



Article

## “To Be, or Not to Be”: Critical Assessment of the Use of $\alpha$ -Acoustic Diversity Indices to Evaluate the Richness and Abundance of Coastal Marine Fish Sounds

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Submitted: 2 November 2022, accepted: 10 January 2023, published: 7 April 2023

**Abstract:** Passive acoustic monitoring can be used to assess the presence of vocal species. Automatic estimation of such information is critical for allowing diversity monitoring over long time spans. Among the existing tools,  $\alpha$ -acoustic indices were originally designed to assess the richness/complexity of terrestrial soundscapes. However, their use in marine environments is impacted by fundamental differences between terrestrial and marine soundscapes. The aim of this study was to determine how they vary depending on the abundance and sound type richness of fish sounds. Fourteen indices used in terrestrial environments were tested. The indices were calculated for files from three sources: a controlled environment (playback of artificial tracks in a pool), in situ playbacks (playback of natural soundscapes), and a natural environment (only natural sounds). The controlled experiment showed that some indices were correlated with the sound abundance but not with the sound type richness, implying that they are not capable of distinguishing the different types of fish sounds. In the in situ playbacks, the indices were not able to capture differences, both in terms of the sound abundance and sound type diversity. In the natural environment, there was no correlation between most of the indices and the abundance of sounds. They were impacted by mass phenomena of biological sounds (e.g., the Pomacentridae sounds in shallow reefs) that cannot inform on fish acoustic diversity. Indices are appropriate when soundscapes are divided into bands. In contrast to terrestrial environments, frequency bands in coastal marine soundscapes do not provide ecologically relevant information on diversity. Overall, indices do not appear to be suitable for inferring marine fish sound diversity.

**Keywords:** passive acoustic monitoring; French Polynesia; acoustic entropy; acoustic evenness; sound type richness; acoustic complexity; bioacoustics; ecoacoustics; fish sounds; biodiversity; remote sensing

**How to cite:** Raick, X.; Di Iorio, L.; Lecchini, D.; Bolgan, M.; Parmentier, E. “To Be, or Not to Be”: Critical Assessment of the Use of  $\alpha$ -Acoustic Diversity Indices to Evaluate the Richness and Abundance of Coastal Marine Fish Sounds. *J. Ecoacoust.* 2023, 7(1), 1; doi:10.35995/jea7010001.

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## 1. Introduction

Biodiversity is directly linked to the resilience of ecosystems (Oliver et al., 2015), and it is declining in many ecosystems around our planet (Hoegh-Guldberg et al., 2007; Marques, 2020). Therefore, there is a need to monitor biodiversity trends over large spatio-temporal scales and to collect comparable and standardized measurements. Biodiversity can be measured by counting the number of different species in a given area, or by taking into account their relative abundance (Whittaker, 1972). The first metric is known as species richness, while the second involves the calculation of diversity indices. In the last 20 years, technological developments in remote sensing have boosted our ability to detect species and to monitor their distribution together with the ecological state of understudied ecosystems (Mooney et al., 2020). Among remote sensing techniques, monitoring the biological sounds present in a habitat is an effective way of measuring biodiversity (Blumstein et al., 2011). The two fundamental aspects of species biodiversity (abundance and richness) are encoded in the biological component of the acoustic environment of a habitat (i.e., the biophony), and they can be measured as the number of different sound types (acoustic richness) and their relative abundances (Celis-Murillo et al., 2009; Desiderà et al., 2019; Mooney et al., 2020; Raick et al., 2023). Technological advancements allow recording for long time periods at large spatial scales, thus requiring the development of adequate standardized, automatic, and quick processing methods, which can inform on biodiversity trends (Mooney et al., 2020). This is a fundamental requirement for meeting international targets of biodiversity monitoring (Maron et al., 2021). In this context, many  $\alpha$ -acoustic indices, representing the  $\alpha$ -diversity measures in a single habitat or sampling unit, have been developed to describe the sonic biodiversity of a soundscape (Sueur et al., 2014). These indices are classically divided into three groups: those describing the intensity of the acoustic scene, those characterizing its complexity, and those on soundscape components (Sueur et al., 2014). **Intensity indices** are based on the measurement of sound intensity, i.e., the ratio of sound pressure relative to a reference value. The sound pressure level (SPL) is a logarithmic measure of the ratio of the sound pressure of a sound to a reference sound pressure. Intensity indices have been used for noise level assessment or in ecological studies, for example, to assess avian biophonies in various environments (Barber et al., 2010; Francis et al., 2011; González-Oreja et al., 2012; Gage and Axel, 2014; Rodríguez et al., 2014). The inconvenience of these indices is that they do not provide any information on the number/identity of sound sources or on the frequency composition of the soundscape, which makes them unsuitable for estimating acoustic richness. This has led to the birth of the first complexity indices based on the frequency composition of the soundscape. These indices postulate that a biophony is more complex when the number of vocal individuals/species increases. **Complexity indices** are computed ( $I$ ) within precise frequency ranges, leading to the

creation of the *bioacoustic index* (= *relative abundance*, **BI** = **Bio**) (Boelman et al., 2007), (2) on the *amplitude index* (**M** = **AI**) based on the median of the amplitude envelope (Depraetere et al., 2012), and (3) on the *acoustic entropy index* (= *total entropy*, **H**) related to the evenness of the acoustic environment (Sueur et al., 2008). It is calculated by multiplying the *temporal entropy* (**TE** = **H<sub>t</sub>**), i.e., measurement of the Shannon evenness of the amplitude envelope, by the *spectral entropy* (**SE** = **H<sub>f</sub>**), i.e., measurement of the Shannon evenness of the frequency spectrum (Sueur et al., 2008). Different indices have also been developed based on entropy: the *Shannon spectral entropy* (= *Pielou's evenness index*, **S**), the *Simpson spectral entropy* (= *Gini–Simpson spectral entropy* = *Gini–Simpson index*, **GS**), the *Renyi spectral entropy* (**R**), the *entropy of spectral variance* (**H<sub>v</sub>**), the *entropy of spectral maxima* (**H<sub>m</sub>**), and the *acoustic diversity index* (**ADI** = **H'**) (Sueur et al., 2008; Pekin et al., 2012; Towsey et al., 2014). More recently, other indices have been created to account for soundscapes that might not be dominated by a biophony and to study noise-like sounds produced by single species (e.g., cicadas). These new indices include the *acoustic richness (index)* (**AR** = **ARic**) (Depraetere et al., 2012), the *acoustic evenness index* (**AEI** = **AEve** = **AE**) (Joo et al., 2011), the *acoustic complexity index* (**ACI**) (Pieretti et al., 2011), and the *number of peaks* (= *frequency peak number*, sometimes confusedly named the *acoustic complexity index*, **NP**) (Gasc et al., 2013). This list is not exhaustive, as other indices (e.g., *mid-band activity*, *spectral diversity*, and *spectral persistence*) have also been developed to determine avian richness (Towsey et al., 2014). The third category of  $\alpha$ -acoustic diversity indices, **soundscape indices**, works on soundscape components by analyzing the biophony (sounds of biological origin) alone or in relation to the anthropophony (sounds produced by humans). To calculate these indices, terrestrial soundscapes are generally split into a frequency band between 0.2 and 2 kHz dominated by the anthropophony, and one between 2 and 8 kHz, generally characterized by the biophony. Some indices use the ratio of anthropophony to biophony, such as the *normalized difference soundscape index* (**NDSI**) (Kasten et al., 2012), while others are based only on the biophony, such as *biophony* or *Biophony Peak* (**bioPeak**) (Krause et al., 2011; Joo et al., 2011).

