

Environmental constraints drive the partitioning of the soundscape in fishes

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The underwater environment is more and more being depicted as particularly noisy, and the inventory of calling fishes is continuously increasing. However, it currently remains unknown how species share the soundscape and are able to communicate without misinterpreting the messages. Different mechanisms of interference avoidance have been documented in birds, mammals, and frogs, but little is known about interference avoidance in fishes. How fish thus partition the soundscape underwater remains unknown, as acoustic communication and its organization have never been studied at the level of fish communities. In this study, passive acoustic recordings were used to inventory sounds produced in a fish community (120 m depth) in an attempt to understand how different species partition the acoustic environment. We uncovered an important diversity of fish sounds, and 16 of the 37 different sounds recorded were sufficiently abundant to use in a quantitative analysis. We show that sonic activity allows a clear distinction between a diurnal and a nocturnal group of fishes. Moreover, frequencies of signals made during the day overlap, whereas there is a clear distinction between the different representatives of the nocturnal callers because of a lack of overlap in sound frequency. This first demonstration, to our knowledge, of interference avoidance in a fish community can be understood by the way sounds are used. In diurnal species, sounds are mostly used to support visual display, whereas nocturnal species are generally deprived of visual cues, resulting in acoustic constraints being more important.

acoustic communication | signal interference | passive acoustic recordings | diversity of sounds | frequency partitioning

The number of studies concerning the soundscape or, more precisely, studies stressing the need for investigations of the soundscape in different environments is growing because the effect of anthropogenic noise is thought to be problematic for many species (1–5). The main reason for this call to action is the crucial role of sound communication in the regulation of different kinds of social relationships, as has been demonstrated in numerous taxa. However, most studies with fish tend to consider species in isolation, and there is a lack of data addressing acoustic communication of fishes living in natural communities (6). As a consequence, how species share the soundscape with other species living in the same habitat remains unknown. This topic has received much more attention in the air, where many mechanisms that animals use to deal with this problem are known (Fig. 1). The Lombard effect, for example, corresponds to an increase in signal amplitude. It was first described for humans, and subsequently in birds, mammals, and fish (5, 7). However, an increase in signal amplitude is a limited solution when the background noise level is important. As a consequence, some frogs, birds, and mammals also increase the call duration, or call rate, to increase the likelihood of being heard (8–10). In complex acoustic environments, such as animal communities characterized by an important quantity of signals, vocalizing animals cope with background noise by inserting their signals in such a way

that signal overlap is avoided (11–15). Moreover, theory predicts that the competition for acoustic space should result in signal divergence, which would increase signal distinctiveness and opportunities for correct signal discrimination (14, 15) and lead to the avoidance of frequency overlap. This strategy predicts that signals produced at a given time and in a given place can be distinguished by their frequency. The frequency partitioning of the acoustic environment was first demonstrated for birds and, more recently, also for frogs (2, 16).

To date, there is little direct evidence of mechanisms of signal interference avoidance in fish. At best, it has been shown that calls of nearby toadfish, *Opsanus beta*, do not overlap. However, this pertains to specimens of the same species (17). Moreover, *O. beta* increases its call rate and changes its call duration during the twilight period (17). Despite the array of behaviors associated with sound production, fish sounds are mainly used during reproduction (courtship, spawning, male competition) or during behaviors related to territoriality (warning, chase, nest defense, fight). During courtship, calls can be used by females to assess species identity and the quality of potential sexual partners (18–21). During agonistic behaviors, sound features enable the receiver to assess the fighting capacity of the opponent because acoustic parameters can provide information on the size, the social status, the motivation, or the physiological state of the emitter (22–25). However, how fish sounds are organized at the level of the community remains unknown.

Passive acoustic recording methods have been developed in recent years (26) and allow not only the detection of a larger

Significance

More and more studies stress the potential deleterious effect of anthropogenic sounds on fish acoustic communication. Paradoxically, how the communication between fishes in a community is organized remains extremely poorly known, as studies using passive acoustic recordings are typically restricted to one or two species. At a single site, we were able to follow 16 different vertebrate sounds for 15 days. We demonstrate that the fish population can be distributed into two groups: one diurnal and one nocturnal. Most interestingly, fish calling at night do not show overlap at the level of the main calling frequency, in contrast to fish calling during the day. This shows that at night, in the absence of visual cues, sound communication is more important.

