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# From the Reef to the Ocean: Revealing the Acoustic Range of the Biophony of a Coral Reef (Moorea Island, French Polynesia)

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**Abstract:** The ability of different marine species to use acoustic cues to locate reefs is known, but the maximal propagation distance of coral reef sounds is still unknown. Using drifting antennas (made of a floater and an autonomous recorder connected to a hydrophone), six transects were realized from the reef crest up to 10 km in the open ocean on Moorea island (French Polynesia). Benthic invertebrates were the major contributors to the ambient noise, producing acoustic mass phenomena (3.5–5.5 kHz) that could propagate at more than 90 km under flat/calm sea conditions and more than 50 km with an average wind regime of 6 knots. However, fish choruses, with frequencies mainly between 200 and 500 Hz would not propagate at distances greater than 2 km. These distances decreased with increasing wind or ship traffic. Using audiograms of different taxa, we estimated that fish post-larvae and invertebrates likely hear the reef at distances up to 0.5 km and some cetaceans would be able to detect reefs up to more than 17 km. These results are an empirically based validation from an example reef and are essential to understanding the effect of soundscape degradation on different zoological groups.

## 1. Introduction

A soundscape is a collection of sounds composed of three acoustic sources: geophony, anthrophony and biophony that reflect important ecosystem processes and human activities [1,2]. In the ocean, the biophony consists of sounds from marine fauna. Fish [3] and invertebrate [4] sounds constitute the most persistent part and the majority of coastal biophonies. Coral reefs are considered to be hotspots of biodiversity [5] and acoustic hotspots [6,7]. In these environments, snapping shrimps tend to dominate reef soundscapes at frequencies above 1 kHz [8], while a band attributed to damselfish is found around 400 Hz [9]. Numerous studies have estimated that these soundscapes may offer a reef orientation cue at relatively large distances [10–12], but there is a lack of empirical studies on reef sound propagation. Measuring the distance over which reef sounds propagate is necessary to determine their relative importance as cues for long-range orientation and habitat choice. However, as reef soundscapes are composed of sounds of different frequencies, they propagate over different distances. Since different species have different hearing frequency ranges, the detection distance (the maximum distance at which a species can perceive a sound above ambient background noise) does not automatically correspond to the propagation distance (the maximum distance at which the ambient background noise masks reef sounds) of the reef sound. The effective use of acoustic cues to detect

the reef requires (1) a loud reef soundscape, (2) low ambient noise (wind and boats), (3) hearing ability in the relevant frequency bands and (4) sound localization.

Propagation and detection distances have been mainly assessed using theoretical spreading models with distances varying from a few hundred meters to a few kilometres [13–16]. In addition, some authors observed a so-called "reef effect"; i.e., sound levels decrease more slowly than expected from a cylindrical spreading model over a distance approximately equal to the length of the reef (≈20 km). The supporting reason is that the reef sound is not located in a single point but results from a series of sources. The high variability in the theoretically estimated propagation distances has highlighted the need to conduct empirical measurements of the soundscape at different distances from a reef [13]. Such empirical studies are fundamental for estimating the distances at which reef sounds can be perceived by marine organisms because they can be useful for many taxa. Many species of cetaceans are known to roam over great distances, for example between mating and feeding areas [17,18]. As lighting conditions are often a constraint, water has excellent sound transmission properties, so the sounds of biotic and abiotic origin can be exploited as acoustic cues for orientation [19]. The routes that cetaceans travel are, in fact, exposed to elevated levels of biological and nonbiological ambient noise [20], and it has been suggested that cetaceans use reef sounds for navigation [20,21].

Many fish species are also known to migrate between spawning and feeding areas [19] or to have distinct migration cycles related to life stages [22]. In coral reefs, most marine organisms (bryozoans, cnidaria, crustaceans, echinoderms, molluscs, polychaetes, sponges, tunicates, teleosts, etc.) have structured life histories with two distinct stages: a relatively benthic/sedentary stage on the reef (usually juveniles and adults), and a pelagic, dispersal larval stage in the ocean [23]. While some species are known to disperse to a maximum of hundreds of meters, other species would travel up to hundreds of kilometres [24]. Their dispersal depends both on hydrodynamic processes and on species-specific behavioural responses to environmental cues [25]. One of the greatest challenges faced by these organisms is relocation to the patchily distributed reef habitats in a vast oceanic matrix once they are ready to transition to demersal habitat [12]. For effective orientation, animals require cues that are heterogeneous in the environment and contain reliable information about potential settlement sites [26,27]. These potential cues include vision [28], olfaction [23,29–31], sounds emanating from reefs [10–12], differences in wind- or wave-induced turbulence [23], gradients in abundance of fish, plankton or reef detritus [23] or a combination of several of them [27,32,33]. Many of these cues, such as vision, are effective only at small distances from the reef [34–36] (a few tens of meters) [23], whereas sounds from the reef (e.g., from benthic invertebrates and fish) are potential cues for larval orientation over long distances. They are thought to assist pelagic larvae of cnidaria [37–39], mollusks [40,41], crustaceans [42–44] and fish [45–50] to locate and orient toward settlement habitat. However, the distances over which pelagic individuals can detect and localize sounds from reefs are still unassessed [13]. A first set of theoretical approaches calculated the distances of detection to be less than 1 km [13] to more than 5 km depending on the hearing ability of the studied species [14,15]. Other studies suggested a distance of detection of 20 km based on the audiogram of a Pomacentridae species on rocky habitats of New Zealand [45].

The aims of the present study are to describe the biophony (sounds of fish and benthic invertebrates) of the barrier reef at Moorea Island (French Polynesia) to (1) measure its propagation distance in the ocean empirically, (2) describe how abiotic and anthropic factors interfere with it and (3) estimate the detection distance based on known audiograms.

## 2. Materials and Methods

### 2.1. Sampling

Data sampling was conducted 13–17 May 2016, on the north coast of Moorea (French Polynesia) (−17.5 S, −149.9 E, Figure 1). Recordings were realized with drifting antennas made of a floater and an autonomous recorder EA-SDA14 (RTSys®, Caudan, France) connected to a wideband low-noise hydrophone HTI-92 (High Tech Inc., Long Beach, MS,

USA) with a sensitivity of $-155 \pm 3$ dB re 1 V µPa$^{-1}$ and a flat frequency response from 2 Hz to 50 kHz. It was placed on a vertical rope at $\approx 5$ m from the surface to minimize sea-surface noise. Sounds were acquired continuously at a 156 kHz sampling rate and 32 bits resolution. Six transects were realized during daytime (8:30 a.m.–5:30 p.m.) with recordings of approximately 600 s duration recorded at 50, 100, 200, 400, 600, 800, 1500, 2000, 3000, 4000, 5000, 7000 and 10,000 m from the reef crest; i.e., a total of 78 stations corresponding to $\approx 13$ h of recordings (Figure 1). The mean depth varied from $-9$ to $-2580$ m. Water depth was measured for each transect using a portable echosounder. These data were completed with bathymetric data obtained from the French Naval Hydrographic and Oceanographic Service (reference: LOTS BATHY S201208100-08, SHOM, France).
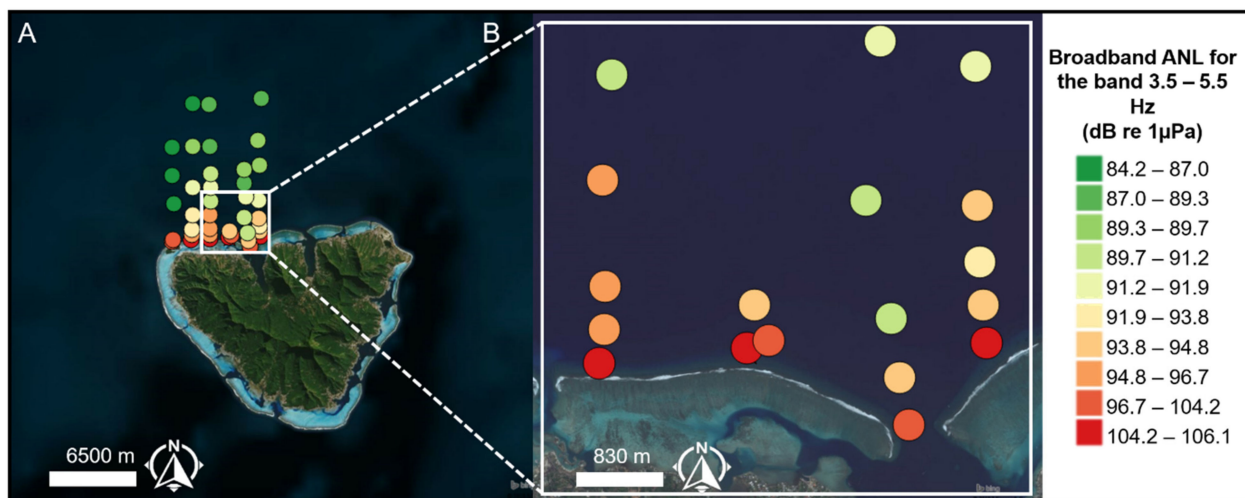


**Figure 1.** (**A**) Distribution of the ambient noise level (ANL) of the benthic transient sounds (BTS) between 3.5 and 5.5 kHz on the 40 stations and (**B**) zoom of the proximal part of the transects. Color scale indicates ambient noise levels.