Because indices are quick and easy to use, they have been widely adopted to study the biophony in a variety of different terrestrial/aerial environments, such as in the Amazon rainforest (Do Nascimento et al., 2020), tropical wet evergreen forests (Buxton et al., 2018), dry tropical forests (Retamosa Izaguirre and Ramírez-Alán, 2018), the Valdivian (Moreno-Gómez et al., 2019) or Atlantic rainforest (Jorge et al., 2018; Campos et al., 2021), savannas (Machado et al., 2017; Campos et al., 2021), Mediterranean forests (Farina et al., 2021), pastures (Gómez et al., 2018), temperate woodlands (Depraetere et al., 2012), cities (Fairbrass et al., 2017; Rajan et al., 2019), and mangroves (Rajan et al., 2019). In comparison to terrestrial soundscapes, sounds at sea include ambient noise caused by thermal agitation, oscillating bubbles, water droplets, surface waves, turbulence, seismic sources, precipitation, and sea-ice movements (Wenz, 1962). Except for sea-ice movements, these sources are less frequency-modulated than sources in terrestrial soundscapes (e.g., birds) and often create broadband noises (similar to white noises) (Bolgan et al., 2018). The soundscapes of marine coastal environments are generally dominated by sounds emitted by invertebrates, such as snapping shrimps or sea urchins, in the frequency band between 1.5 and 40 kHz (Johnson et al., 1947; Coquereau et al., 2016). Below 2 kHz, that is, within a very narrow frequency band, marine coastal biophonies are dominated by fish and marine mammal sounds (Staaterman et al., 2014). This makes coastal marine soundscapes profoundly different

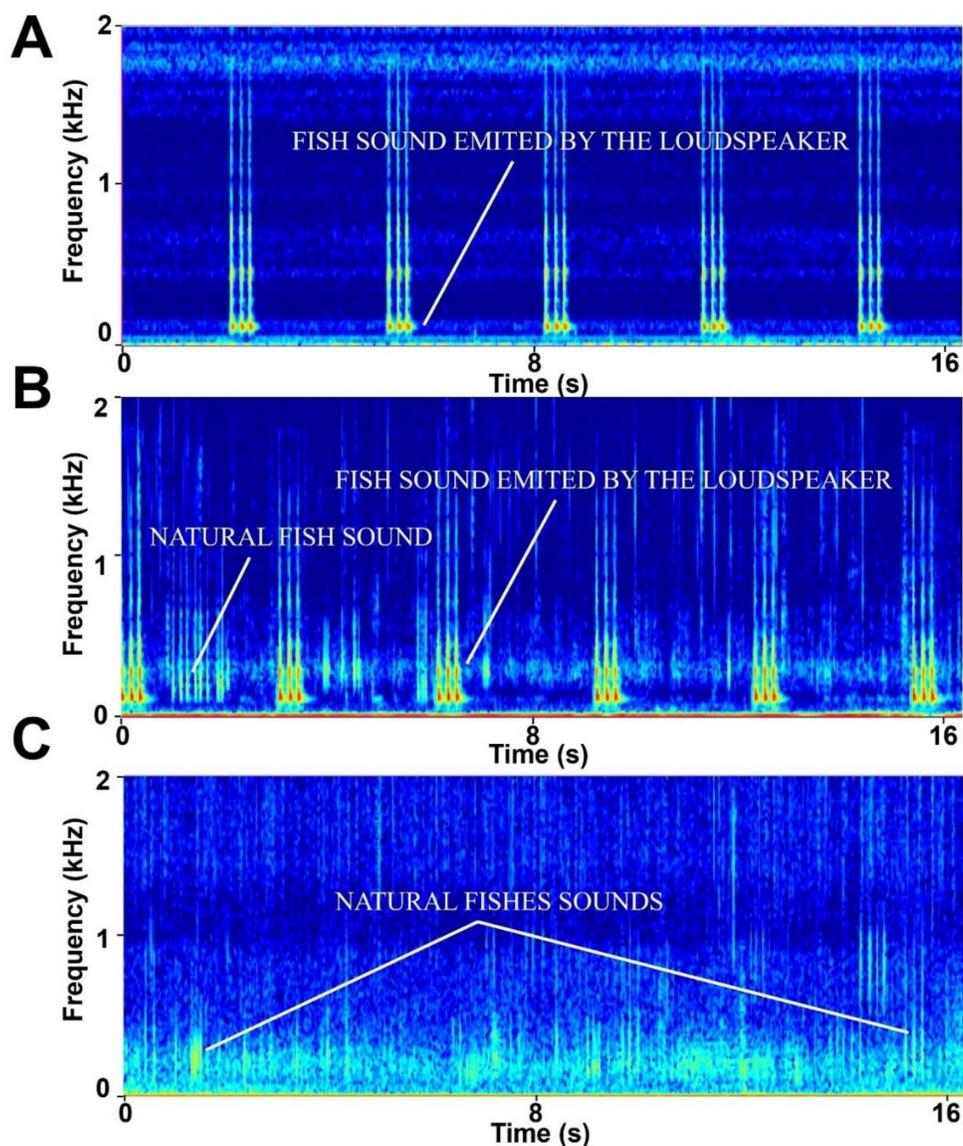
from terrestrial soundscapes. Despite these considerations, indices have been used in different environments such as mangroves (Staaterman et al., 2017), streams (Decker et al., 2020), ponds (Desjonquères et al., 2015), seagrass meadows (Staaterman et al., 2017; Ceraulo et al., 2018), sandy bottoms (Staaterman et al., 2017; Ceraulo et al., 2018), deep seamounts (Cariço et al., 2020), temperate reefs (Harris et al., 2016), and coral reefs (Bertucci et al., 2016; Staaterman et al., 2017; élise, 2019).

Although highly informative, one of the biggest challenges with the use of acoustic indices, particularly in the marine environment, is identifying the extent to which they are representative of the acoustic richness and diversity of an environment. Among all indices, the **ACI**, **H**, **AEI**, and **ADI** have often been applied to study acoustic fish communities. However, controlled experiments have shown the difficulty in discriminating between sound abundance and sound type richness (Bolgan et al., 2018). Furthermore, the **ACI**, for instance, has been shown to be unrelated to fish sound diversity (Bohnenstiehl et al., 2018; Dimoff et al., 2021). Depending on the settings, the **ACI** increases or decreases when the sound abundance increases, but **H** always decreases (Bohnenstiehl et al., 2018). For Indonesian reefs, the **AEI** and **ADI** (band: 1.2–11 kHz) are considered good predictors of fish abundance and/or richness (explaining 19% to 40% of the deviance) (Peck et al., 2021). However, it is difficult to fully appreciate these relationships since the band used for the analysis (1.2–11 kHz) does not correspond to the frequency band of fish vocalizations, but to the frequency band of invertebrate activity. Similar to what has been carried out in terrestrial environments (Zhao et al., 2019), experimental tests of acoustic indices are required (Minello et al., 2021) to understand if they are representative of fish biophony diversity. In this work, we focused on fish sounds, because fish are the only taxa with species-specific vocalizations that are always present on reefs (contrary to marine mammals). The aim of this study was to experimentally determine if  $\alpha$ -acoustic diversity indices can reflect the abundance and sound type richness of marine fish sounds.

## 2. Methods

### 2.1. Experimental Conditions

The  $\alpha$ -acoustic indices were studied under three experimental conditions: a controlled environment (with artificial tracks only), in situ playbacks (with artificial tracks played back over natural sounds), and a natural environment (only with natural sounds) (Figure 1).

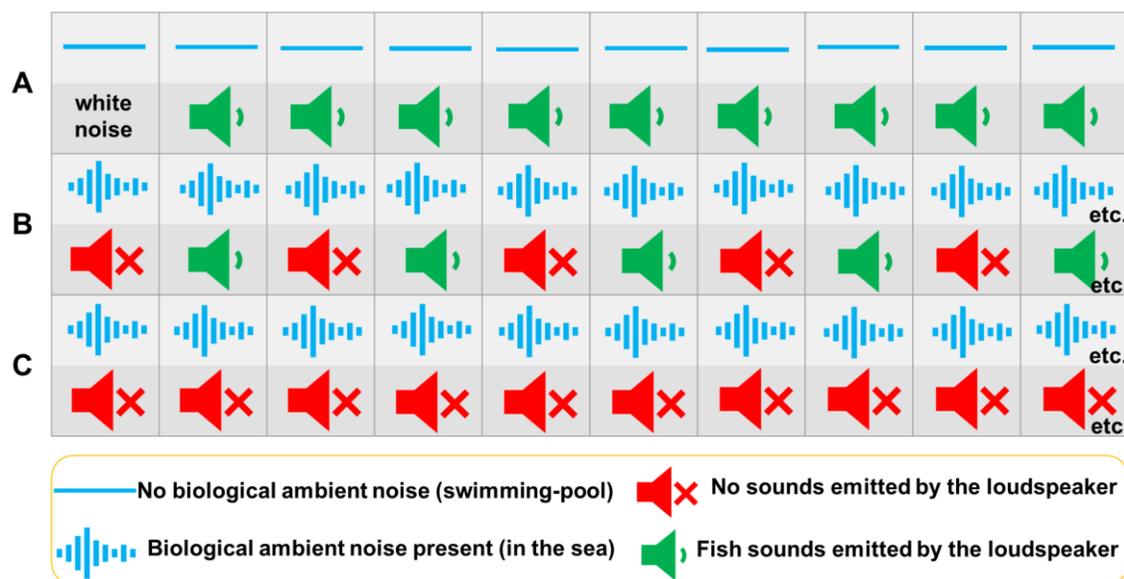


**Figure 1. Acoustic background variation depending on the environment:** (A) controlled environment, (B) in situ playbacks, and (C) natural environment. For all the spectrograms: files were subsampled at 4 kHz, FFT = 256, window = Hann, overlap = 0.50.