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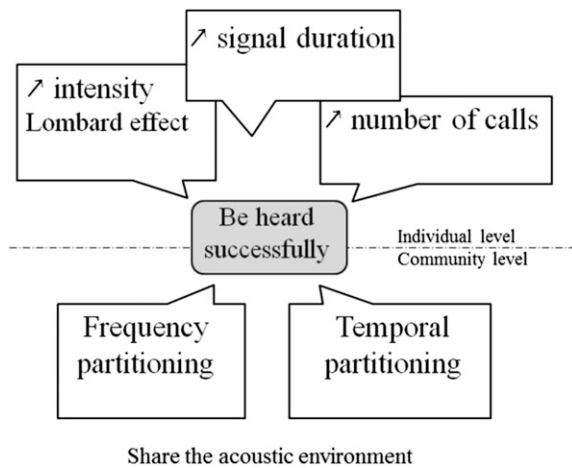


Fig. 1. Mechanisms to ensure the signal transfer in the soundscape on land.

number of individuals than by the use of visual methods but also a continuous day and night monitoring. Moreover, passive acoustic recording methods can be used at depths not accessible to humans, independent of weather conditions, and for a long-term period (27, 28). These methods are based on the deployment of one or more hydrophones scheduled to record sounds during various periods in the natural habitat. These methods have been successfully used to demonstrate temporal partitioning by several cooccurring species (29). Passive acoustic methods have many applications in the field of conservation, population

monitoring, migration studies, and so on. However, most of the passive acoustic studies have restricted their investigations to the monitoring of one or two aquatic species or to the description of acoustic characteristics. The biological sound environment (soundscape) and its partitioning have rarely been studied in fish communities, although some studies have reported that fish share the acoustic space (6, 30–32). As such, the mechanisms of signal interference avoidance remain unknown and will be addressed in the present study. In other words, we here ask ourselves whether fish sound production is a cacophony, or whether there is an organization of sound production in the marine environment.

In spring 2013, an autonomous recording device was placed in a cave at a depth of 120 m off the coast of South Africa that was sheltering a great species diversity. A census performed in 2006 revealed 70 vertebrate groups including 136 teleost species, the coelacanth *Latimeria chalumnae*, and 19 chondrichthyan species (33). The goal of the present study was to categorize the sounds to understand how the different species share the acoustic environment.

Results and Discussion

Description of Sounds. The present analysis concerned 2,793 sounds. These sounds were divided into 17 groups on the basis of the similarity in their characteristics (Table 1 and Fig. S1). These 17 groups were composed of 25–398 sounds. All the sounds of each group were analyzed, but the inequality between groups makes the statistical analysis of these data complex. Thus, a random sample of 10 sounds for each group was taken and analyzed. The acoustic features of each sample and its corresponding group were statistically compared, and no significant differences for any