GPS positions of the drifting antennas were recorded both when they were deployed and when they were recovered. The drift distances were not uniform, but the error caused by the uncertainty of the hydrophone position due to drift was inferior to 1.8 dB for all the data. In addition, to record the diel variability of the biophony during the recording period, a fixed recording station, composed of the same type of recorder and hydrophone, was bottom-moored on the external slope, at a depth $\approx 12$ m and 127 m distant from the reef crest on the same dates as the transects.

### 2.2. Analyses

The recordings were visually and aurally inspected with RavenPro Sound Analysis Software 1.5 (Cornell Lab of Ornithology, Ithaca, NY, USA). Only transect stations with low noise levels from buoy strumming (e.g., not in the presence of high swells) were considered (40 out of 79). For each of the selected stations, only sections without boat noises were analysed. Long-term spectrograms, sound pressure spectrum levels and graphics were realized with custom-made Matlab® R2014b routines (MathWorks, Natick, MA, USA).

### 2.3. Benthic Invertebrate Sounds

To assess the temporal variability of the benthic invertebrate biophony (the sum of the many isolated broadband transient sounds (BTS) produced by benthic invertebrates [51] (Figure 2A)) recordings from the fixed station were analysed (Figures 1 and 2). BTS were grouped into four frequency "bands" (3.5–5.5 kHz, 6–8 kHz, 10–13 kHz and 14–17 kHz). These bands were chosen based on peaks in 24 h power spectra. An automatic BTS detector (see [52] for details of the algorithm) was run for each of the selected bands. In addition to the four bands, the same algorithm was run on the BTS between 570 and 2000 Hz, because these frequencies corresponded to sounds that appeared to be more attractive to larvae of

different fish families [26]. The three features calculated were the number of detected BTS (NoBTS) having a minimal signal-to-noise ratio (SNR) of 10 dB, the peak-to-peak sound pressure level (SPL), and the ambient noise level (ANL), both in dB re 1 µPa for each band (Figure 2A). The ANL is the background SPL modelled with a $\chi^2$ distribution on the 20th percentile (*cf.* [53] for the definition and [54] for the formula). It represented the overall energy of distant BTS emanating from the reef without the individually identifiable high-energetic BTS. The SPL is the sum of both individualizable sounds and the ANL. Wenz's ambient noise curves [55], calculated on the same bands as the BTS, were superposed to the sound levels to estimate attenuation due to wind regime or ship traffic [56]. The flat sea state condition corresponded to a wind speed of 0 kn while the average condition corresponded to 6 kn; that is, the average wind speed of the study area (annual mean at the Tahiti island meteorological station between 2008 and 2019). To compare the different acoustic features between day and night recordings of the fixed station at the barrier reef, Student's *t*-tests were realized using the R software version 3.3.0. (R Core Team, 2016).
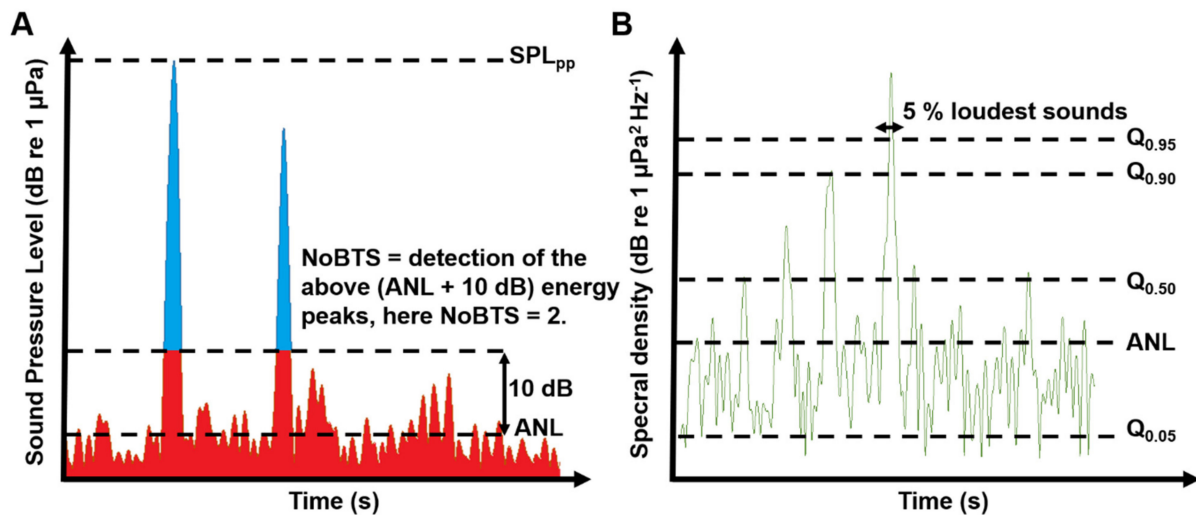


**Figure 2.** Description of the acoustic features for (**A**) benthic invertebrates sounds (for each BTS band) and (**B**) fish sounds (200–500 Hz). In blue: nearby sources producing loud and short individual energy peaks; in red, a collection of a large number of distant unidentified sources producing a background chorus. SPL = Sound Pressure Level, pp = peak to peak, NoBTS = number of Broadband Transient Sounds, ANL = ambient noise level, Q = percentile, with $Q_{0.05}$ = 5% faintest sounds, $Q_{0.50}$ = median levels, $Q_{0.90}$ = 10% loudest sounds and $Q_{0.95}$ = 5% loudest sounds.

### 2.4. Fish Sounds

To characterize fish sounds, the mean sound pressure level of the frequency band comprised between 200 and 500 Hz was analysed because it corresponded to the frequency band in which a fish chorus [57,58] was present. The features measured were the spectral ANL, the 50th percentile ($Q_{0.50}$), the 90th percentile ($Q_{0.90}$) (representative of the 10% loudest sounds), and individual sounds, represented as the 90th percentile with 10 dB above the Wenz background noise ($Q_{0.90} - 10$) in dB re 1 µPa$^2$ Hz$^{-1}$ (Figure 2B). Wenz's ambient noise spectra were superposed to the calculated spectra [56] to estimate the wind- or shipping noise-dependent effect on reef sound propagation. To compare the different acoustic features between day and night recordings of the fixed station at the barrier reef, Mann-Whitney *U* tests were conducted using the R software version 3.3.0. (R Core Team, 2016).

### 2.5. Propagation Distances of Reef Sounds

To account for complex local conditions of propagation near the shore, logarithmic linear regressions were obtained from sound levels measured in situ from the reef up to

10 km offshore as $y = a \log_{10} r + b$ for $r < 10$ km. Sounds below 200 Hz were affected by the strumming noise produced by the drifting systems and were not considered. Distances between locations of the drifting recording devices and the reef crest were measured using QGIS 2.14.3 (Open Source Geospatial Foundation Project).

For distances greater than 10 km, a theorical cylindrical propagation loss (=transmission loss, TL) was calculated from 10 km to range $r$, with $TL = 10\log\left(r{\cdot}r_0^{-1}\right) + \alpha(r - r_0)$ for $r \geq 10$ km and $r_0 = 10$ km. The attenuation of sound in seawater ($\alpha$ in dB km$^{-1}$) was calculated using the model of Ainslie and McColm (1998) [59] to fit the average temperature of 26 °C. Reference values were used for the pH and salinity (pH = 8; S = 35) [59]. This propagation model was chosen because the majority of the regression equations for distances shorter than 10 km were closer to a cylindrical than a spherical propagation (Table S2). The difference between day and night recordings of the fixed station were used to infer the difference between diurnal and nocturnal propagation.