### 2.1.1. Controlled Environment

Trials were conducted in a large pool during the experiment presented in [Bolgan et al. \(2018\)](#). We focused only on stimuli emitted by a single loudspeaker, which were recorded as part of a broader experiment, but were not presented in the resulting article. An HTI-94 SSQ hydrophone (High Tech INC; Long Beach, MS, USA; sensitivity  $-162$  dB re  $1$  V  $\mu\text{Pa}^{-1}$ ) connected to a USB A–D converter (Edirol U25-EX, 48 kHz, 16 bits) and controlled by a laptop running Adobe Audition 3.0 (Adobe Systems Inc., Mountain View, CA, USA) was placed in the middle of the pool ( $6$  m  $\times$   $9$  m  $\times$   $1.30$  m) at  $0.9$  m from a UW-30 loudspeaker (Electrovoice, Burnsville, MN, USA)

attached to a GTA 260 amplifier (Blaupunkt, Hildesheim, Germany) connected to a U25-EX USB D–A converter (Edirol, Hamamatsu, Japan) controlled by a laptop running Adobe Audition 3.0 (Adobe Systems Inc., Mountain View, CA, USA), which produced the sound stimuli (Figure 2A). The sound stimulus was a sound file (WAV format, 48 kHz, 16 bit) composed of 10 blocks of 2 min duration. The first block was white noise (WN) (Bolgan et al., 2018). The other nine blocks had a known sound abundance and a known sound type richness (Table S1). Three ranges of sound abundance were tested: low (20 sounds min<sup>-1</sup> in total, regardless of the number of sound types), medium (60 sounds min<sup>-1</sup>), and high (100 sounds min<sup>-1</sup>), as well as three ranges of sound type richness: low (one sound type), medium (two sound types), and high (three sound types, Table S1) (Bolgan et al., 2018). The sound types used were isolated fish calls from three different species (Bolgan et al., 2018). All the sounds had the same amplitude (see Bolgan et al. (2018) for the complete procedure). Within each block, fish sounds were separated by white noise (signal-to-noise ratio > 48 dB). The durations of the three sound types were equalized in order to occupy the same period of time (for details, see (Bolgan et al., 2018)).



**Figure 2. Schematization of the experimental design.** (A) Controlled environment. (B) In situ playbacks. (C) Natural environment. Blocks are indicated by the gray cases. For A, within each block, fish sounds were separated by white noise, while for B, they were separated by silence.

### 2.1.2. In situ Playback

Trials were conducted in December 2020 in coral reefs at Moorea Island (Temae lagoon, French Polynesia; 17.50° S; 149.76° W, 2 to 4 m depth). This area was chosen because this part of the lagoon has a reduced anthropophony because of the absence of a boat channel. The loudspeaker was attached to a GTA 260 amplifier (Blaupunkt, Hildesheim, Germany) connected to a DR5 recorder (TASCAM, Wiesbaden, Germany) playing back the recorded soundtrack. The soundtrack was a sound file (WAV format, 44.1 kHz, 16 bit) composed of 9 blocks of 6 min duration each. Replicates were realized at five locations in the lagoon (Table S2). The sounds

used in the playbacks were the same as those used in the experimental design of the controlled environment (Table S1). However, because the ambient noise of in situ playbacks could vary between the beginning and the end of the session, each block was composed of 3 min of silence followed by 3 min of sounds, thus allowing for pairwise comparisons (Figure 2B). The order of the blocks was random and was always different from one replicate to another.

A SNAP autonomous underwater acoustic recorder (Loggerhead Instruments, Sarasota, USA; sensitivities of the hydrophones:  $-169.6$  to  $-169.7$  dB re 1 V for a sound pressure of  $1 \mu\text{Pa}$ , flat frequency response 2 Hz to 30 kHz, WAV format, 44.1 kHz, 16 bit) was placed on the bottom at 1 m from a UW-30 loudspeaker (Electrovoice, Burnsville, MN, USA). It recorded during the entire session to obtain acoustic recordings with both natural sounds (emitted by fishes present on the reef) and sounds broadcasted by the loudspeaker. The signal-to-noise ratios of the broadcasted sounds were overall equivalent to those of natural sounds. All the individually identifiable fish sounds were selected and classified through visual and aural inspection using RavenPro Sound Analysis Software 1.5 (Cornell Lab of Ornithology, Ithaca, NY, USA). Then, the natural fish sound abundance (total number of sounds per minute) and sound type richness (one value per minute) were calculated.

### 2.1.3. Natural Environment

Acoustic recordings were collected in March 2018 on the external slope of Raroia Island (French Polynesia) ( $S 16.02310^\circ$ ,  $W 142.46327^\circ$ ) during the study presented in Raick et al. (2023). Three SNAP autonomous underwater acoustic recorders (Loggerhead Instruments, Sarasota, USA; sensitivities of the hydrophones:  $-170.5$ ,  $-170.2$  and  $-169.7$  dB re 1 V for a sound pressure of  $1 \mu\text{Pa}$ , flat frequency response 2 Hz to 30 kHz, WAV format, 44.1 kHz, 16 bit) were deployed during three consecutive sunsets (05:00 PM–06:59 PM) at  $-20$  m,  $-60$  m, and  $-120$  m. A total of 108 recording files of 1 min were visually and aurally inspected with RavenPro Sound Analysis Software 1.5 (Cornell Lab of Ornithology, Ithaca, NY, USA) to assess the fish sound abundance and sound type richness (Figure 2C). Fish sounds were classified into 45 different sound types (Raick et al., 2023).

## 2.2. Acoustic Indices of $\alpha$ -Diversity

Fourteen  $\alpha$ -acoustic diversity indices were calculated for tracks from the controlled environment, in situ playbacks, and natural environment: two intensity indices, eleven complexity indices, and one soundscape index. The used indices are summarized in Table 1, along with their bibliographic references: (1) the peak-to-peak sound pressure level ( $\text{SPL}_{\text{pp}}$ ); (2) the root mean square sound pressure level ( $\text{SPL}_{\text{rms}}$ ); (3) the amplitude index, calculated as the median of the amplitude envelope ( $\mathbf{M} = \text{AI}$ ); (4) the bioacoustic index, which measures the area under the power spectrum ( $\mathbf{BI} = \text{Bio}$ ); (5) the temporal entropy ( $\mathbf{TE} = H_t$ ), which measures the envelope complexity; (6) the spectral entropy (also named the Shannon spectral entropy and Pielou's evenness index,  $\mathbf{SE} = S = H_f$ ), which measures the spectral complexity; (7) the Gini–Simpson spectral entropy (also named the Simpson spectral entropy, Gini–Simpson spectral index, or Simpson spectral index,

**GS**), which is derived from the spectral entropy; (8) the acoustic entropy index (also named total entropy or acoustic entropy, **H**), which measures both the envelope and spectrum; (9) the acoustic richness index (also named acoustic richness, **AR**), which measures the envelope complexity and intensity; (10) the acoustic diversity index (**ADI** =  $H'$ ), which measures the spectrum complexity; (11) the acoustic evenness index (**AEI** =  $A_{eve}$  =  $AE$ ), which applies the Gini index to a frequency spectrum; (12) the number of peaks in a frequency spectrum (also named frequency peak number, **NP**); (13) the acoustic complexity index (**ACI**); and (14) the normalized difference soundscape index (**NDSI**), which measures the ratio between two frequency bands (Table 1, Equations (S1) to (S10)). All the indices were calculated in R software version 3.6.1. (R Core Team, 2019) with the libraries seewave, signal, sound, and soundecology. The functions used are detailed in Table 1.

