Gulf and Caribbean Research

Volume 36 | Issue 1

2025

# Lack of Consistent Diurnal Trends in Acoustic Metrics from Restored Coral Reefs

Jeremy Velázquez-Alvarado
*Sociedad Ambiente Marino, Universidad Ana G. Mendez*

Valentina Pérez-García
*Universidad Ana G. Mendez*

Javier S. Tellechea
*4Laboratorio de Acústica Ultrasonora, Instituto de Física, Universidad de la República, Uruguay.*

Joni T. Backstrom
*University of North Carolina Wilmington*

*See next page for additional authors*

## Recommended Citation

Velázquez-Alvarado, J., V. Pérez-García, J. S. Tellechea, J. T. Backstrom and A. Mercado-Molina. 2025. Lack of Consistent Diurnal Trends in Acoustic Metrics from Restored Coral Reefs. Gulf and Caribbean Research 36 (1): 71-88.
Retrieved from https://aquila.usm.edu/gcr/vol36/iss1/17
DOI: https://doi.org/10.18785/gcr.3601.16

# Lack of Consistent Diurnal Trends in Acoustic Metrics from Restored Coral Reefs

## Authors

Jeremy Velázquez-Alvarado, *Sociedad Ambiente Marino, Universidad Ana G. Mendez*; Valentina Pérez-García, *Universidad Ana G. Mendez*; Javier S. Tellechea, *4Laboratorio de Acústica Ultrasonora, Instituto de Física, Universidad de la República, Uruguay.*; Joni T. Backstrom, *University of North Carolina Wilmington*; and Alex Mercado-Molina, *University of Puerto Rico-Bayamon*

# GULF AND CARIBBEAN
## RESEARCH

Volume 36
2025
ISSN: 2572-1410

*Published by*
THE UNIVERSITY OF
SOUTHERN MISSISSIPPI

GULF COAST RESEARCH LABORATORY
Ocean Springs, Mississippi

Gulf and Caribbean Research Vol 36, 71–88, 2025
DOI: 10.18785/gcr.3601.16

Manuscript received January 10, 2025; accepted November 27, 2025

# LACK OF CONSISTENT DIURNAL TRENDS IN ACOUSTIC METRICS FROM RESTORED CORAL REEFS

**Jeremy Velázquez–Alvarado[1*], Valentina Pérez–García[2], Joni T. Backstrom[3], Javier S. Tellechea[4], and Alex E. Mercado–Molina[1,5,*]**

*[1]Sociedad Ambiente Marino, Calle–3 #1130, Urbanización Villa Nevárez, San Juan, Puerto Rico, 00927 USA; [2]Universidad Ana G. Méndez–Gurabo, Carretera #189, Km. 3.3, Gurabo, Puerto Rico, 00777 USA; [3]University of North Carolina Wilmington, Dobo Hall, Room 2006 601 S. College Road, Wilmington, North Carolina 28403, USA; [4]Instituto de Ciencias Oceánicas, Universidad de la República, Campus Luisi Janicki: pioneras universitarias, Alberto Lasplaces 1620, Montevideo 11600, Uruguay; [5]Universidad de Puerto Rico–Bayamón, Carretera #174. 170, Industrial Minillas 1911 Bayamón, Puerto Rico, 00959 USA; *Corresponding authors, emails: avelazquezsoundscapes@gmail.com; balex.mercado1@upr.edu*