### 2.6. Comparisons with Audiograms

Regressions of the biophony reef spectra against distance from the reef (Table S2) were compared to audiograms from cetaceans, invertebrates and (post-)larval fish in the literature. Polynesian coral reef species were used except when little data were available, in which case we used audiograms reported for others species (e.g., *Stenella coeruleoalba* was used instead of the one of *S. longirostris*). Values in particle motion from the literature were converted to pressure values assuming a plane-wave propagation [60]. To compare audiogram values at one given frequency (dB re 1 µPa) to the spectra (dB re 1 µPa$^2$ Hz$^{-1}$), it was necessary to adjust the audiogram thresholds [61] by lowering them by 10 log$_{10}$ (Critical Bandwidth, CBW) [62,63] with CBW estimated to 10% of the centre frequency as in Egner and Mann 2005. According to the literature [64,65], for both fish and invertebrates, a correction factor of 10 to 30 dB was applied to compare methods. In contrast, in cetaceans, the results of the different methods were comparable [66]. The biophony spectra used were the 90th percentile (Q$_{0.90}$, the 10% loudest sounds), the 50$^{\text{th}}$ percentile (the median) and the ANL on the basis of the regressions (calculated on each frequency used in the audiograms, Figure 2B). When propagation distances were beyond 10 km (i.e., the greatest distance at which recordings were acquired), the theoretical TL model was used with an $\alpha$ calculated for each frequency of the audiograms. The distances obtained were compared to the background noise of the Wenz model.

## 3. Results

The soundscape of the barrier reef of Moorea was characterized by fish sounds between 200 and 500 Hz and by a high number of broadband transient sounds (NoBTS) between 3.5 and 17 kHz (Figure 3).

### 3.1. Benthic Invertebrate Sounds

The NoBTS ranged from 106 ± 6 (mean ± SD) per second in the 3.5–5.5 kHz band; 96 ± 9 per second in the 6–8 kHz; 86 ± 4 in the 10–13 kHz and 83 ± 3 in the 14–17 kHz. The NoBTS was 8% greater during the night for the band 3.5–5.5 kHz ($\Delta$ = 8.12, t = –5.64, df = 23, $p < 10^{-5}$, Student's *t*-test), 14% and 5% smaller during the night within the band 6–8 kHz ($\Delta$ = 14.05, t = 7.67, df = 23, $p < 10^{-6}$, Student's *t*-test) and the band 10–13 kHz respectively ($\Delta$ = 4.42, t = 3.15, df = 22, $p$ = 0.0046, Student's *t*-test), and similar for the band 14–17 kHz (t = 0.59, df = 23, $p$ = 0.56, Student's *t*-test, Figures 3A and 4).
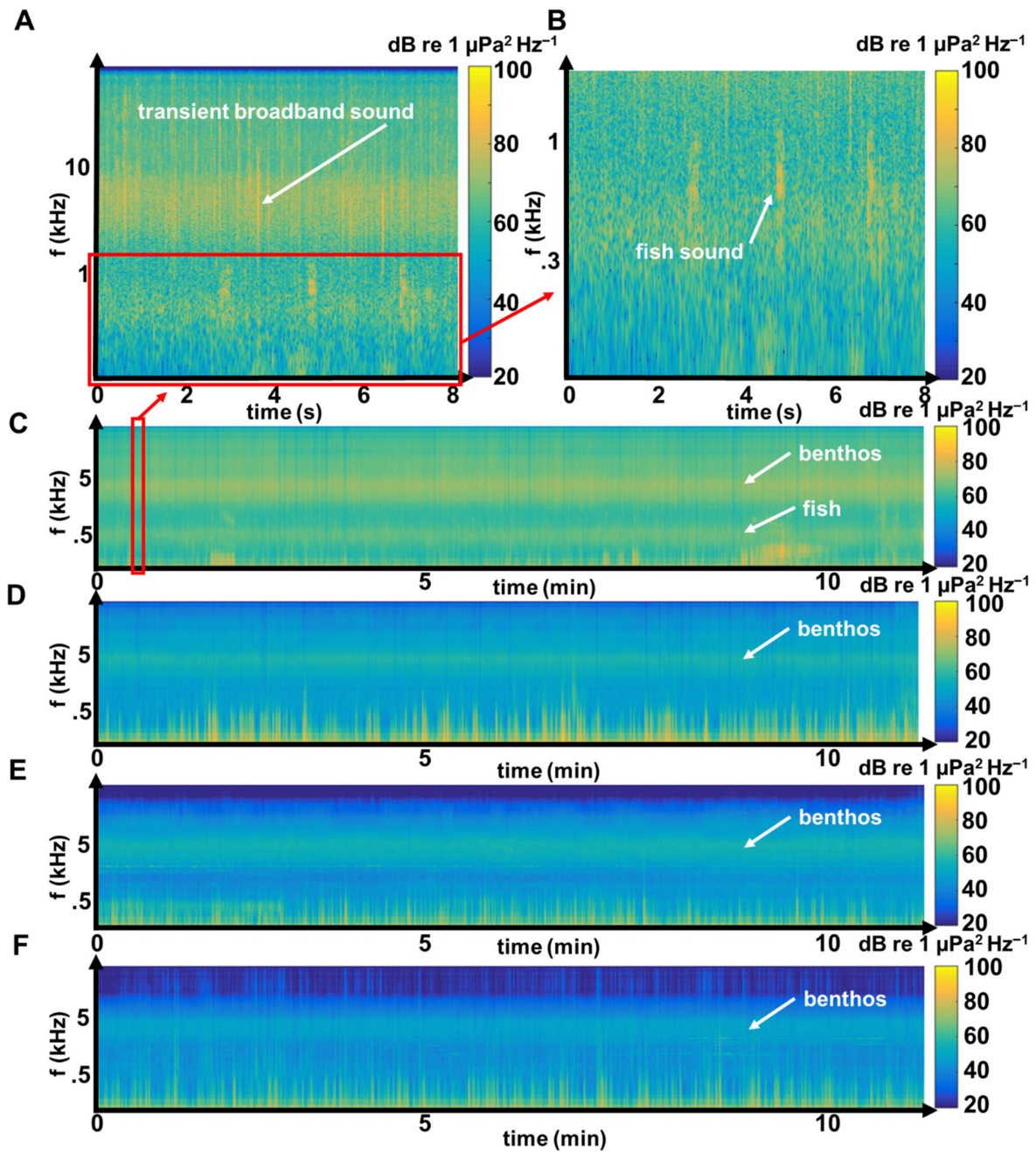
**Figure 3.** Spectrograms of the soundscapes recorded at different distances from the reef. A and B illustrate subsections of spectrogram C highlighting invertebrate (**A**) and fish sounds (**B**). (**C**) was recorded at $138 \pm 11$ m from the reef, (**D**) $964 \pm 138$ m, (**E**) $3896 \pm 3$ m and (**F**) $9866 \pm 43$ m from the reef crest. For A and B: LFFT = 16,384, overlap = 75%, window = Kaiser. For C, D, E and F: LFFT = 65,536, overlap = 50%, window = Kaiser.