**Table 1.**  $\alpha$ -Acoustic diversity indices calculated in this study.

Name	Library	Function	Référence
<b>Intensity indices</b>			
<b>SPL<sub>pp</sub></b> <i>Peak-to-peak sound pressure level</i>			
<b>SPL<sub>rms</sub></b> <i>Root mean square sound pressure level</i>			
<b>Complexity indices</b>			
<b>M</b> <i>Amplitude index = median of the amplitude envelope</i>	Seewave	M	(Depraetere et al., 2012)
<b>BI</b> <i>Bioacoustic index = relative abundance</i>	Soundecology	bioacoustic_index	(Boelman et al., 2007)
<b>TE</b> <i>Temporal entropy</i>	Seewave	Th	(Sueur et al., 2008)
<b>SE</b> <i>(Shannon) Spectral entropy</i>	Seewave	Sh	(Sueur et al., 2008)
<b>GS</b> <i>(Gini-)Simpson spectral entropy</i>	Seewave	Sh	(Sueur et al., 2008)
<b>H</b> <i>Acoustic entropy index = total entropy</i>	Seewave	H	(Sueur et al., 2008)
<b>AR</b> <i>Acoustic richness (index)</i>	Seewave	AR	(Depraetere et al., 2012)
<b>ADI</b> <i>Acoustic diversity index</i>	Soundecology	acoustic_diversity	(Villanueva-Rivera et al., 2011; Pekin et al., 2012)
<b>AEI</b> <i>Acoustic evenness index</i>	Soundecology	acoustic_evenness	(Villanueva-Rivera et al., 2011)
<b>NP</b> <i>Number of peaks</i>	Seewave	fpeaks	(Gasc et al., 2013)
<b>ACI</b> <i>Acoustic complexity index</i>	Seewave	ACI	(Pieretti et al., 2011)
<b>Soundscape indices</b>			
<b>NDSI</b> <i>Normalized difference soundscape index</i>	Seewave	NDSI	(Kasten et al., 2012)

### 2.3. Calculation of the Indices

Prior to analysis, the files recorded by the hydrophone in the controlled environment were subsampled at 44.1 kHz to be comparable with the soundtracks recorded during the in situ playbacks, and in the natural environment.

The indices were calculated for the 50–2000 Hz frequency band. For the **NDSI**, the so-called “anthropophony band” was the band of interest (fish sounds, 50–2000 Hz), while the so-called “biophony band” was the band occupied by benthic invertebrate snaps (mainly snapping shrimps, 2.5–8.5 kHz). Out of the eleven tested complexity indices, specific settings were necessary for three of them (**ACI**, **ADI**, and **AEI**). To examine the effect of the settings on the **ADI** and **AEI**, the following frequency bandwidths and threshold were tested: 10, 50, 100, 500, and 1000 Hz; −10, −25, −50, and −75 dB. These tests were realized on the three datasets (controlled, in situ playbacks, and natural environments). The effect of settings was not tested on the **ACI** as previously done by [Bolgan et al. \(2018\)](#). For the **ADI** and **AEI**, two “optimal” settings, obtained from the controlled environment, were kept because one of them was more representative of the sound abundance, while the other was more representative of the sound type richness. Consequently, the following settings were used for the calculations: FFT window = 2048, window name = Hanning, size of frequency bands (for the **ADI** and **AEI**) = step = 100 and 500 Hz, threshold (for the **ADI** and **AEI**) = −25 and −50 dB (referred to as “**ADI\_v1**, **ADI\_v2**, **AEI\_v1**, and **AEI\_v2**” throughout the document; v1 = 100 Hz and −50 dB, and v2 = 500 Hz and −25 dB), overlap = 75%, number of windows (for the **ACI**) = 120 for 1 min files and 360 for 3 min files.

The indices were calculated for each file, i.e., each block from the controlled environment (Figure 2), five replicates of each block for the in situ playbacks, and 108 files of 1 min for the natural environment (Figure 2). In addition, for the in situ playbacks, a second analysis was realized: the indices were calculated for each “background block” (i.e., natural acoustic environment without playbacks) and for each “playback block” (i.e., blocks with both natural acoustic environment and playback sounds) from each replicate. Then, the values from each “background block” were subtracted from those of the adjacent “playback block” to obtain a delta, referred to as “delta sounds” throughout the document. For graphical visualization, the deltas of all the replicates were averaged together.

### 2.4. Graphical Representation and Statistics

The values of the different indices were standardized between 0 and 1 with the formula “standardized(x) = [(x − min(x)) (max(x) − min(x))<sup>−1</sup>]”. These standardized values were plotted as “bubble graphs”. Standard Z-scores greater than |3| were considered as outliers. The correlation between each index with both the sound abundance and the sound type richness was assessed using Spearman’s rank correlation  $\rho$  with the associated p-values corrected with the Benjamini–Yekutieli method. This method was used rather than the Benjamini–Hochberg method because of the non-independence of the tests. Then, the coefficient of multiple correlation (R) was calculated for each index (Equation (1)). For the in situ playbacks, both the artificial

abundance/richness (from the stimuli) and the total abundance/richness (including both stimuli and natural sounds) were examined.

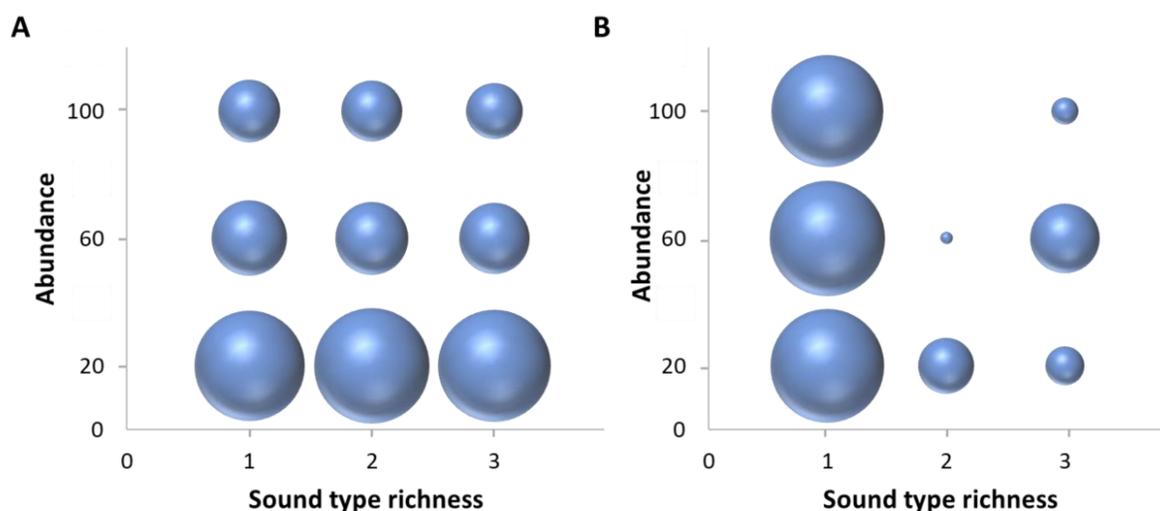
$$R_{i,a,d}^2 = \frac{\rho_{a,i}^2 + \rho_{d,i}^2 - 2\rho_{a,i}\rho_{d,i}\rho_{a,d}}{1 - \rho_{a,d}^2} \tag{1}$$

**Calculation of the coefficient of multiple correlation (R).** *i* = index; *a* = sound abundance; *d* = sound type richness.

### 3. Results

#### 3.1. Controlled Environment

In the controlled environment, no index was significantly correlated with the sound type richness (Table 2). The **ACI**, **GS**, **H**, and **SE** showed positive correlations with the sound type richness that were, however, not statistically significant (Table 2). The **ADI**, **M**, and **TE** were strongly correlated with the sound abundance ( $\rho = 0.95, 0.90, \text{ and } 0.90, p = 0.0062, 0.036, \text{ and } 0.036$ ), while a negative correlation was observed for the **AEI** ( $\rho = -0.95, P = 0.0062$ ; Table 2). The correlation between the sound abundance and **ADI** was observed with a threshold of  $-50$  dB, but not with smaller ( $-10$  or  $-25$  dB) or higher thresholds ( $-75$  dB) ( $\rho = 0.95, p = 0.0044$ ; Table S3). No effect of the step (i.e., the size of the frequency bands) was observed. No correlation was observed with the default settings. The same results were obtained for the **AEI** (Figure 3, Table S4).



**Figure 3. Bubble graph for the standardized AEI as a function of the sound abundance and sound type richness.** (A) Step = 1000 Hz, threshold =  $-50$  dB; (B) step = 500 Hz, threshold =  $-25$  dB. Range: between 0 and 1. This figure highlights the importance of the settings. In panel A, the sound type richness does not affect the AEI, while the contrary is shown in panel B.

**Table 2. Correlation coefficients and associated *p*-values between  $\alpha$ -acoustic indices, sound abundance, and sound type richness in the controlled environment.** Statistically significant *p*-values are in bold. Both = both abundance and richness; BY = Benjamini–Yekutieli.