Table 1. Mean values of measured acoustic parameters for the 17 groups

Group	Total duration, s	Peak frequency, Hz	Pulse number	Pulse period, pulse·s ⁻¹	General pattern
1	0.33 ± 0.12	490 ± 281	6.80 ± 2.25	23.11 ± 11.67	One pulse followed by a train of around six pulses (pulse period: 50 ms). Sometimes, the previous pulse is absent
2	0.65 ± 0.09	480 ± 227	28.82 ± 4.49	44.75 ± 6.79	Two parts. The first one is composed of around 20–25 pulses (pulse period: 10–15 ms). The second part is around five pulses (pulse period: 30–35 ms)
3	0.07 ± 0.02	2,803 ± 277	2.20 ± 0.42	33.72 ± 7.83	Two or three clear pulses separated by 45–50 ms
4	0.16 ± 0.03	66 ± 5	1.00 ± 0	—	Isolated boom
5	0.08 ± 0.05	158 ± 69	1.00 ± 0	—	Isolated pulse
6	1.16 ± 0.31	274 ± 137	4.10 ± 0.74	3.65 ± 0.68	Coarse pulses with a small growl at the front of the pulse (pulse period: around 200 ms)
7	0.78 ± 0.25	762 ± 122	4.50 ± 0.97	6.04 ± 1.26	Long pulse. High-frequency whistle.
8	1.14 ± 0.36	1,630 ± 401	10.30 ± 3.33	9.27 ± 1.71	Three or four groups of pulses separated by around 250 ms. The first one is often composed of one pulse, and the next groups of three to four pulses (pulse period: around 10–15 ms)
9	1.08 ± 0.64	2,641 ± 257	6.70 ± 3.27	6.38 ± 0.60	Clear pulses, regular
10	0.51 ± 0.12	162 ± 102	4.70 ± 1.16	9.33 ± 1.55	Coarse pulses grouped with a number of pulses, increasing for the next one
11	0.82 ± 0.35	429 ± 267	19.80 ± 7.76	25.16 ± 6.29	Pulses separated by around 50 ms. Amplitude relative variation: increase then decrease
12	0.35 ± 0.15	446 ± 299	16.82 ± 4.96	52.87 ± 15.44	One large pulse followed by smaller pulses with an increasing pulse period
13	1.49 ± 0.70	1,088 ± 214	5.10 ± 2.18	3.58 ± 0.60	Series of grunts
14	1.30 ± 0.23	263 ± 114	Tonal	—	Long tonal sound with an increasing of the intensity. At the end, some more isolated pulses are observable
15	0.49 ± 0.08	290 ± 198	6.90 ± 1.20	14.26 ± 2.35	One or two pulses grouped following by a train of around eight pulses. Sometimes the first group of pulses is absent
16	1.65 ± 0.74	427 ± 204	4.1 ± 1.20	2.75 ± 0.93	Clear pulses
17	0.24 ± 0.13	1,056 ± 151	6.4 ± 3.37	27.13 ± 2.53	Coarse pulses in regular series

Values are mean ± SD. An oscillogram is presented in Fig. S1 for each group.

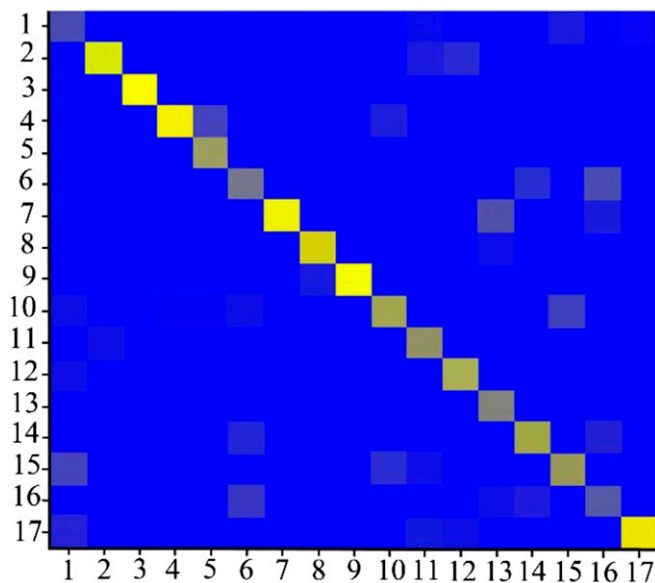


Fig. 2. Confusion matrix summarizing the result of the cross-validation discriminant function analysis test. The horizontal axis represents the actual group to which the sound belongs, and the vertical axis represents the assignment of a sound to a group by the model. The more yellow the color, the higher the proportion of correct assignments (Table S2).

of the acoustic parameters were found (Wilcoxon test, $P > 0.05$ in all cases), showing each sampling is representative and does not influence the results. Statistical analyses were performed to estimate the validity and consistency of these groups. In a principal component analysis, $\sim 71.1\%$ of the variability is explained by the first two principal components (43.2% by principal component 1 and 27.9% by principal component 2). Principal component 1 describes the pulse period and the number of pulses. The second component describes the sound duration and the peak frequency. All groups are homogeneous, and Kruskal Wallis tests were significant for each acoustic parameter between groups (pulse period: $\chi^2 = 161.2$; $df = 16$; $P < 0.001$;

number of pulses: $\chi^2 = 149.6$; $df = 16$; $P < 0.001$; peak frequency: $\chi^2 = 141.2$; $df = 16$; $P < 0.001$; sound duration: $\chi^2 = 144.7$; $df = 16$; $P < 0.001$). The results of the honest significant difference (HSD) Tukey post hoc tests show that, in most cases, groups are distinguishable by their acoustic parameters (Table S1). However, a minority of groups are not distinct (such as 1 and 15 or 6 and 16).

