virtual symphony of animal sounds, the origins of musical expression and the health of habitats. Soundscape Newslett 6:6-10

Krause BL (2002) Wild soundscapes: discovering the voice of the natural world. Wild Sanctuary Books, Berkeley

Lima MSCS, Pederassi J, Pineschi RB, Barbosa DBS (2019) Acoustic niche partitioning in an anuran community from the municipality of Floriano, Piaui, Brazil. Brazil J Biol 79(4):566-576

Lobel PS, Kaatz IM, Rice AN (2010) Acoustical behavior of coral reef fishes. In: Cole KS (ed) Reproduction and sexuality in marine fishes: patterns and processes. University of California Press, Oakland, pp 307-386

Lobel PS (2013) In: Lang MA, Sayer M (eds) Joint international scientific diving symposium AAUS & ESDP, Curaçao, pp 179-184

Luczkovich JJ, Mann DA, Rountree RA (2008) Passive acoustics as a tool in fisheries: an introduction to the American Fisheries Society Symposium. Trans Am Fish Soc 137:533-541

Luther D (2009) The influence of the acoustic community on songs of birds in a neotropical rain forest. Behav Ecol 20(4):864-871

Miller J (1982) Divided attention: evidence for coactivation with redundant signals. Cognit Psychol 14(2):247-279

Mossbridge JA, Thomas JA (1999) An "acoustic niche" for Antarctic killer whale and leopard seal sounds. Mar Mam Sci 15(4):1351-1357

Mouy X, Rountree R, Juanes F, Dosso SE (2018) Cataloging fish sounds in the wild using combined acoustic and video recordings. J Acoust Soc Am 143:EL333

Mullet TC, Farina A, Gage SH (2017) The acoustic habitat hypothesis: an ecoacoustics perspective on species habitat selection. Biosemiotics 10:319-336

Myrberg AA (1981) Sound communication and interception in fishes. In: Tavolga W, Popper AN, Fay RR (eds) Hearing and sound communication in fishes. Springer, New York, pp 395-426

Naugler CT, Ratcliffe L (1994) Character release in bird song: a test of the acoustic competition hypothesis using American Tree Sparrows Spizella arborea. J Avian Biol 25(2):142-148

Parmentier E, Vandewalle P, Brié C, Diranths L, Lecchini D (2011) Comparative study on sound production in different Holocentridae species. Front Zool 8:1-12

Parmentier E, Lecchini D, Mann D (2016) Sound production in damselfishes. In: Parmentier E, Frédérich B (eds) Biology of damselfishes. CRC Press, New York, pp 204-228

Parmentier E, Raick X, Lecchini D, Boyle KS, Van Wassenbergh S, Bertucci F, Kever L (2017) Unusual sound production mechanism in the triggerfish Rhinecanthus aculeatus (Balistidae). J Exp Biol 220:186-193

Parmentier E, Solagna L, Bertucci F, Fine ML, Nakae M, Compère P, Smeets S, Raick X, Lecchini D (2019) Simultaneous production of two kinds of sounds in relation with sonic mechanism in the boxfish Ostracion meleagris and O. cubicus. Sci Rep 9:4962

Parsons MJ, Salgado Kent CP, Recalde-Salas A, McCauley RD (2016) Fish choruses off Port Hedland, Western Australia. Bioacoustics 26(2):135-152

Planqué R, Slabbekoorn H (2008) Spectral overlap in songs and temporal avoidance in a Peruvian bird assemblage. Ethology 114(3):262-271

Rice AN, Soldevilla MS, Quinlan JA (2017) Nocturnal patterns in fish chorusing off the coasts of Georgia and eastern Florida. Bull Mar Sci 93(2):455-474

Römer H (2020) Insect acoustic communication: the role of transmission channel and the sensory system and brain of receivers. Funct Ecol 34(2):310-321

Rountree RA, Gilmore RG, Goudey CA, Hawkins AD, Luczkovich J, Mann D (2006) Listening to fish: applications of passive acoustics to fisheries science. Fisheries 31:433-446

Ruppé L, Clément G, Herrel A, Ballesta L, Décamps T, Kéver L, Parmentier E (2015) Environmental constraints drive the partitioning of the soundscape in fishes. Proc Natl Acad Sci 112(19):6092-6097

Staaterman E, Rice AN, Mann DA, Paris CB (2013) Soundscapes from a Tropical Eastern Pacific reef and a Caribbean Sea reef. Coral Reefs 32(2):553-557

Schmidt AK, Balakrishnan R (2015) Ecology of acoustic signalling and the problem of masking interference in insects. J Comp Physiol A 201(1):133-142

Schmidt AK, Römer H (2011) Solutions to the cocktail party problem in insects: selective filters, spatial release from masking and gain control in tropical crickets. PLoS ONE 6(12):e28593

Schmidt AKD, Römer H, Riede K (2013) Spectral niche segregation and community organization in a tropical cricket assemblage. Behav Ecol 24(2):470-480

Shieh BS, Liang SH, Chiu YW (2015) Acoustic and temporal partitioning of cicada assemblages in city and mountain environments. PLoS ONE 10(1):e0116794

Sinsch U, Lümkemann K, Rosar K, Schwarz C, Dehling JM (2012) Acoustic niche partitioning in an anuran community inhabiting an Afromontane wetland (Butare, Rwanda). Afr Zool 47(1):60-73 Siu G, Bacchet P, Bernardi G, Brooks AJ, Carlot J, Causse R, Claudet J, Clua E, Delrieu-Trottin E, Espiau B, Harmelin-Vivien M, Keith P, Lecchini D, Madi-Moussa R, Parravicini V, Planes S, Ponsonnet C, Randall JE, Sasal P, Taquet M, Williams JT, Galzin R (2017) Shore fishes of French Polynesia. Cybium 41(3):245-278

Stone E (2015) Separating the noise from the noise: a finding in support of the "Niche Hypothesis," that birds are influenced by human- induced noise in natural habitats. Anthrozoös 13(4):225-231

Sueur J, Krause B, Farina A (2019) Climate change is breaking Earth'beat. Trends Ecol Evol 34(11):971-973

Tavolga WN, Popper AN, Fay RR (2012) Hearing and sound communication in fishes. Springer, New York

Thorson RF, Fine ML (2002) Acoustic competition in the gulf toadfish Opsanus beta : acoustic tagging. J Acoust Soc Am 111(5):2302-2307

Tobias JA, Planqué R, Cram DL, Seddon N (2014) Species interactions and the structure of complex communication networks. Proc Natl Acad Sci 111(3):1020-1025

Tricas T, Boyle K (2014) Acoustic behaviors in Hawaiian coral reef fish communities. Mar Ecol Prog Ser 511:1-16

Vokurkovùá J, Motombi F, Ferenc M, Hořák D, Sedláćek O (2018) Seasonality of vocal activity of a bird community in an Afrotropical lowland rain forest. J Trop Ecol 34(1):53-64