**ABSTRACT:** Once vibrant ecosystems, coral reefs are degrading at unprecedented rates due to natural and human–induced disturbances, necessitating immediate restoration and conservation efforts. Evaluating the success of these projects often involves assessing changes in reef biodiversity. Bioacoustics has emerged as a promising, non–invasive method for such evaluations, though its efficacy remains debated. This study aimed to determine whether the diurnal soundscapes of restored coral reefs are consistent across different time frames (months) and spatial scales (reefs), which is crucial for developing reliable monitoring tools for reef health. To achieve this, 2 commonly used acoustic indices, the Acoustic Complexity Index (ACI) and Mean Sound Pressure Level (SPL), were employed to describe the underwater soundscape of 3 restored coral reefs in Culebra, Puerto Rico. The results showed that neither acoustic index followed a clear diurnal pattern, with considerable variation across studied locations and sampling days. The lack of consistent diurnal patterns across space and time suggests that ACI and SPL alone may not be ideal for comparing coral reef health, particularly as indicators of biodiversity. Instead, these sound metrics should complement other monitoring methods, such as visual and video census techniques, when evaluating the biodiversity of coral reef ecosystems.

**KEY WORDS:** Acoustic Biodiversity, Acoustic Complexity Index, Passive Acoustic Monitoring, Sound Pressure Level, Underwater Soundscape

## INTRODUCTION

The generation of sound is important in the lives of numerous marine organisms, as it plays a pivotal role in their survival, communication, and reproductive behavior. Large marine mammals like whales utilize sound for various purposes, including avoiding predatory risks, orientation, and prey detection (Tyack 2008, Radford et al. 2011, Parks et al. 2014). Similarly, several fish species incorporate sound production into their mating rituals, covering the courtship and mate selection processes (Lobel 1992, Schärer et al. 2014, Tellechea et al. 2022, Popper et al. 2024). Evidence suggests that some marine bottom–dwelling species (i.e., crabs) use sound to defend their territories (Radford and Stanley 2023). Sounds are vital even in species that do not generate them directly. For instance, pelagic larvae of certain marine invertebrates, including corals and crustaceans, rely on sounds to settle on appropriate substrates (Tolimieri et al. 2002, Simpson et al. 2008, Vermeij et al. 2010, Radford et al. 2011). These examples underscore the potential significance of sound in shaping the structure of marine populations and communities.

Animal sounds are pervasive in marine ecosystems (Mooney et al. 2020, Lin et al. 2021). Consequently, underwater soundscapes can offer valuable insights into the dynamics and health of marine environments (Duarte et al. 2021, Williams et al. 2022). The study of marine underwater sounds has increased exponentially since the early 2000s, reflecting an increased focus on understanding the acoustic dimensions of aquatic ecosystems (Lindseth and Lobel 2018). To characterize marine bioacoustic environments, scientists have turned to using sound recorders or acoustic sensors, which can be deployed in the field for prolonged periods (Browning et al. 2017). This approach, known as Passive Acoustic Monitoring (PAM), is not only a non–invasive method for long–term monitoring, but because various organisms often produce sounds, it can also complement the measurement of marine biodiversity. In particular, PAM enhances the probability of detecting the presence of cryptic species that are often challenging to survey using traditional visual methods. Hence, the data generated through PAM can inform evidence–based management decisions with the potential to contribute to preserving marine biodiversity (Nedelec et al. 2015).

In the Caribbean, several bioacoustics studies have been undertaken to characterize spatiotemporal variations in biodiversity (Freeman and Freeman 2016, Kaplan et al. 2018, La Manna et al. 2021, Lin et al. 2021), establish connections between the underwater soundscape and coral reef health (Piercy et al. 2014, Lamont et al. 2022) and assess how anthropogenic sounds, such as noise, affect the biology and ecology of coral reef communities (Simpson et al. 2016, Ferrier–Pagès et al. 2021). Despite these efforts, a definitive pattern regarding the diel trends in sound production within coral reefs remains elusive, limiting the applicability of PAM for monitoring purposes in the region.

While the innovative use of sounds as an alternative metric for evaluating coral reef diversity has gained attention, debate persists regarding the efficacy of PAMs in accurately reflecting reef biodiversity (Mooney et al. 2020, Dimoff et al. 2021). Thus, before achieving widespread acceptance as a method for estimating biodiversity, several critical issues must be carefully considered. These encompass the interpretation of diverse sound sources, comprehension of potential variations in sound production driven by environmental changes, and the necessity for standardized analysis methods (Mooney et al. 2020, Dimoff et al. 2021).