The SPL and ANL of all the bands of BTS were significantly higher during the night (for all: $t < -16.79$, $20 < df < 23$, & $p < 10^{-13}$, Student's *t*-test) with a 6.7 to 9.2 dB difference between 5 and 6 p.m. (Figure 4C). This means that sounds were four to eight times louder at dusk. There was a peak at dusk and dawn with a higher difference between day and night for BTS in the 3.5–5.5 Hz band (SPL: $126.90 \pm 0.86$ dB re1 µPa during the day and $133.72 \pm 0.88$ dB re1 µPa during the night) (Figure 4C). The SPL and the ANL of the 6–8 kHz band were always smaller than those of the other bands (Figure 4C).
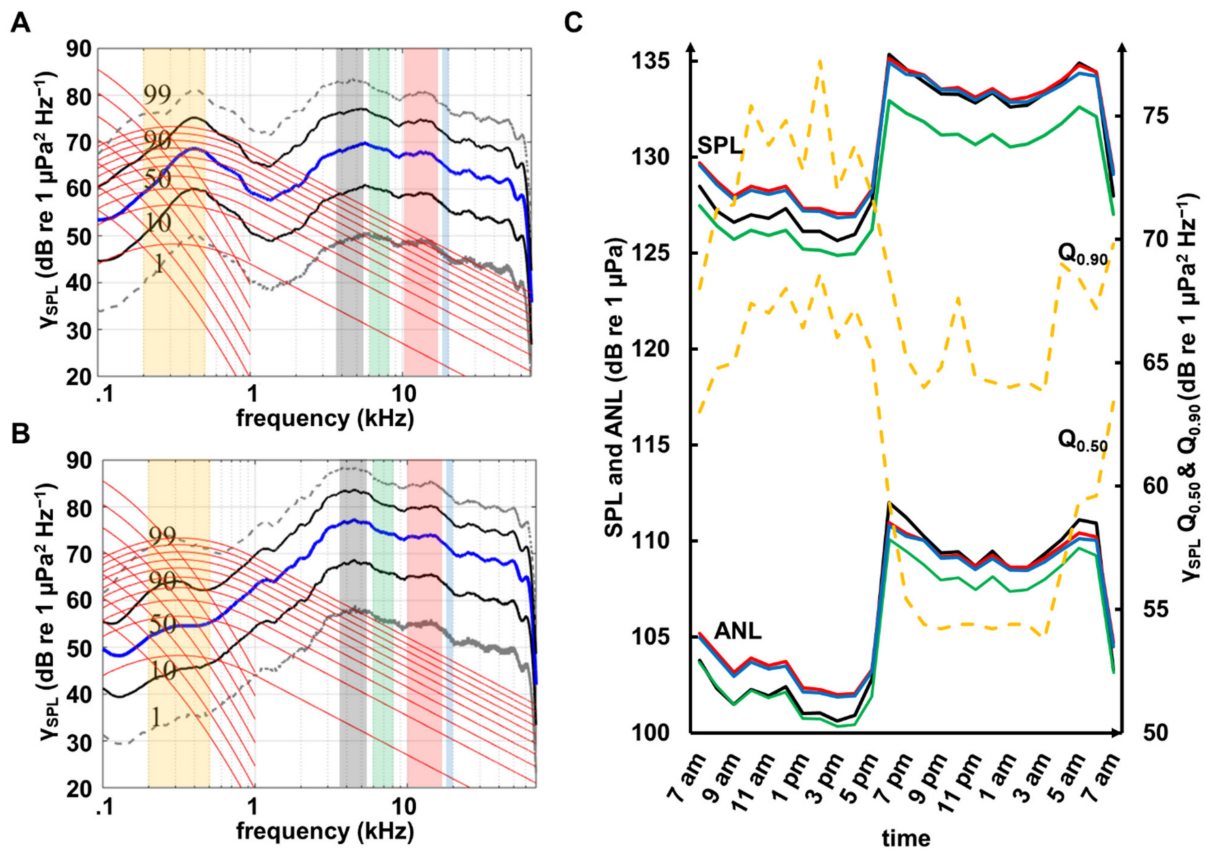
**Figure 4.** Power spectral density at the fixed recording station at –12 m depth and 127 m distance from the reef crest at (**A**) 2 p.m. and (**B**) midnight. In dashed grey, percentiles $Q_{0.01}$ and $Q_{0.99}$; in black, percentiles $Q_{0.10}$ and $Q_{0.90}$; in bold blue, the median $Q_{0.50}$ and in red, Wenz background noise for wind speeds between 0 and 30 kn and ship traffic index between 1 and 7. (**C**) Diel pattern of sound pressure level (SPL) and ambient noise level (ANL) (left scale) for benthic BTS bands (3.5–5.5 kHz, 6–8 kHz, 10–13 kHz and 14–17 kHz) highlighted respectively in black, green, red and blue non-dashed lines (also highlighted in the vertical rectangles in (**A**,**B**)). Diel pattern of $Q_{0.50}$ and $Q_{0.90}$ of power spectral density ($\gamma$SPL) (right scale) for the frequency band between 200 and 500 Hz corresponding to the daytime fish chorus highlighted in orange (dashed lines).

### 3.2. Fish Sounds

The band between 200 and 500 Hz presented a diel pattern with higher values of sound pressure spectrum level during the day: $Q_{0.50} = 66.02 \pm 1.74$ dB re 1 $\mu$Pa$^2$ Hz$^{-1}$ (day) and $55.92 \pm 2.40$ dB re 1 $\mu$Pa$^2$ Hz$^{-1}$ (night); $Q_{0.90} = 72.58 \pm 2.29$ dB re 1 $\mu$Pa$^2$ Hz$^{-1}$ (day), and $65.76 \pm 2.12$ dB re 1 $\mu$Pa$^2$ Hz$^{-1}$ (night) ($W = 918$ and 901; both $p < 10^{-5}$, Mann–Whitney $U$ test for $Q_{0.50}$; Figure 4). The spectra presented differences between day and night: a peak between 400 and 500 Hz was present during the day both for intense (percentile $Q_{0.99}$) and median sounds ($Q_{0.50}$), while during the night, peaks were always observed between 250 and 280 Hz for $Q_{0.99}$ and were never observed for $Q_{0.50}$ (Figure 4) Other peaks were punctually observed at dusk and dawn, especially for lower frequencies. This suggests that vocal species produce sounds with different diel patterns.

### 3.3. Propagation Distances of Reef Sounds

A decrease of the sound spectrum level from the shore to the open ocean was observed for sounds between 200 and 70,000 Hz (Figures 1 and 3). ANL and SPL of BTS showed a constant logarithmic decrease with distance from the reef crest (Figure 5A). From the slope of the regressions, TL was estimated to vary from −8.99 to −16.80 dB decade$^{-1}$ (a decade corresponds to a factor-of-ten increase) for BTS depending on the noise levels (i.e., SPL or

ANL) and the band of BTS used (Table 1). There was a positive relationship between TL and frequency except for frequencies between 600 and 2100 Hz, for which a decrease in TL was observed. At 10 km, the measured ANL of the four bands of BTS was between 70 and 86 dB re 1 µPa and the SPL between 93 and 107 dB re 1 µPa (Figure 5).
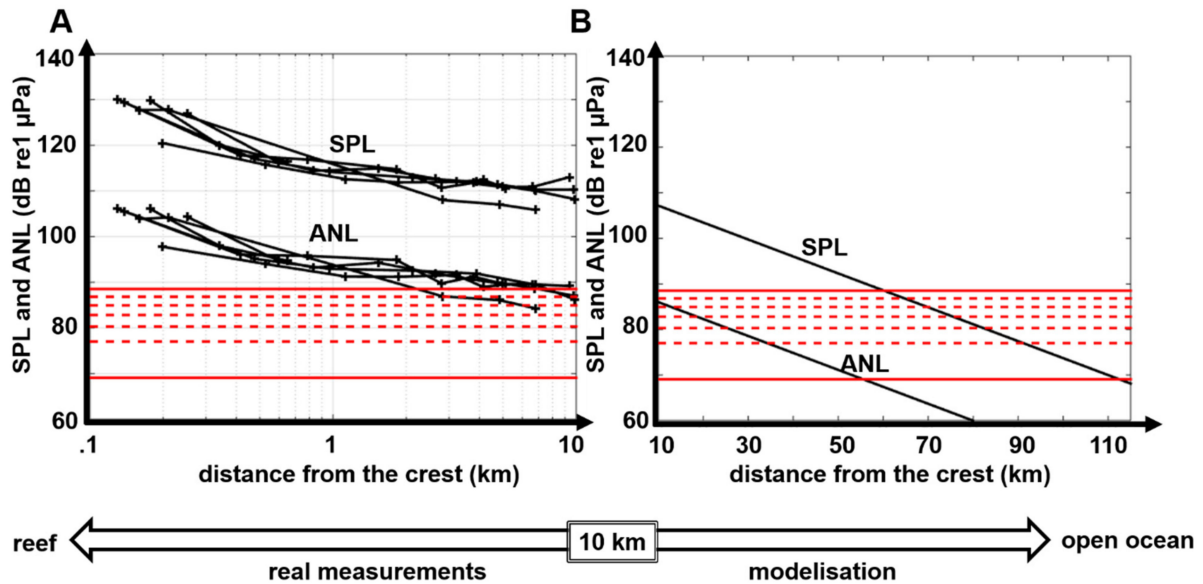


**Figure 5.** (**A**) In situ measurements of the sound pressure level (SPL) and ambient noise level (ANL) for the band 3.5–5.5 kHz for each of the six transects up to 10 km. (**B**) Logarithmic regression with a modelled propagation loss (= transmission loss, TL): $TL = 10\log\left(r \cdot r_0^{-1}\right) + \alpha(r - r_0)$ with $r_0 = 10$ km and $\alpha = 0.274$ dB km$^{-1}$ for distances beyond 10 km. In red, Wenz background noise for wind speeds between 0 and 18 kn (from bottom to top: 0, 3, 6, 9, 12, 15 and 18 kn).