A discriminant function analysis was then performed to complement the principal component analysis. A mean cross-validation matrix was calculated after 1,000 cross-validation tests. In addition, the discriminant function analysis was performed on random groups (all sounds were mixed, and 17 groups created randomly). After the cross-validation test, 70% of sounds were correctly assigned to their group (Table S2), which is significantly greater than expected by chance (χ^2 test: $\chi^2 = 51.11$; $df = 16$; $P < 0.001$). Fig. 2 represents the confusion matrix obtained from the result of the cross-validation tests. The confusion matrix diagonal is well discerned ($>50\%$ of correct assignment) with the exception of groups 1, 6, 13, and 16. For these latter groups, the acoustic parameters are not sufficient to distinguish the sounds. However, sound description is not only restricted to the data used in the analysis; it appears other features allow support of group validity. Groups 1 and 15 were confused by the model; for these two groups, the general pattern of sound (oscillogram shape) is similar, but the hours of activity are opposed (sounds of group 1 occur mainly during the day, whereas sounds of group 15 occur mainly at night). Two hypotheses can be proposed: these sounds are produced by two different species, one diurnal and one nocturnal, thus avoiding acoustic interference, or these sounds are produced by a single species with a large activity period. At this point, we cannot distinguish between these two possibilities.

Some sounds belonging to group 6 were assigned to group 16 by the model. The general pattern of these two groups is, however, different. Sounds belonging to group 6 show long pulses with small growls, whereas sounds belonging to group 16 are composed of clear and short pulses (Table 1 and Fig. S1). These sounds cannot be produced by an identical mechanism, and thus not by the same species. The same holds for group 13 (sounds of “grunt” type), from which some sounds were assigned to group 7 (sounds of “whistle” type).

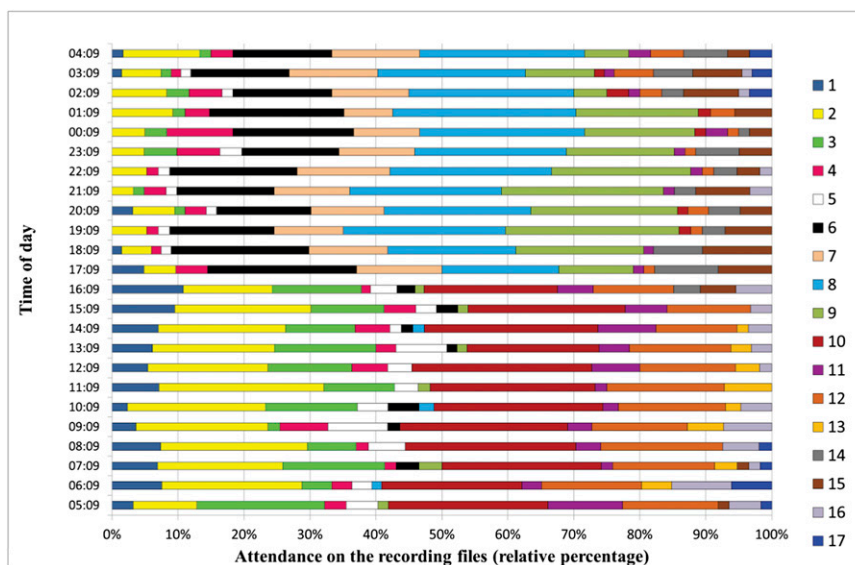


Fig. 3. Distribution of the different groups during the day. Daytime was between 05:00 and 16:30. Each group is represented by its relative percentage of presence per hour. The longer the rectangle, the more likely the presence of the group at this hour is.