Determining whether bioacoustic signals show spatiotemporal consistency in restored coral reefs also holds significant implications for developing effective biodiversity monitoring protocols. For instance, if bioacoustic signals exhibit spatiotemporal specificity, monitoring efforts could be concentrated during these periods, thereby maximizing the efficient allocation of resources such as funding and manpower. Furthermore, establishing a baseline for the diel patterns of reef soundscapes is a crucial reference point, not only for identifying normal variations but also enabling the detection of abnormal patterns that may indicate changes in the composition or behavior of marine organisms.

The primary objective of this study is to contribute to the existing body of knowledge on the spatiotemporal dynamics of coral reef soundscapes. Specifically, our investigation focused on determining whether patterns of biological sounds exhibit diurnal consistency across sampling days and reefs. While many bioacoustic studies emphasize crepuscular periods, acoustic activity during daylight hours can also reveal essential ecological dynamics on coral reefs. Diurnal fluctuations in sound production are shaped by processes such as grazing, invertebrate movement, predator—prey interactions, competition, and reproductive behaviors (Remage—Healey et al. 2006, Kennedy et al. 2010). Hence, capturing these intra—daily variations is particularly important when assessing the soundscape of restored reefs and evaluating their ecological function.

We chose to concentrate on coral reefs because of their status as highly productive and biodiverse ecosystems, offering crucial ecological services such as food provision, coastal protection, and employment opportunities. Despite their significant contribution, coral reefs face severe threats and are among the most endangered ecosystems. Recent estimates indicate a staggering loss of 63% of global coral reef biodiversity since the 1950s (Eddy et al. 2021). To develop effective management and conservation strategies for these imperiled ecosystems, accurate measurements of reef biodiversity are essential.

The study was conducted in 3 reef areas within the island municipality of Culebra, Puerto Rico. Given the differences in reef geomorphology (i.e., topographic relief), we expected spatial variability in acoustic signals both within and across sites. Areas with greater structural complexity were anticipated to exhibit richer and more variable soundscapes, whereas reefs with comparable benthic composition and topography were expected to produce more uniform acoustic patterns. We also anticipated diurnal variability in soundscapes, as it is well established that many reef—associated organisms, including soniferous fishes, vary in acoustic activity throughout the day. In contrast, we did not expect significant differences in diurnal patterns across sampling days, as we assumed that community composition and abiotic conditions would remain relatively stable over the short duration of the study, particularly in the absence of major disturbances. We believe that the findings of our research will provide valuable insights into the use of coral reef bioacoustics surveys to describe the complex dynamics of coral reef soundscapes, contributing to the foundation for informed conservation and management strategies.

## Materials and Methods

### Study Sites

This study was performed at 9 substations across 3 coral reef sites along the western coast of the island municipality of Culebra, Puerto Rico (Figure 1). The 3 reef sites were Punta Maguey (MAG), Punta Melones (MEL), and Punta Tampico (TAM). At each site, and before the study started, populations of the threatened