	Correlation			Non-Adjusted <i>p</i>		BY-Adjusted <i>p</i>	
	$\rho$		R	Abundance	Richness	Abundance	Richness
	Abundance	Richness	Both				
<b>ACI</b>	−0.05	0.84	0.84	0.89	<b>0.0043</b>	1.00	0.11
<b>ADI_v1</b>	0.95	0.11	0.96	< <b>0.0001</b>	0.79	<b>0.0062</b>	1.00
<b>ADI_v2</b>	0.32	0.58	0.66	0.41	0.10	1.00	1.00
<b>AEI_v1</b>	−0.95	−0.16	0.96	< <b>0.0001</b>	0.68	<b>0.0062</b>	1.00
<b>AEI_v2</b>	−0.32	−0.58	0.66	0.41	0.10	1.00	1.00
<b>AR</b>	0.19	0.48	0.52	0.63	0.19	1.00	1.00
<b>BI</b>	0.37	0.26	0.45	0.33	0.49	1.00	1.00
<b>GS</b>	−0.16	0.74	0.76	0.68	<b>0.023</b>	1.00	0.38
<b>H</b>	0.16	0.69	0.71	0.68	<b>0.042</b>	1.00	0.60
<b>M</b>	0.90	0.32	0.96	<b>0.0011</b>	0.41	<b>0.036</b>	1.00
<b>NDSI</b>	−0.32	−0.63	0.71	0.41	0.07	1.00	0.80
<b>NP</b>	−0.74	−0.16	0.76	<b>0.022</b>	0.68	0.38	1.00
<b>SE</b>	−0.21	0.79	0.82	0.59	<b>0.011</b>	1.00	0.24
<b>SPL<sub>pp</sub></b>	0.05	0.63	0.63	0.89	0.07	1.00	0.80
<b>SPL<sub>rms</sub></b>	0.47	0.42	0.63	0.20	0.26	1.00	1.00
<b>TE</b>	0.90	0.32	0.96	<b>0.0011</b>	0.41	<b>0.036</b>	1.00

### 3.2. In situ Playback

In the in situ playbacks, **M** and **TE** were both correlated with the playback sound abundance (both  $\rho = 0.82$ , both  $p < 0.0001$ ; Table S5), and total sound abundance (i.e., playback and natural fish sounds) ( $\rho = 0.84$  and  $0.80$ , both  $p < 0.0001$ ; Table 3). In contrast, **NP** was negatively correlated with the total sound abundance ( $\rho = -0.56$ ,  $P = 0.0032$ ; Table 3). When considering the “delta sounds”, only **M** was correlated with the sound abundance ( $\rho = 0.90$ ,  $p < 0.0001$ ; Table S6). In all cases, the **ADI** never correlated with the sound abundance or sound type richness (Tables S7–S9). Similar observations were obtained for the **AEI**, but with negative signs (Tables S10–S12).

**Table 3. Correlation coefficients and associated *P*-values between  $\alpha$ -acoustic indices, sound abundance, and sound type richness per minute (natural + played back) for the in situ playbacks.** Statistically significant *P*-values are in bold. Both = both abundance and richness; BY = Benjamini–Yekutieli. The correlation between the sound abundance and sound type richness was almost null ( $\rho = 0.045$ ).

	Correlation			Non-Adjusted <i>p</i>		BY-Adjusted <i>p</i>	
	$\rho$		R	Abundance	Richness	Abundance	Richness
	Abundance	Richness	Both				
ACI	−0.28	0.38	0.48	0.063	<b>0.011</b>	0.85	0.35
ADI_v1	0.21	0.26	0.33	0.16	0.082	1	0.97
ADI_v2	−0.17	−0.16	0.23	0.27	0.29	1	1
AEI_v1	−0.22	−0.23	0.31	0.14	0.13	1	1
AEI_v2	0.20	0.13	0.23	0.20	0.39	1	1
AR	−0.28	−0.057	0.28	0.066	0.71	0.85	1
BI	0.058	−0.30	0.31	0.71	<b>0.047</b>	1	0.76
GS	−0.32	0.018	0.32	0.034	0.91	0.73	1
H	−0.15	0.18	0.24	0.31	0.25	1	1
M	0.84	0.047	0.84	<b>&lt;0.0001</b>	0.76	<b>&lt;0.0001</b>	1
NDSI	−0.14	−0.18	0.23	0.35	0.24	1	1
NP	−0.56	−0.076	0.56	<b>&lt;0.0001</b>	0.62	<b>0.0032</b>	1
SE	−0.31	0.14	0.35	<b>0.039</b>	0.35	0.73	1
SPLpp_	−0.0055	−0.041	0.042	0.97	0.79	1	1
SPLrms_	−0.16	−0.31	0.34	0.31	<b>0.039</b>	1	0.73
TE	0.80	−0.0077	0.80	<b>&lt;0.0001</b>	0.96	<b>&lt;0.0001</b>	1