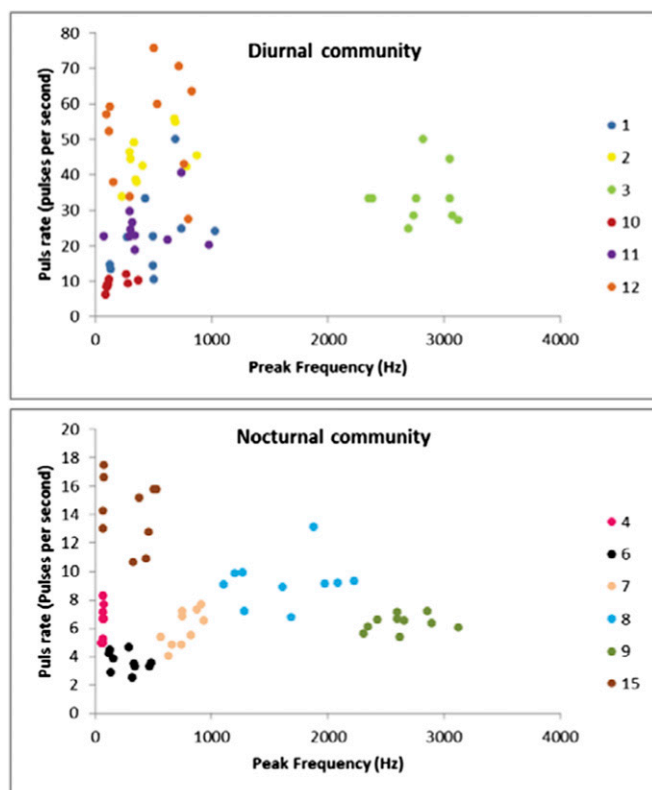


Fig. 4. Overlap analysis on the diurnal community (*Upper*) and the nocturnal community (*Lower*) in terms of peak frequency and pulse period. Note that whereas sound characteristics overlap strongly during the day, calls are clearly separated by frequency and pulse period at night.

In summary, 17 groups of sounds can be clearly distinguished, and each would therefore at best represent a sound-producing marine species. Note, however, that some species are able to produce different kinds of sounds (34). Fish sounds are mainly characterized by low frequencies (<1,000 Hz), are limited in intensity, and are pulsed and produced routinely for long periods of time during the day (27). All groups have the characteristics of fish sounds with the exception of group 3. This group presents a very fast pulse rate and a high frequency (>2,500 Hz). These characteristics are reminiscent of cetacean clicks. Calls of group 9 also have high frequencies (>2,500 Hz). However, these calls were recorded continuously from 17h00 to 04h00, highlighting that they were produced by sedentary species living permanently in or around the cave. These data indicate it cannot be cetacean clicks, the sound emission of which is more sporadic. Therefore, the acoustic analysis allowed us to identify 16 different fish-like sounds and one cetacean-like sound (group 3). The important number of different sounds obtained here highlights the incredible diversity of sounds produced in the aquatic environment, particularly in a relatively deep-water habitat. The fact that sounds were recorded at a depth of 120 m explains why it was impossible to visually identify the calling species, and additional studies are required to identify the species producing the calls. Comparisons of our acoustic data with the literature suggest groups 2 and 14 could belong to *Batrachoididae* (35–37), groups 1 and 15 to *Holocentridae* (38), and group 4 to the serranid genus *Epinephelus* (39).

Frequency Partitioning of the Acoustic Environment. For each group, the probability of its presence in the recording files was calculated. Two distinct groups could thus be highlighted (Fig. 3): a nocturnal group and a diurnal group. The diurnal group is active

between 05:00 and 17:00. During our recording, the sun rose around 06:30, and sunset was around 17:30. This is compatible with our result because many species deploy peaks of activities around these periods of the day, and there is not a strict limit (40, 41). The diurnal group is composed of calls 1, 3, 5, 10, 11, 12, 13, and 16. At 17:00, there is a drastic change in the acoustic environment. Between 17:00 and 05:00, a nocturnal group of callers is being established and is composed of calls 6, 7, 8, 9, 14, and 15. Calls 2, 4, and 17 occur during both night and day, but call 2 presents its maximal activity during the daytime, whereas the maximal activity of call 4 is during the nighttime. Call 17 shows only a restricted activity at sunrise.