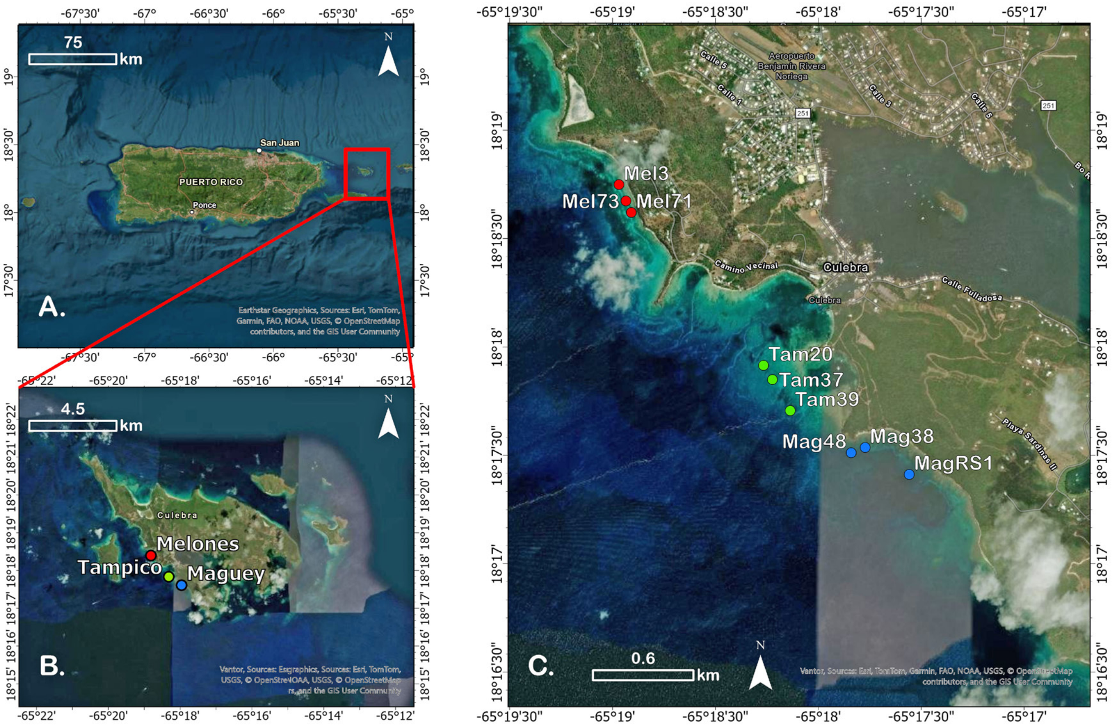

***Figure 1.*** *Study area. A. The study was conducted at 3 coral reef systems located along the west coast of the Island municipality of Culebra, Puerto Rico. B. Melones (MEL = red), Tampico (TAM = green), and Maguey (MAG = blue). C. The 3 subareas used for the photography survey and hydrophones deployment at MEL (red dots), TAM (green dots) and Maguey (blue dots).*

coral species *Acropora cervicornis* and *A. palmata* were restored through the outplanting of nursery—reared colonies. These 2 coral species provide habitat for multiple reef—dwelling organisms, including fish (Hernández—Delgado et al. 2025). Hence, their presence could play a role in the soundscape dynamics of the studied sites. The density of coral outplants was similar across the 3 reef areas, averaging about one colony/m$^2$. Prior to deploying the hydrophones, the benthic composition of the reef areas was described by photographic surveys using 1 m$^2$ quadrats. Each of the 3 reefs was surveyed at 3 replicate substations (Figure 1C), where the hydrophones were later deployed. The substations within each reef were spaced about 100 m apart. Images of the quadrats (n = 30—40 per site) were analyzed using the free software Coral Point Count with Excel Extension (CPCe; Kohler and Gill 2006). For each image, 100 random points were superimposed, and the benthic component beneath each point was identified. Percent cover was then calculated by dividing the number of points assigned to each category by 100 and multiplying by 100. Rugosity of each substation was based on Santiago—Padua et al. (2023) (i.e., MEL) or calculated *in—situ* using the chain methodology (see Supplemental Table S1).