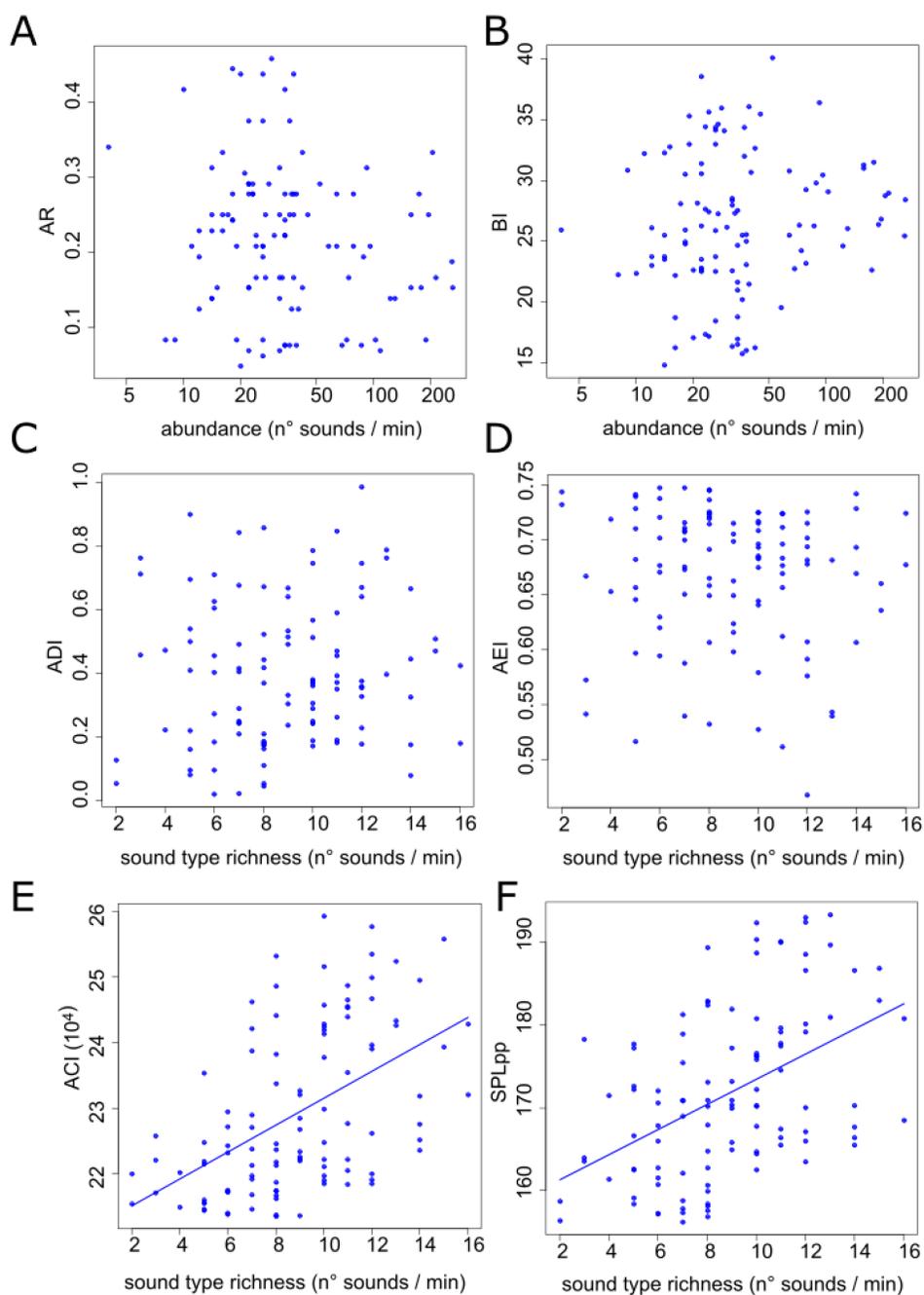
### 3.3. Natural Environment

In the natural environment, when considering the optimal settings, no index showed any statistically significant correlation with the sound abundance (Figure 4, Table 4). Four indices (ADI\_v1, NP, SPLrms, and TE) were negatively correlated with the sound type richness ( $\rho = -0.43, -0.52, -0.35,$  and  $-0.57,$  all  $p < 0.001$ ), while six indices (ACI, AEI\_v1, BI, M, NDSI, and SPLpp) were positively correlated with the sound type richness ( $\rho = 0.53, 0.43, 0.36, 0.55, 0.35,$  and  $0.47,$  all  $p < 0.05$ ; Figure 4, Table 4). In the natural environment, the sound abundance and sound type richness were not independent ( $\rho = 0.53, p < 0.0001$ ). When considering a broader range of settings, the ADI was positively correlated with the sound abundance ( $\rho = 0.33$  to  $0.34,$  all  $p < 0.006$ ), but only with a low threshold ( $-10$  dB) and low step values (10, 50, and 100 Hz). With this low threshold ( $-10$  dB), a positive correlation with the sound type richness was found ( $\rho = 0.29, p = 0.031$ ), but only with low step values (10 and 100 Hz). In contrast, with

high thresholds (−50 and −75 dB), the correlations between the sound type richness and **ADI** were generally all negative ( $-0.51 < \rho < -0.34$ , all  $p < 0.004$ ) (Table S13). Similar results were obtained for the **AEI** (Table S14). When using a low threshold (−10 dB) with low step values (10, 50, and 100 Hz), the **AEI** appeared to be negatively correlated with the sound abundance ( $\rho = -0.32$ ,  $p = 0.012$ ), while with higher thresholds, it was generally positively correlated with the sound type richness ( $0.36 < \rho < 0.51$ , all  $p < 0.004$ ) (Table S14).

**Table 4. Correlation coefficients and associated p-values between  $\alpha$ -acoustic indices, sound abundance, and sound type richness in the natural environment.** Statistically significant p-values are in bold. Both = both abundance and richness; BY = Benjamini–Yekutieli.

	Correlation			Non-Adjusted $p$		BY-Adjusted $p$	
	$\rho$		R	Abundance	Richness	Abundance	Richness
	Abundance	Richness	Both				
<b>ACI</b>	0.060	0.53	0.60	0.54	<b>&lt;0.0001</b>	1	<b>&lt;0.0001</b>
<b>ADI_v1</b>	−0.066	−0.43	0.47	0.50	<b>&lt;0.0001</b>	1	<b>&lt;0.0001</b>
<b>ADI_v2</b>	−0.018	0.10	0.14	0.85	0.28	1	1
<b>AEI_v1</b>	0.066	0.43	0.47	0.50	<b>&lt;0.0001</b>	1	<b>&lt;0.0001</b>
<b>AEI_v2</b>	0.038	−0.10	0.15	0.70	0.30	1	1
<b>AR</b>	−0.15	−0.024	0.17	0.12	0.81	0.95	1
<b>BI</b>	0.13	0.36	0.37	0.19	<b>0.0001</b>	1	<b>0.0016</b>
<b>GS</b>	0.073	0.27	0.29	0.45	<b>0.0043</b>	1	0.051
<b>H</b>	0.014	0.092	0.10	0.89	0.35	1	1
<b>M</b>	0.21	0.55	0.55	0.030	<b>&lt;0.0001</b>	0.30	<b>&lt;0.0001</b>
<b>NDSI</b>	0.031	0.35	0.40	0.75	<b>0.0002</b>	1	<b>0.026</b>
<b>NP</b>	−0.21	−0.52	0.52	0.029	<b>&lt;0.0001</b>	0.30	<b>&lt;0.0001</b>
<b>SE</b>	0.055	0.19	0.20	0.57	<b>0.043</b>	1	0.40
<b>SPL<sub>pp</sub></b>	0.018	0.47	0.54	0.86	<b>&lt;0.0001</b>	1	<b>&lt;0.0001</b>
<b>SPL<sub>rms</sub></b>	0.16	−0.35	0.54	0.11	<b>0.0002</b>	0.93	<b>0.0026</b>
<b>TE</b>	−0.13	−0.57	0.60	0.20	<b>&lt;0.0001</b>	1	<b>&lt;0.0001</b>



**Figure 4. Scatterplots of the indices as a function of the sound abundance or sound type richness, in the natural environment.** (A) AR and (B) BI as a function of the sound abundance (logarithmic scale). (C) ADI\_v2 (step = 500 Hz, threshold = -25 dB), (D) AEI\_v2 (step = 500 Hz, threshold = -25 dB), (E) ACI, and (F) SPL<sub>pp</sub> as a function of the sound type richness. Regression lines are presented for cases where a significant correlation was observed.

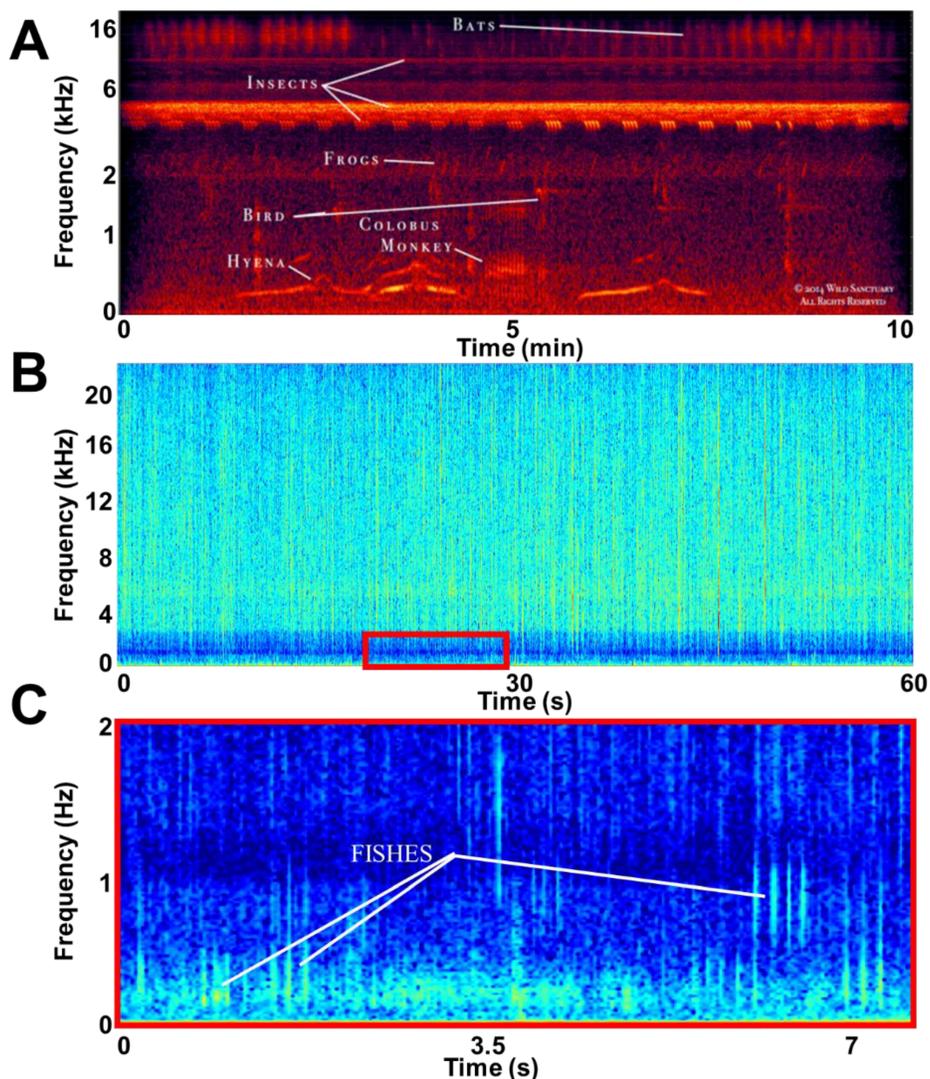
## 4. Discussion

The aim of this study was to determine whether, and how,  $\alpha$ -acoustic diversity indices, which are easily and rapidly applicable on large datasets, discriminate between the sound abundance and sound type richness of coastal marine fish sounds, and whether they are appropriate as proxies of species diversity for environmental monitoring.