The division of the calls into two distinct groups can be related to environmental constraints and the need for different kinds of strategies to avoid species misidentification by the receiver. To study the sound overlap between calls within each group, different analyses were performed, using the calls that are most representative: calls 1, 2, 3, 10, 11, and 12 for the diurnal group and calls 4, 6, 7, 8, 9, and 15 for the nocturnal group. These calls represent 90% of the total vocal activity. Data pertaining to frequency and pulse periods were used because these characters are usually involved in the coding of information (42, 43). Within the diurnal group, sounds produced by different species overlap at the level of the pulse period and frequency (Fig. 4). In this group, only call 3 constitutes an exception, showing high pulse periods and high peak frequencies, which are acoustic characters known from cetaceans. In contrast, these acoustic parameters allow a clear distinction between the different representatives of the nocturnal group (Fig. 4). This distinction is mostly a result of differences in peak frequencies, as there is little overlap between sounds produced by nocturnal species (Fig. 5).

In diurnal fishes, sounds are often associated with a particular behavior to reinforce visual stimuli. For example, courtship in *Dascyllus* (*Pomacentridae*) species is characterized by consecutive dances (called dips) performed by the courting male and by modifications of the color pattern. The male rises first in the water column and then falls off, rapidly emitting a pulsed sound (42, 44). In gobiids, the sound can be accompanied by nodding movements (45). In contrast, visual stimuli cannot be used to transfer information in nocturnal fishes. This implies greater constraints on the acoustic channel, with the need to be able to distinguish species on the basis of sound only. The use of different frequencies should allow the fish to identify conspecifics and allows for the simultaneous presence of the calls of different species without generating crosstalk.

Conclusion

The use of passive recording methods highlighted an important diversity of sounds produced by fishes at a depth of 120 m off the coast of Sodwana Bay, southeastern South Africa. Sixteen different fish sounds were described. The analysis of the temporal occurrence of these sounds shows the partitioning of the acoustic window with a diurnal and a nocturnal pattern. During the day, the different sounds overlap at the level of the pulse period and frequency. In contrast, there is a clear distinction between the different representatives that call at night, where species do not overlap in frequency characteristics. This call partitioning at night could help prevent signal interference and likely compensates for the lack of visibility.

Materials and Methods

Study Site. The study was conducted at Sodwana Bay, KwaZulu Natal Province, Ezemvelo Nature Reserve, Isimangaliso Wetland Park, southeastern South Africa. Twelve large and many small submarine canyons running along a stretch of coastline ~78 km in length characterize this area. The canyons are oriented perpendicularly to the shoreline and can reach more than 700 m in depth (46). The specificity of these canyons is the presence of numerous moderate-sized