### Acoustic Recordings

At each substation, a recording unit consisting of an SQ26—08 hydrophone (Cetacean Research Technology) paired with a Tascam DR—05X recorder was deployed (Supplemental Figure S1). The hydrophones were factory—calibrated with a frequency response up to ~100 kHz and a sensitivity of −193 dB re 1 V/µPa. At each of the substations in MEL, hydrophones were deployed in sand patches located about 2 m from the reef. Hydrophones were not placed directly on the reef structure because it is a shallow fringing reef with depths ranging from < 1 m to about 5 m. The reef is characterized by a gentle slope extending roughly 15 m from the shore. Given this shallow and variable bathymetry, placing hydrophones directly on the reef would have risked contact with the substrate. Instead, hydrophones were suspended at least 1 m above the seafloor to prevent them from striking corals, rocks, or other benthic structures. At the MAG and TAM sites, restoration efforts were conducted within delineated 100 m$^2$ areas (10 m × 10 m). We leveraged these predefined zones by deploying hydrophones near the center of each restored area to ensure proximity to coral outplants while avoiding contact with any benthic structures.

Because we did not have access to underwater housings that could protect the recorders from long—term submersion, they were placed in floating, waterproof casings (Supplemental Figure S1) anchored to the seafloor using paracord lines tied to cement blocks. A rebar was installed at each substation to mark the exact deployment location. The hydrophones, connected to the recorders inside the casings, were suspended about 1 m above the seabed. The cables were left with sufficient slack to allow free movement with water motion, minimizing the risk of tension—induced vibrations. The recorder units were labeled with unique identification numbers to ensure that the same unit was placed at its respective location during subsequent surveys. Throughout the recording period, no strumming or vibration—induced noise was detected in the spectrograms. Spectrograms were reviewed for signs of vibrational artifacts (e.g., tonal bands or harmonic structures typical of line strumming), and none were observed.

Due to the considerable boat traffic in the study area, leaving surface—floating recording units unattended at night posed a significant risk of collision or interference. Therefore, deployments were conducted only during daylight hours on sunny and calm days to minimize noise from external metocean influences such as waves, wind, and rain. Recordings were conducted from 7:00 a.m. to 5:00 p.m. in July 2022, August 2022, September 2022, and January 2023 (see Supplemental Table S2 for specific sampling dates). However, the January recording for substation TAM—20 was lost when the recorder became submerged and damaged. Each site was recorded for one day during each sampling date, with all substations within a reef recorded on the same day.

The sampling rate was 96 kHz, enabling detection of acoustic signals up to 48 kHz (Nyquist frequency). All recorded reef sound data were subsampled to assess daily variability and differences among sites. One minute representative subsamples were extracted from each recorded hour using a Fast Fourier Transform (FFT) window size of 2048 samples. The software Raven Pro was used to select one-minute sub-samples, which were subsequently analyzed acoustically following the methods described by Lamont et al. (2022). Each 1 min subsample was visually inspected and audited using spectrograms to identify and exclude segments containing anthropogenic noise. While we did not quantify the exact number of excluded samples, those showing clear signs of interference (e.g., boat engines or aircraft) were removed to ensure the analysis focused on biologically relevant reef sounds. The first minute free of anthropogenic noise was selected for analysis.

### Acoustic Complexity Index and Sound Pressure Level

Two of the most common acoustic indices (Acoustic Complexity Index: ACI and Sound Pressure level: SPL) used to describe underwater soundscape were examined within 3 different frequency bands (Pieretti and Danovaro 2020, Lamont et al. 2022). These included 1) the low—frequency band between 20 and 1000 Hz, 2) the mid—range frequency band between 2000 and 7000 Hz, and 3) the whole (i.e., full) frequency band, ranging from 20 Hz to 48000 Hz. To avoid aliasing, we limited our analysis to frequencies below the Nyquist limit, which for our 96,000 Hz sampling rate was 48,000 Hz (96,000 Hz/2 = 48,000 Hz). The frequency bandwidths were specifically chosen because of their capacity to obtain information about ecosystem functions and communities (Nedelec et al. 2015, Bertucci et al. 2016, Pieretti et al. 2017, Lamont et al. 2022). For example, fish vocalizations have been identified in the low—frequency band with sounds < 800 Hz (Tricas and Boyle 2014), while frequencies between 2000–7000 Hz are dominated by sounds produced by benthic invertebrates (i.e., shrimps, Nedelec et al. 2015, Lamont et al. 2022).