### 4.1. Use of $\alpha$ -Acoustic Diversity Indices to Assess Sound Abundance and Sound Type Richness

In both the controlled environment and in situ playbacks, no index was correlated with the sound type richness. **M** and **TE** were correlated with the sound abundance in both the controlled environment and in situ playbacks. Similarly, the **ADI** and **AEI** were also correlated with the sound abundance, but only in the controlled environment. In the natural environment, the opposite was observed: no index was correlated with the sound abundance, but many (**ACI**, **ADI**, **AEI**, **BI**, **M**, **NDSI**, **NP**, **SPL<sub>rms</sub>**, **SPL<sub>pp</sub>**, and **TE**) were correlated with the sound type richness. These results are therefore contradictory and can lead to misinterpretation.

The controlled experiments showed that the indices were correlated with the sound abundance but not with the sound type richness, implying that they are sensitive to the number of sounds but are not capable of distinguishing the different types of fish sounds. In the in situ playbacks, the indices were not able to capture those differences, both in terms of the sound abundance and sound type diversity of the played-back and naturally occurring fish sounds. This is of critical importance, because it clearly shows that indices are incapable of discerning subtle modifications of a subset of a soundscape (i.e., fish frequency band), being intended, rather, to describe soundscape phenomena over a wide and often diverse frequency bandwidth. The disappearance of a species or arrival of an invasive species within the fish frequency band would therefore be difficult to assess, unless it produced mass phenomena. Marine coastal soundscapes are always noisy and distinct from terrestrial soundscapes because they show limited frequency partitioning. In contrast, in terrestrial soundscapes, frequency partitioning is often linked to species or a group of animals (Figure 5) (Krause, 2012). Coastal biological soundscapes are dominated by a broad band range (>30 kHz) of short transient snaps of invertebrates, with a low frequency resolution (Lossent et al., 2017) and a narrow (<2 kHz) low-frequency band occupied mainly by fish sounds. Coastal soundscapes, especially in coral reefs, are therefore characterized by mass biophonic phenomena with little frequency partitioning (Figure 5).



**Figure 5. Difference between terrestrial and coastal marine soundscapes:** (A) spectrogram in a savanna (Courtesy Bernie Krause. © 2021 Wild Sanctuary. All Rights Reserved (Krause, 2012)); (B) a coral reef dominated by benthic transient sounds mainly produced by snapping shrimps; (C) zoom-in of the low-frequency part (0–2 kHz) of the spectrogram, dominated by fish sounds (subsampled at 4 kHz, FFT = 256).

In some terrestrial environments, indices are not suitable for biodiversity monitoring without prior removal of biasing sounds, such as the anthropophony (Fairbrass et al., 2017) or anuran sounds in tropical forests (Eldridge et al., 2018). In a study on terrestrial soundscapes conducted in Japan, the comparison between acoustic indices and acoustic richness (i.e., the number of different sounds produced by animals) under different sonic conditions (e.g., presence or absence of wind, rain, and anthropophony) revealed that only two (AR and TE) out of the eleven tested indices reflected the measured richness across all the sonic conditions. Moreover, none of these indices correlated with the measured richness when masked by broadband insect stridulations (Ross et al., 2021). In our study, the indices were affected by background noise (Figure 1). In coral

reefs, the major contributor to background noise is the biophony, such as sounds from snapping shrimps that are always present (Johnson et al., 1947; Au and Banks, 1998). Although their peak frequency is above 2 kHz, these sounds are usually broadband sounds and overlap the fish band (0.05–2 kHz). These broadband sounds affect indices, particularly those detecting peaks, such as NP. In addition, in coral reefs, a diurnal “background noise” band around 400 to 500 Hz is present and composed of transient short pulses attributed to Pomacentridae sounds (Figure 1) (Staaterman et al., 2013; Raick et al., 2023). This mass phenomenon in the fish band influences the indices. In the Polynesian Islands, the intensity of this “fish noise” was higher in shallow reefs than in deeper reefs (Raick et al., 2023), but the indices did not show the same trends depending on the depth. For example, the ACI and  $SPL_{pp}$ , which were positively correlated with the sound type richness, were higher at shallow depths, while the contrary was found for the  $SPL_{rms}$ , which was negatively correlated with the sound type richness. The indices that were positively correlated with the sound type richness, i.e., the number of fish sound types that were clearly identified and into which the detected sounds were classified, did not reflect this sound type richness, but they did quantify biological mass phenomena (e.g., the Pomacentridae sounds in shallow reefs). Consequently, none of the acoustic indices tested can inform on fish acoustic diversity. Even a combination of indices (Williams et al., 2022) within such a small, poorly stratified frequency band dominated by biophonic background noise cannot inform on fish sound acoustic diversity because it is not suitable for depicting subtle changes in sound types.

In addition, there was no correlation between most of the indices and the measured sound abundance in the natural environment. This is because the number of sounds in the background noise was higher than the number of sounds manually selected to measure the abundance and richness, i.e., those with a high signal-to-noise ratio allowing for the identification and classification of sounds into types. When testing the settings of the ADI and AEI, the only threshold that showed a link with the sound abundance was  $-10$  dB, while in the controlled environment, this threshold was  $-50$  dB, which implies an influence of the presence of mass acoustic phenomena. Moreover, to establish a link with the sound abundance, the ADI and AEI frequency bands (i.e., steps) had to be small (bandwidths of 10 to 100 Hz). Small bands also better correlated with the sound type richness, but both positively and negatively depending on the threshold. However, indices that work on frequency bands, such as the AEI or ADI, are appropriate when soundscapes are divided into bands, which is not the case in marine coastal soundscapes (or only partly the case). Indeed, coastal marine soundscapes, contrary to terrestrial soundscapes, are generally divided into a few overlapping bands: a low-frequency band (mainly fish sounds, some crustacean sounds, and sometimes whale sounds) and a high-frequency band (transient benthic sounds, and occasionally small cetacean sounds) (Figure 4). The band occupied by fish sounds (mainly below 2 kHz) is narrow and shows little frequency partitioning. Contrary to terrestrial environments, frequency bands in coastal marine soundscapes provide only poor ecologically relevant information on diversity.

Moreover, the use of the tested indices to assess fish sound diversity is problematic because fish sounds are typically drum-like sounds, of similar frequencies, composed of pulses or (pseudo-)harmonic sounds. If the frequency bands chosen in the settings are too small, such sounds would be detected in several bands. Bands would therefore “decompose” a sound type

in different bands but would not be representative of different fish sound types. The type of fish sounds (e.g., knocks and herbivorous sounds vs. grunts, buzzes, and chirps) has been shown to impact some indices' values (Bolgan et al., 2018; Dimoff et al., 2021). Similarly, in fish and frogs, indices have been suggested to be more limited with harmonic sounds than with single-pulsed sounds (Bolgan et al., 2018; Indraswari et al., 2020). Therefore, as dominating fish sounds are not the same everywhere, this can impact the indices and comparisons between sites. For example, in French Polynesia, the proportion of pulse series is known to vary between the photic and mesophotic reefs (Raick et al., 2023). Therefore, caution is needed when comparing the values of indices from one environment to another.

These different considerations lead to the conclusion that acoustic indices are not appropriate for studying fish sound diversity in marine coastal environments such as coral reefs. Indices, for example, may be used to report on the anthropophony, to study the geophony, to focus on high-frequency sounds produced by benthic invertebrates, or to study fish mass phenomena, but such usage was not inspected in the present study.

#### 4.2. Effect of the Settings

In this study, the use of manually chosen settings compared to default settings considerably increased the values of the correlations. Depending on the settings used, indices such as the **ADI** or the **AEI** could be correlated with the sound abundance or with the sound type richness. In addition, the sign of the correlation changed depending on the settings and, more importantly, the threshold used: low (around  $-10$  dB) or high (under  $-50$  dB). The same observations were made by Bohnenstiehl et al. (2018) with the **ACI**. They found negative correlations between the **ACI** and sound abundance of harmonic fish calls with a low frequency resolution (47–94 Hz), and positive correlations with a high frequency resolution (23 Hz). This is in agreement with other studies showing the high sensitivity of the **ACI** to settings such as the frequency resolution (Bolgan et al., 2018; Dimoff et al., 2021). When comparing the results of the controlled experiment in this study with those reported in 2018 for similar tracks (Bolgan et al., 2018), the correlation between the **ACI** and the sound abundance is completely different ( $\rho = 0.66$  vs.  $\rho = -0.05$ ). The differences could be due to slight changes in the software used (R vs. SoundscapeMeter (Farina et al., 2012)), which measure different **ACI** metrics (e.g.,  $ACI_f$  vs.  $ACI_{tot}$ ) and allow slightly different settings (e.g., presence or absence of a noise filter). In addition, the settings that allow the best representation of the sound abundance and sound type richness vary depending on the environment, e.g., temperate seas vs. coral reefs (Dimoff et al., 2021). This high sensitivity of the settings would pose a risk if acoustic diversity indices were to be widely used for habitat management or for informing on marine spatial planning.