**Table 1.** Regressions of benthic transient sounds (BTS) levels (dB re 1 µPa) at 1 m and 10 km from the reef crest for the ambient noise level (ANL) and the sound pressure level (SPL). Equations correspond to propagation loss regression equations assessed form the empirical data.

| Band (kHz) | Feature | Equation | R$^2$ | Value at 1 m | Value at 10 km | Δ Night |
|---|---|---|---|---|---|---|
| | | | | (dB re 1 µPa) | | |
| 3.5–5.5 | ANL | y = −8.99 log$_{10}$x + 121.97 | 0.85 | 121.97 | 86.01 | 7.92 |
| | SPL | y = −10.01 log$_{10}$x + 147.23 | 0.83 | 147.23 | 107.19 | 6.81 |
| 6–8 | ANL | y = −10.22 log$_{10}$x + 121.79 | 0.88 | 121.79 | 80.91 | 6.73 |
| | SPL | y = −11.13 log$_{10}$x + 146.72 | 0.84 | 146.72 | 102.20 | 5.60 |
| 10–13 | ANL | y = −13.84 log$_{10}$x + 130.29 | 0.94 | 130.29 | 74.93 | 6.22 |
| | SPL | y = −14.50 log$_{10}$x + 155.64 | 0.93 | 155.64 | 97.64 | 5.72 |
| 14–17 | ANL | y = −16.42 log$_{10}$x + 135.74 | 0.96 | 135.74 | 70.06 | 6.24 |
| | SPL | y = −16.80 log$_{10}$x + 160.45 | 0.95 | 160.45 | 93.25 | 5.71 |

At 10 km, the ANL of the dominant BTS band 3.5–5.5 Hz was 86.01 dB re 1 µPa (Table 1). Its estimated propagation range was 65 km under a low wind regime (0 kn) and decreased to 28 km with a 6 kn wind (Figure 5). During the day, the SPL of the BTS in the 3.5–5.5 kHz band under 0 kn wind conditions was 10 dB re 1 µPa above the background noise and detectable by hydrophone at 101 km. During the night, the intensity of these BTS was higher. Consequently, the estimated distances were higher: 90 km for the ANL under flat-sea conditions and 54 km with a 6 kn wind.

Propagation distances decreased with increasing BTS frequency band (Table 2). The ANL of the BTS between 570 and 2000 Hz (the band described to be attractive to fish larvae [26]) was detectable up to 55 km (day) and up to 90 km (night) with 0 kn of wind

and to 0.9 km (day) and 3.4 km (night) with an average wind speed of 6 kn. Similar results were obtained for the spectral density values (Table 1) except for the 570–2000 Hz band. Propagation distances of all analysed BTS bands were likely poorly affected by ship traffic. In fact, based on Wenz's ship traffic spectra, if the index increased from 0 to 2, the ANL of the 570–2000 Hz band decreased by less than 1% (Figure 6A) while with an index of 6, the ANL decreased by 50% (Figure 6A).

**Table 2.** Distance of detection (km) of the investigated Broadband Transient Sounds (BTS) frequency bands at day and night under different wind regimes as reported by Wenz (1962). ANL = ambient noise level, SPL = sound pressure level, both measured in dB re 1 μPa, kn = knot. γANL, $\gamma Q_{0.50}$ = 50th percentile and $\gamma Q_{0.90}$ = 90th percentile, measured as dB re $1\ \mu Pa^2\ Hz^{-1}$ from the power spectra.

| | | Distance from the Reef Crest (km) | | | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | | Day | | | | | Night | | | | |
| Band (kHz) | Feature | 0 kn | 3 kn | 6 kn | 9 kn | 12 kn | 0 kn | 3 kn | 6 kn | 9 kn | 12 kn |
| 3.5–5.5 | ANL | 65 | 39 | 28 | 20 | 13 | 90 | 65 | 54 | 46 | 39 |
| | SPL | 134 | 108 | 97 | 90 | 82 | 156 | 130 | 120 | 111 | 104 |
| | SPL–10 | 101 | 75 | 65 | 56 | 50 | 123 | 97 | 87 | 79 | 72 |
| | γANL | 59 | 33 | 22 | 15 | 8.4 | 81 | 55 | 45 | 36 | 30 |
| | γQ0.50 | 54 | 28 | 18 | 9.8 | 6.0 | 76 | 50 | 39 | 31 | 24 |
| | γQ0.90 | 71 | 46 | 35 | 27 | 20 | 92 | 66 | 56 | 47 | 40 |
| 6–8 | ANL | 43 | 26 | 19 | 13 | < 10 | 58 | 40 | 33 | 28 | 23 |
| | SPL | 90 | 72 | 65 | 60 | 55 | 102 | 84 | 77 | 72 | 67 |
| | SPL–10 | 68 | 50 | 43 | 38 | 33 | 80 | 63 | 55 | 50 | 45 |
| | γANL | 40 | 22 | 15 | 9.7 | 7.0 | 52 | 35 | 27 | 22 | 17 |
| | γQ0.50 | 36 | 19 | 12 | 6.1 | 4.4 | 48 | 31 | 24 | 18 | 14 |
| | γQ0.90 | 48 | 30 | 23 | 18 | 13 | 59 | 42 | 35 | 29 | 25 |
| 10–13 | ANL | 23 | 14 | <10 | <10 | <10 | 31 | 21 | 17 | 14 | 12 |
| | SPL | 50 | 41 | 37 | 34 | 31 | 57 | 48 | 44 | 41 | 38 |
| | SPL–10 | 38 | 29 | 25 | 22 | 19 | 45 | 36 | 32 | 29 | 26 |
| | γANL | 21 | 12 | 7.5 | 5.0 | 3.5 | 28 | 18 | 15 | 12 | <10 |
| | γQ0.50 | 19 | 10 | 5.9 | 4.0 | 2.8 | 26 | 17 | 13 | <10 | <10 |
| | γQ0.90 | 26 | 16 | 13 | 9.6 | 6.9 | 32 | 23 | 19 | 16 | 14 |
| 14–17 | ANL | 16 | 10 | <10 | <10 | <10 | 21 | 15 | 13 | 11 | <10 |
| | SPL | 34 | 28 | 26 | 24 | 22 | 38 | 32 | 30 | 28 | 26 |
| | SPL–10 | 26 | 20 | 18 | 16 | 14 | 31 | 25 | 22 | 20 | 19 |
| | γANL | 15 | 9.0 | 5.7 | 4.0 | 3.0 | 20 | 14 | 11 | <10 | <10 |
| | γQ0.50 | 14 | 7.4 | 4.7 | 3.3 | 2.5 | 19 | 13 | 10 | <10 | <10 |
| | γQ0.90 | 19 | 13 | 10 | 7.5 | 5.6 | 23 | 17 | 14 | 13 | 11 |