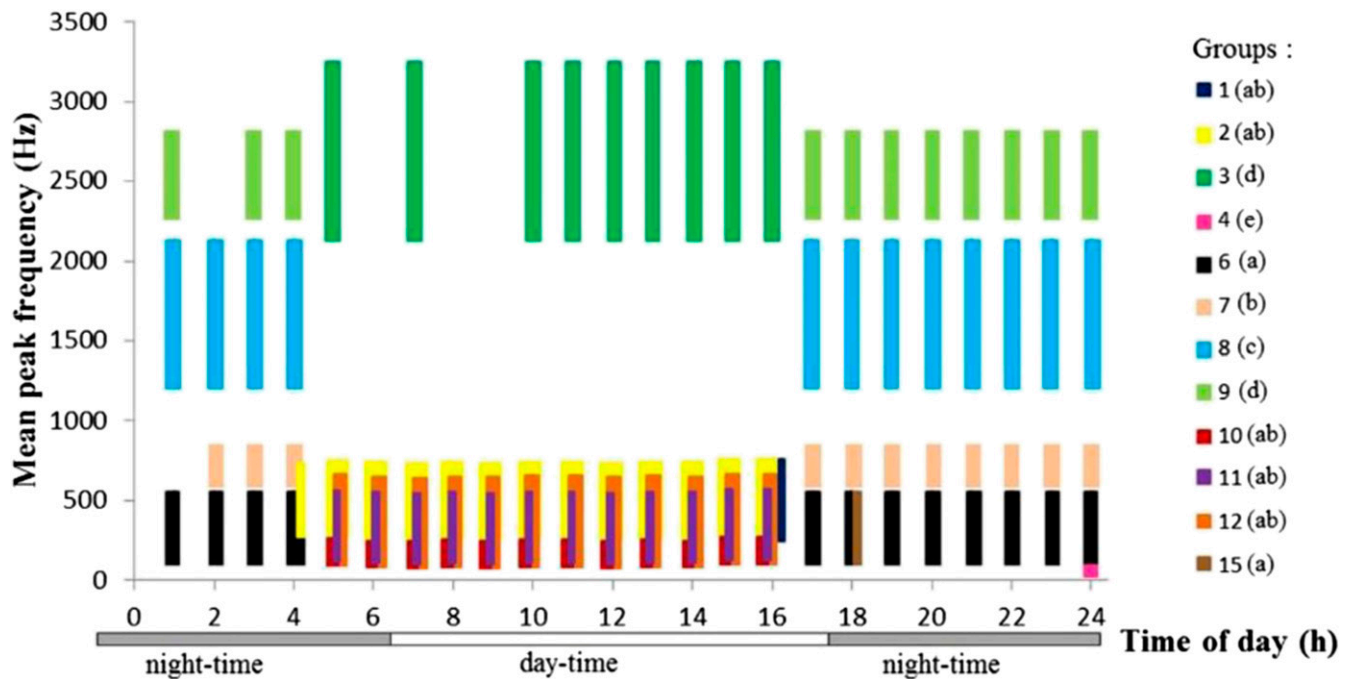


Fig. 5. Mean peak frequency distribution between the nocturnal community and diurnal community at each hour. The center of the rectangles represents the mean peak frequency of the group. The SD is represented by the vertical extent of rectangles. In the legend, the name of the group is associated with letters representing the significant difference. Two groups sharing a letter have no significant difference in peak frequency. A difference is considered significant when $P < 0.05$.

caves sheltering many species, including coelacanths. The device was placed in a submarine cave (called U-cave or cave 2) localized at 113 m in depth at the head of the Jesser Canyon, about 4 km from the shoreline.

Acoustic Recordings. The Digital SpectroGram Recorder system is an autonomous acoustic recording system. It enables users to save acoustic recordings on a 32-GB SD memory card and is controlled by an on-board real-time clock. In this study, a Digital SpectroGram Recorder system (Loggerhead Instruments) was positioned in a crevice of the submarine cave wall. Sounds were recorded for 9 min every 10 min by the hydrophone (-186 dB re $1\text{V}/\mu\text{Pa}$, sample rate of 20 kHz) during a total of 19 nonconsecutive days from April through May 2013. Files were automatically saved with temporal data. A total of 2,273 acoustic files were recorded during this study. Given the large number of files, only the first 9 min of each hour were analyzed (387 files). Acoustical analyses were conducted manually with Avisoft-SASLab Pro-5.2.07 software. For each distinct sound, the following acoustic parameters were measured: total sound duration (s), number of pulses, pulse period (i.e., the ratio between the pulse number and the sound duration, in pulses per second), and the peak frequency in hertz (i.e., the frequency of greatest amplitude). The temporal features were measured from oscillograms (44.1 kHz, 16 bit), whereas the peak frequency was obtained from the logarithmic power spectra (Hamming window, FFT Fast Fourier Transform, FFT Length 64, 689-Hz resolution).

Statistical Analyses. A principal component analysis and a discriminant function analysis were conducted to discriminate and determine the validity of our sound groups. These tests were coupled to Kruskal Wallis tests, χ^2 test, and Tukey HSD post hoc tests. To study the emission of sounds during daytime and nighttime, the same tests were used. A nonparametric test on paired data (Wilcoxon test) was used to justify the use of a raw data sample. All these tests were conducted with R i386 3.0.2 software.

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