#### 4.3. Comparison of the Different Indices

**TE** was one of the two indices correlated with the sound abundance in both the controlled environment and in situ playbacks. In the natural environment, this index was the most impacted by biological “background” noise (i.e., the highest correlation observed with the sound type

richness). The higher performance of **TE** compared to other indices and the impact of background noise have been underlined in terrestrial environments too (Ross et al., 2021). **TE** is known to perform well in the presence of a geophony (Ross et al., 2021) and anthropophony (Depraetere et al., 2012; Ross et al., 2021), which appear as temporally invariable low-frequency patterns in the soundscape (Pieretti et al., 2011). On the other hand, **TE** is known to be affected by background noise, the sound duration, and overlap (Gasc et al., 2017).

Correlations between **H** and the fish sound type richness were not observed, not even in the natural environment, where many of the indices were impacted by biological “background” noise. Similar observations were made in temperate reefs (Harris et al., 2016). These results are not caused by the absence of a link but by the intrinsic calculation of the index. **H** is designed to have low values for pure tones and high values for almost silent soundscapes or, on the contrary, noisy soundscapes across frequency bands. In the in situ playbacks, the values of **H** were always higher when the loudspeaker was silent. In addition, when the number of sound types emitted by the loudspeaker was increased from 1 to 2, **H** increased, but when the number of sounds was increased from 2 to 3, **H** decreased (Figure S1). This was observed for all the sound abundances tested. This shows that this index is not representative of the sound type richness because there is no linear relation between them.

The **ADI** and **AEI** were only correlated with the sound abundance in the controlled environment. In Indonesian coral reefs, the **ADI** and **AEI** were correlated with fish species richness (19% to 24% of the deviance explained), when calculated for a higher-frequency band: 1.2–11 kHz (Peck et al., 2021), which is the frequency band covered by benthic invertebrates’ snapping sounds (Nedelec et al., 2015; Raick et al., 2021). Similar to what is observed with **H**, low values of the **AEI** could relate to a near-silent, saturated, or windy terrestrial soundscape, while high values of the **ADI** could relate to a completely silent or a noisy soundscape.

At low frequencies (band: 0.1–1.2 kHz), Peck et al. (2021) found that only the **ACI** was affected by fish abundance (38% of the deviance explained). However, the use of the **ACI** in coral reefs is known to be impacted by a masking effect (Dimoff et al., 2021), for example, in chorus events (Staaterman et al., 2017). Therefore, a single fish species can have a considerable effect on indices because they respond to mass phenomena (Staaterman et al., 2017; Bolgan et al., 2018). Moreover, when considering higher-frequency bands, typically dominated by snapping shrimps’ broadband sounds, indices such as the **ACI** saturate at high snap rates (Bohnenstiehl et al., 2018).

Using simulated bird recordings, Gasc et al. (2015) showed that some indices are affected by the sound duration in comparison to the file duration (**S/R** ratio; **H**, **SE**, **TE**, **M**, and **ACI**), background noise (**H**, **SE**, **TE**, **M**, **AR**, and **ACI**), type of sound (**NP** and **ACI**), relative amplitude (**AR**), and overlap (**H**, **SE**, **TE**, **M**, and **ACI**) (Gasc et al., 2015). Therefore, to correctly reflect the acoustic biodiversity, particularly of a group of animals, indices should be insensitive to the (1) **S/R** ratio, (2) background noise, (3) type of sound (i.e., should be equally sensitive to different types of sounds (e.g., pulse series vs. upsweeps)), (4) relative amplitude of the sounds, and (5) sound overlap (Gasc et al., 2015).

## 5. Conclusions

In coral reefs, which are hotspots of biodiversity, indices do not appear to be suitable for inferring information on fish acoustic diversity, because they are affected by naturally highly abundant sounds. In this sense, indices rather describe mass phenomena, and thus the activity of a group of sound-producing organisms (e.g., Pomacentridae or snapping shrimps), that are limited in diversity. Overall, this study clearly suggests that the use of acoustic indices to study fish sound diversity is inappropriate.

**Supplementary Materials:** The following supporting information can be downloaded at: <https://journals.jams.pub/user/manuscripts/displayFile/643fd555cd2d08fa84fb14c0f4418aa5/supplementary>, Figure S1. H values for three different abundances (20, 60 and 100 fish sounds  $\text{min}^{-1}$ ) with the loudspeaker silent (in blue) and with the loudspeaker emitting 1, 2 or 3 different fish sound types (in orange). Table S1. Abundance and sound type species richness of each sound stimuli file created. Table S2. Location of sampling sites in the lagoon of Temae (Moorea, French Polynesia). Table S3. Correlation coefficients and associated P-values between the ADI, abundance, and sound type richness in the controlled environment. Table S4. Correlation coefficients and associated P-values between the AEI, abundance, and sound type richness in the controlled environment. Table S5. Correlation coefficients and associated P-values between  $\alpha$ -acoustic indices, artificial (= introduced) abundance and artificial sound type species richness with in situ playbacks. Table S6. Correlation coefficients and associated P-values between  $\alpha$ -acoustic indices, abundance, and sound type richness with in situ playbacks (delta sounds). Table S7. Correlation coefficients and associated P-values between the ADI, artificial (= introduced) abundance, and artificial sound type richness with in situ playbacks. Table S8. Correlation coefficients and associated P-values between the ADI, abundance, and sound type richness per minute (natural + introduced) with in situ playbacks. Table S9. Correlation coefficients and associated P-values between the ADI, abundance, and sound type richness with in-situ playbacks (delta sounds). Table S10. Correlation coefficients and associated P-values between the AEI, artificial (= introduced) abundance, and artificial sound type richness with in situ playbacks. Table S11. Correlation coefficients and associated P-values between the AEI, abundance, and sound type richness per minute (natural and introduced) with in situ playbacks. Table S12. Correlation coefficients and associated P-values between the AEI, abundance, and sound type richness with in situ playbacks (delta sounds). Table S13. Correlation coefficients and associated P-values between the ADI, abundance, and sound type richness in the natural environment. Table S14. Correlation coefficients and associated P-values between the AEI, abundance, and sound type richness in the natural environment. Experimental data supporting the findings of this study are available in open access online. <https://doi.org/10.5281/zenodo.7789403>.

**Author Contributions:** Conceptualization, X.R. and E.P.; Methodology, X.R. and E.P.; Software, X.R.; Validation, X.R., L.D.I. and E.P.; Formal Analysis, X.R.; Investigation, X.R.; Resources, X.R., M.B., D.L., E.P.; Data Curation, X.R.; Writing—Original Draft Preparation, X.R.; Writing—Review & Editing, X.R., E.P. and L.D.I.; Visualization, X.R.; Supervision, X.R., E.P. and L.D.I.; Project Administration, X.R.; Funding Acquisition, X.R. and D.L. All authors have read and agreed to the published version of the manuscript.

**Funding:** This work was supported by the King Leopold III Fund for Nature Exploration and Conservation (X.R.), the University of Liège (X.R., “financement mission scientifique”), the Fondation de France (D.L., 2019-08602), the Ministère de l’Economie verte et du domaine—Délégation à la recherche de Polynésie française (D.L., contrat N3622 MED-EPHE), the Office Français de la Biodiversité (D.L., AFB/2019/385—OFB.20.0888) and the Agence Nationale de la Recherche (D.L., ANR-19-CE34-0006-Manini).

**Acknowledgments:** We thank Aurélie Aqua, Kim Eustache, Pierrick Hy, Guillaume Iwankow, Frank Lerouvreur and Chloé Pozas for their help as safety operator during fieldwork in Moorea Island. We are grateful to all Under The Pole III Expedition members for the positioning of the autonomous recorders in Raroia Island. Sonic data used in the controlled experiment were realized in collaboration with M. Clara P. Amorim and Paulo J. Fonseca in the framework of a previous study (Bolgan et al. 2018). We thank Frédéric Bertucci and Ben Williams for their help with R codes. Finally, we thank Gentiane Haesbroeck and Sophie Klenkenberg for their advice on correlations. We thank William Shakespeare for the ‘The Tragedy of Hamlet, Prince of Denmark’ that inspired the title.

**Conflicts of Interest:** The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

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