Diurnal fish sounds (between 200 and 500 Hz) presented a logarithmic decrease in both ANL and $Q_{0.50}$, up to 1 km from the reef crest. Between 1 and 10 km, a logarithmic decrease of the sound pressure spectrum level was observed only in calm sea conditions. In presence of high swells up to 2 m, the sound pressure spectrum level of the transects was higher because it included hydrodynamic noises. Therefore, only transects under a calm sea state were used for the analyses (40 out of 79). This result indicated a limitation of the drifting method for low-frequency sounds in the presence of a significant swell. For the flattest sea-state transect, the distance of detection of the fish chorus frequencies (200–500 Hz) was found between 1322 m (for $Q_{0.50}$) and 1501 m (for ANL) with no wind ($y = -13.00 \log_{10} x + 91.82$, $R^2 = 0.96$, for $Q_{0.50}$, and $y = -13.42 \log_{10} x + 93.87$, $R^2 = 0.95$, for ANL; between the crest and 2 km, Table S1). The 10% loudest sounds ($Q_{0.90}$) were detected at 3.5 km from the crest and individual sounds ($Q_{0.90}$ with 10 dB above the Wenz background noise, named $Q_{0.90}$–10) at 793 m from the crest ($y = -14.62 \log_{10} x + 103.63$, $R^2 = 0.94$ between the crest and 1 km on the descending portions of all the transects, Table S1). Propagation distance decreased by a factor ≈4 (for $Q_{0.50}$ & ANL) or 3.5 (for $Q_{0.90}$) with

a 3 kn increase in wind speed (Table S1). With an average wind speed of 6 kn, these four distances decreased to 180, 217, 654 and 134 m for $Q_{0.50}$, ANL, $Q_{0.90}$ and $Q_{0.90}-10$ respectively. Under no-wind conditions, the increase of the level of Wenz's ship traffic index from 1 to 2 decreased the distance between 187 and 207 m (for $Q_{0.50}$ & ANL) and 491 to 102 m (for $Q_{0.90}$ and $Q_{0.90}-10$); however, this decrease was less important when wind speeds were higher as there was a combined effect of wind and boats on detection distance during the day (Figure 6B, Table S1).
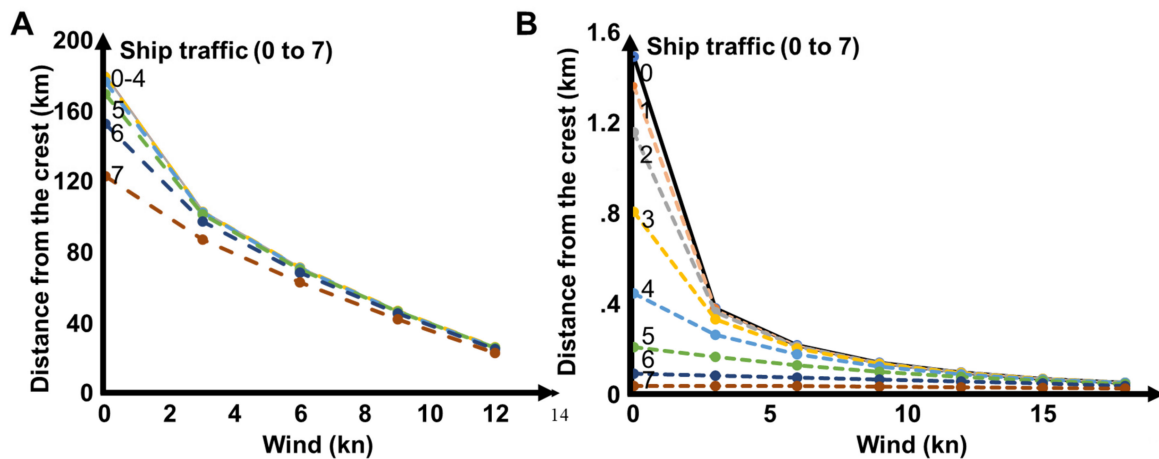


**Figure 6.** Detection distance of (**A**) the individual sounds represented as the 90th percentile with 10 dB above the Wenz background noise ($Q_{0.90}-10$) between 570 and 2000 Hz (**B**) and fish ambient noise level (ANL) as a function of the wind in knots. The solid line is without considering boats and dashed lines are when considering ship traffic from the Wenz model; each colour corresponds to a ship traffic regime also numbered from 1 (upper line) to 7 (bottom line).

### 3.4. Comparisons with Audiograms: Fish

In post-larval reef fish, audiograms based on sound pressure showed that the best hearing sensitivity is between 200 and 600 Hz [15,61,64,67–69]. The frequencies that allowed them to hear the reef from the greatest distance during daytime were in the same frequency range. Based on the audiograms (SPL) of post-larval reef fish [15,61,64,65,67–69], the estimated detection distances ranged from 0 to 65 m (median) and 80 m (ANL) for the six species of Pomacentridae, 8 to 336 m (median) and 11 to 401 m (ANL) for *Myripristis kuntee* (Holocentridae); 4 to 191 m (median) and 6 to 234 m (ANL) for *Acanthurus triostegus* (Acanthuridae); 23 to 455 m (median) and 28 to 560 m (ANL) for *Chaetodon citrinellus* (Chaetodontidae); 19 to 392 m (median) and 24 to 482 m (ANL) for *Rhinecanthus aculeatus* (Balistidae) and 0 to 4–5 m for the two Lutjanidae and the four Serranidae species analyzed (Figure 4B, Tables S2 and S3). These distances were smaller during the night except for species such as *M. kuntee*, which are able to hear higher frequencies (Figures 7A and 8). For this species, frequencies between 2.7 and 3 kHz were the ones showing the greatest detection distances ranging from 2 to 337 m (median) and from 3 to 498 m for the ANL. For fish, the detection of low frequencies 300 and 600 Hz was limited by ambient noise values, as maximal detection distances both at day and night for an average wind of 6 kn can decrease up to 54% (Figures 7A and 8).
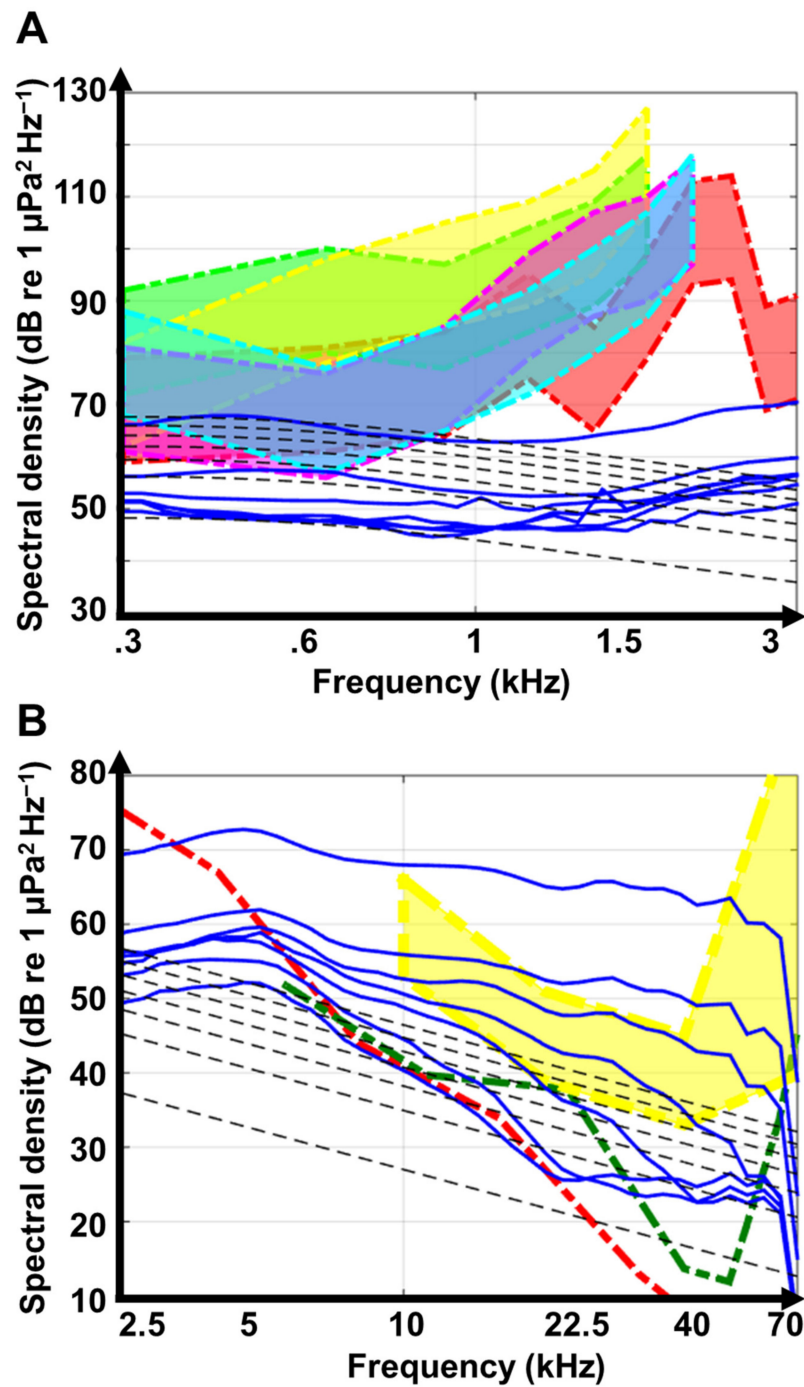
**Figure 7.** Audiograms of (**A**) fish post-larvae and (**B**) cetaceans compared to spectrum level of ambient noise level (ANL) at different distances from the barrier reef. Solid blue line: measured ANL on one of the six transects; from top to bottom: at 138, 476, 964, 2134, 3896, 6831, 9866 m from the reef crest. Dashed black line: Wenz's ambient noise curves; from bottom to top: 0, 3, 6, 9, 12, 15 and 18 kn of wind. Equivalent threshold (for details of the transformations, see Table S3). (**A**) Red: *Myripristis kuntee*, green: *Abudefduf vaigiensis*, yellow: *Acanthurus triostegus*, magenta: *Chaetodon citrinellus* and cyan: *Rhinecanthus aculeatus*; (**B**) Red: *Stenella coeruleoalba*, green: *Mesoplodon densirostris* and yellow: *Globicephala macrorhynchus* [69,74–76].
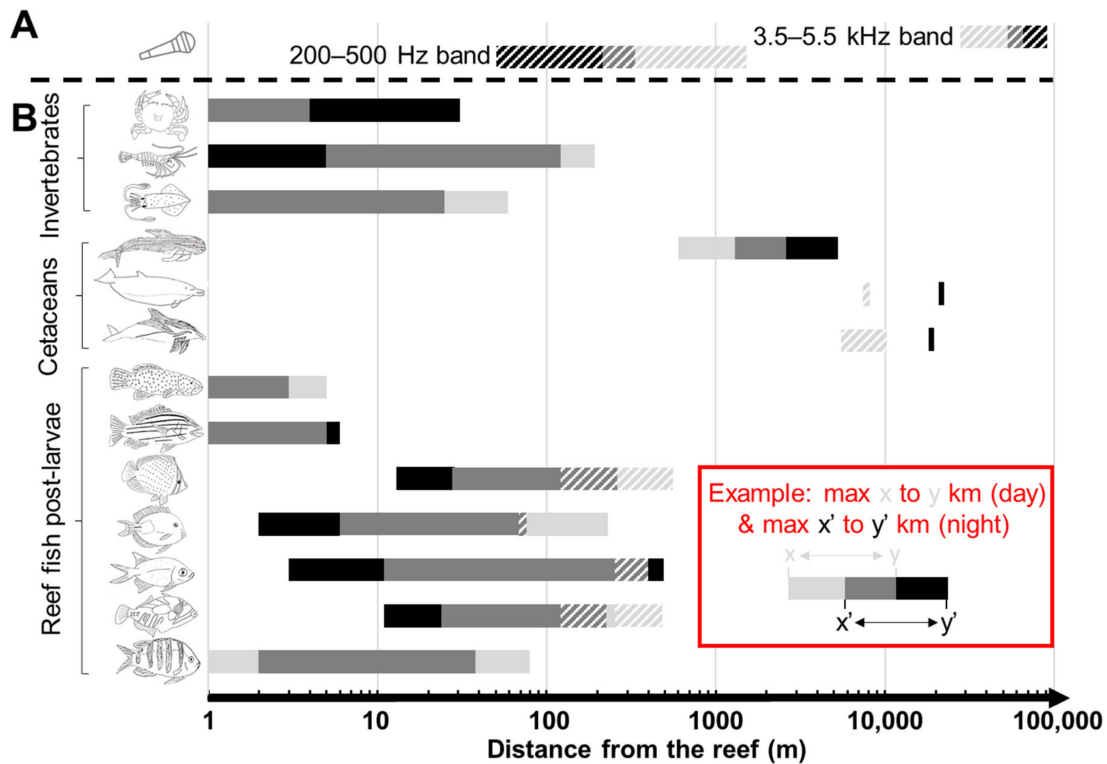
**Figure 8.** (**A**) Maximal distance of detection of the ambient noise level (ANL) of the fish chorus (200–500 Hz) and benthic invertebrate (3.5–5.5 kHz) bands and (**B**) Maximal distance of detection of the ANL of the reef by different species from the literature, from bottom to top: fish (Pomacentridae, Balistidae, Holocentridae, Acanthuridae, Chaetodontidae, Lutjanidae and Serranidae), cetaceans (*Stenella*, *Mesoplodon* and *Globicephala*) and invertebrates (squid *Loligo*, shrimp *Palaemon* and crab *Ovalipes*). See Table S3 for details of the individuals used. Light grey = diurnal values, black = nocturnal values, dark grey = overlap between diurnal and nocturnal values. Hatched parts correspond to values possible only when the wind is less than 6 knots, the average speed in Polynesia). The red box is an example to show how to read the figure.

However, for the majority of fish species, particle motion seems to be more appropriate for evaluating hearing thresholds [70]. As only little is known about particle motion perception on fish post-larvae, adult thresholds [71–73] were also used for comparisons with soundscape data (particle motion thresholds converted to pressure thresholds) as assumed in several studies [45,72]. Distances below 13 m were found for all the considered species except for the temperate *Sciaena umbra* (Sciaenidae): 13 to 344 m (median) and 16 to 430 m (ANL) at 500 Hz (maximum 217 and 271 if there are 6 kn of wind). For adult fish hearing specialists species, these distances are higher; for example, *Pempheris adspersa* (Pempheridae) could detect the pressure component of the reef at 49 to 1389 m (median) and 59 to 1710 m (ANL) (maximum 207 and 258 m in a 6 kn wind).

*3.5. Comparisons with Audiograms: Cetaceans*

Odontocetes have their maximum hearing sensitivity around 40 and 64 kHz [74–76]. However, the audiogram comparison [74–76] indicated that the frequency range that would allow them to perceive reef sounds from a greater distance is between 5.6 and 20 kHz (Figure 7). The maximal detection distance of the median reef sounds ($Q_{0.50}$) ranged between 7.6 km (day) and 15.9 km (night) for the striped dolphin *Stenella coeruleoalba*, while the ambient noise level (ANL) emanating from the reef could be heard up to 9.2 km (day) to 19.0 km (night) (Figures 7 and 8). With an average wind of 6 kn, diurnal values decreased to 4.5 km and 5.5 km while nocturnal values did not change (Figure 8). Similar results were obtained for the Blainville's beaked whale *Mesoplodon densirostris* (median: 6.4 km (5.8 km if 6 kn of wind (day)) to 17.5 km (night); ANL: 8.2 km (7.3 km if 6 kn of wind

(day)) to 21.8 km (night)) while smaller maximum distances were estimated for the short-finned pilot whale *Globicephala macrorhynchus* (median: 0.5 to 2.2 km (day) to 1.1 to 4.5 km (night); ANL: 0.6 to 2.6 km (day) to 1.3 to 5.3 km (night)) (Figure 4B, Tables S2 and S3). In contrast to odontocetes, mysticetes are sensitive to lower frequencies, around 0.7 to 10 kHz with best values between 2 and 6 kHz [77]. However, as the exact auditory sensitivity of mysticetes is unknown (the frequency range is based on a mathematical function describing frequency sensitivity by the position along the basilar membrane coupled with data from other mammals [77]), detection range estimates could not be calculated.

### 3.6. Comparisons with Audiograms: Invertebrates

To the best of our knowledge, there are no available audiograms of post-larval marine invertebrates. Based on audiograms of adult individuals from the literature [78–83], different detection distances were estimated: some species such as *Panopeus* spp. crabs could perceive reef sounds with a maximal detection distance smaller than 1 m. Other species such as the crab *Ovalipes catharus* likely attained higher maximal detection distances at high frequencies (2000 Hz) and during the night (median: 0–21 m, ANL: 0–31 m) (Figure 8). For cephalopods, the maximal detection distances were found for lower frequencies between 200 and 600 Hz. These distances were estimated between 0 and 59 m. Finally, some species such as the prawn *Palaemon serratus* were likely capable of detecting reef sounds at 4–159 m (median) and 5–195 m (ANL) at 300 Hz during the day (Figure 8). During the night, maximal distances could be achieved for higher frequencies (3000 Hz; between 1 and 121 m) (Figure 4B, Tables S2 and S3).

## 4. Discussion

### 4.1. Diel Pattern

Sounds emitted by coral reefs are complex signals since they are generated by numerous species and affected by physical processes [13]. The source level of the barrier reef of Moorea (SPL at 1 m) was estimated to be 147 dB re 1 μPa for the most energetic frequency band 3.5–5.5 kHz and was of 136 dB re 1 μPa for larger BTS band (1–70 kHz). These values are within the range of source levels usually found in coral reefs [84] and healthy temperate rocky reefs [51]. In this study, there was an increase in low frequency sounds emitted by fish (200–500 Hz) during the day and an increase of high frequencies emitted by benthic invertebrates (3.5–5.5 kHz) during the night. Moreover, a peak in this higher frequency band was observed at both dawn and dusk. Similar diel patterns have been previously described from Polynesian [7,85] and non-Polynesian coral reefs [9,86].

### 4.2. Propagation Distances

In the literature, the estimation of the propagation distances of biogenic reef sounds varies greatly according to the use of a spherical or cylindrical spreading model [87]. Moreover, different studies [45,87] assumed, without experimental demonstration, that acoustic cues could be detected at several tens of kilometres. (See Mann et al. (2007) and Kaplan and Mooney (2016) for exceptions.) Therefore, measurements of sound fields at different distances from the reef were required to establish an empirical propagation model based on in situ noise measurements [13]. This was the scope of this study. We showed that sound pressure and ambient noise levels decreased linearly. Transmission losses up to 10 km from the reef crest were intermediate between values from cylindrical and spherical models. On average, transmission losses up to 10 km from the reef crest varied between −9 and −17 dB decade$^{-1}$, depending on the source level and frequency band. The differences between these empirically estimated transmission losses and the ones of cylindrical or spherical models were likely a consequence of the acoustic reef effect [45]. This effect is observed because the recorder placed near the reef mainly records the nearby sounds, whereas a hydrophone placed further away from the reef records sounds coming from a larger portion of the reef.

Based on the empirical models, we found distinct propagation distances according to the nature of the sounds that form the reef soundscapes, i.e., fish choruses or the sum of benthic transient sounds (BTS). BTS from Moorea reefs (band: 3.5–5.5 kHz, ambient noise level) at 65 km (day) propagated up to 90 km (night) in optimal sea state conditions. In comparison, for the lower frequency band corresponding to fish choruses (200–500 Hz, spectral ambient noise level), the propagation distance in optimal sea state conditions was 1.5 km. These empirically assessed propagation distances are necessary to understand how the species could use reef sound and to provide a first prediction of detection distance of sounds by marine organisms.

### 4.3. Wind and Anthropogenic Noise

In the ocean off Moorea reef, with an average wind regime of 6 kn, propagation distances of BTS (band: 3.5–5.5 kHz, ANL) decreased by a factor between 2.3 (day) and 1.7 (night) while fish sounds (200–500 Hz, spectral ANL) propagation distances decreased by a factor of 6.9 compared to optimal sea state conditions. Propagation distances with a Wenz's ship traffic index of 2 decreased by less than 1% for BTS (band: 3.5–5.5 kHz, ANL) and of a factor of 8 for fish sounds (200–500 Hz, spectral ANL). Moreover, the fact that the fish chorus occurred during the day, when vessel traffic and noise is highest, implies a greater impact on the propagation distances of the low-frequency component of the reef's biophony. The quantification of this influence is important because previous studies have shown that soundscape degradation by boat noise can reduce settlement success in different larvae of coral reef fish [88,89]. Increases in ambient background noise levels caused by wind speed or anthropogenic noise may also interfere with the localization of suitable habitats as they reduce the intensity of natural reef sound that limits or impairs perception by marine organisms [90].

### 4.4. Comparisons with Audiograms

Detection distances of reef sounds do, however, depend not only on geophysical or bathymetric conditions that affect propagation loss and on background noise masking, but also on the hearing sensitivity of the animal (e.g., auditory threshold) and the sensory mechanisms of signal perception that determine the ability of aurally detecting reef sounds from the ocean (e.g., critical bands). These distances are automatically lower than propagation distances. In our study, comparisons with audiograms indicated detection distances of less than 22 km for odontocetes and less than 0.5 km for fish post-larvae and invertebrates. The detection distances for fish reported here are in accordance with a previous study on the damselfish *Abudefduf saxatilis* (Pomacentridae), where Egner & Mann (2005) have estimated that reef sounds from the Great Barrier Reef can be aurally detected at a distance between 0.54 km and 2.15 km [61].

Previous studies, based on soundscapes recorded in New Zealand temperate waters, suggested greater detection distances up to 50 km [45]. The soundscapes of the two environments showed important differences. Typical soundscapes of New Zealand rocky reefs have peak intensities between 1 and 1.9 kHz [91]. These peaks are generally absent in coral reefs soundscapes [7,9,85,86] where they usually occupy frequencies between 3 and 6 kHz. As these peaks in temperate water are within the audible range of several of species of fish, cetaceans and invertebrates, they likely affect detection distances.

The uncertainty in estimating the detection distance of numerous species is largely the result of a lack of information on their hearing abilities. Although fish and invertebrate species use particle motion and to some extent sound pressure, current audiograms are mainly based on sound pressure [71] and few studies described the contribution of direct particle motion and pressure detection separately in the auditory response [71,92,93]. In Hawaii, Kaplan and Mooney (2016) measured reef particle acceleration in the field. Average levels were found to be generally below these published hearing thresholds, meaning that particle motion may not play a major role as long-range orientation and settlement cue [86]. Because particle motion will attenuate more rapidly than acoustic pressure and is therefore

not as likely to propagate as far as acoustic pressure, the estimated distances should likely be considered maximal values. Nevertheless, individual sounds that exceed the mean ambient noise values, may also play a role in reef detection [86]. For example, when considering SPL of high-energetic BTS (3.5–5.5 kHz), propagation distances increased by a factor of 1.6 to 2.1 (day) and 1.4 to 1.7 (night) under flat sea state conditions.

Not only larvae use reef sound to detect suitable habitats. In the 1960s, Norris speculated that migrating cetaceans could use consistent sound sources as acoustic marks [94]. Subsequent observations showed that cetaceans may use the sound of snapping shrimp to orient themselves toward shallow water [20]. Depending on the species' audiograms and wind regimes, we found maximal detection distances for odontocetes (*Globicephala macrorhynchus*, *Mesoplodon densirostris* and *Stenella coeruleoalba*) in a range from 2 to 22 km for sounds between 5.6 and 20 kHz, which represents the frequency range of best hearing for reef sounds. In odontocetes, maximum hearing sensitivities between 34 and 55 dB re 1 µPa are found between 3 and 35 kHz and between 30 and 110 kHz [95]. Consequently, cetaceans are able to hear higher frequencies than fish and their frequency range of audition overlaps with the intense BTS emitted by benthic invertebrates from the coral reef, which are the ones for which we reported the greatest propagation distances (up to 20 km). Although the attenuation in seawater increases with increasing frequency (e.g., $\alpha = 0.005$ dB km$^{-1}$ at 300 Hz vs. $\alpha = 0.3$ dB km$^{-1}$ at 4.5 kHz), ambient noise is naturally lower at high frequencies (e.g., 51 dB re 1 µPa$^2$ Hz$^{-1}$ at 300 Hz vs. 36 dB re 1 µPa$^2$ Hz$^{-1}$ at 4.5 kHz; both with a wind regime of 0 knots). As a consequence, detection distances are higher for cetaceans than for fish and invertebrates. To which extent different species of cetaceans use reef sounds for orientation remains unknown [19]. But considering their responses to playbacks of biological and industrial sounds [90] and considering their hearing abilities, it constitutes an interesting subject for investigation.

## 5. Conclusions

In conclusion, Moorea reef biophony can propagate up to 90 km from the coast, but depending on the species and life stage, maximal detection distances range from less than 0.5 km to 22 km. Furthermore, these distances can be reduced if reef noise is masked by meteorological conditions and anthropic noise. Therefore, the reduction of the distance of detection both by changing the soundscape or by masking can directly affect a variety of biological processes and reduce habitat sustainability.

**Author Contributions:** Conceptualization, É.P., D.L., C.G., J.L., L.D.I. and X.R.; methodology, C.G., L.D.I., J.L., É.P. and X.R.; software, C.G.; validation, É.P., L.D.I., X.R. and C.G.; formal analysis, X.R.; investigation, X.R., L.D.I., C.G., J.L. and É.P.; resources, C.G. and L.D.I.; data curation, X.R.;

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