The ACI is an algorithm designed to directly quantify complex biotic sounds by assessing the variability of the intensities recorded in audio recordings, even amidst continuous human—generated noise. The ACI is calculated following a series of equations based on a matrix of sound intensity values that are extrapolated from sound spectrograms. From the matrix, the absolute differences between adjacent values in a frequency bin are calculated and then summed for specific time segments. This step is followed by dividing the resulting sum by the total intensity values for the specific segment. The ACI is then calculated by combining the values from all frequency bins for the entire recording (Pieretti et al. 2011). ACI values were obtained using the Soundecology R v.4.1.2 package, with a default j=60s cluster size (www.r—project.org/; Sueur et al. 2008, Villanueva—Rivera et al. 2018).

The SPL, the most ubiquitously employed acoustic metric, expresses the root—mean—square (RMS) sound amplitude within a given time window and frequency range as a single—decibel (dB) level (Merchant et al. 2015, Pieretti et al. 2017). A Hamming Fast—Fourier Transform (FFT) window of 512 samples and 50% overlap was used for both computation analyses. The SPL was analyzed using the PAM Guide (Nedelec et al. 2015).

### Data Analysis

Following previous studies focusing on coral reef soundscapes (Ferguson et al. 2022, Lamont et al. 2022), we modelled the response variable (ACI, SPL) using a generalized linear mixed—effects model (GLMM). The GLMMs are well—suited for analyzing hierarchical (i.e., substations nested within reefs) data by accounting for random effects at multiple levels. Moreover, GLMMs provide a flexible framework for analyzing non—normal data by relaxing traditional assumptions such as normality and homoscedasticity (Bolker et al. 2009, Bolker 2015). This framework also allows for the comparison of alternative models using information—theoretic criteria such as AIC.

The GLMMs were fitted using a Gamma distribution with a log link, implemented via the glmmTMB package in R (Brooks et al. 2017). Although lme4 can also fit Gamma GLMMs, glmmTMB was selected because it offers greater flexibility for non—Gaussian models and often provides more stable estimation for complex model structures, including those with multiple random effects or interaction terms. Additionally, glmmTMB allows more explicit control over dispersion and model specification, which can be advantageous for continuous, positively skewed acoustic metrics. We also used the glmmTMBControl function to increase the maximum number of iterations (iter.max = 10000, eval.max = 10000) to ensure model convergence given the model structure (Brooks et al. 2025). Fixed effects included Substation and Hour, while Sampling Date (i.e., date of data collection) was included as a random intercept to account for repeated measures across sampling days.

We focused our spatial analysis at the substation level rather than at the broader reef scale because we expected that microhabitat features such as depth, rugosity, and benthic composition would influence acoustic variation. As noted above, we anticipated spatial heterogeneity even within individual reefs. Therefore, we considered "Substation" to be the more appropriate spatial unit for testing predictive capability in our models.

We fitted several candidate models to evaluate the influence of substation, hour, and their interaction on the response variables (Table 1). Model selection was based on Akaike's Information Criterion corrected for small sample size (AICc), using the AICcmodavg package (Mazerolle 2017). The model with the lowest AICc and highest Akaike weight was considered the best—supported model.

To further investigate whether there were consistent diurnal patterns (i.e., by hour) in acoustic indices, we conducted pairwise correlation comparisons (p—values adjusted using Holm's method for multiple comparisons) between all 4 sampling dates at each substation using Spearman's rank correlation. This non—parametric method was chosen because it does not assume linear relationships and is robust to non—normal data distributions. By evaluating the strength and significance of these pairwise correlations, we assessed the temporal coherence of acoustic index values (e.g., ACI, SPL) throughout daylight hours. This approach allowed us to identify whether soundscape activity followed predictable diurnal (i.e. hourly) patterns or exhibited irregular fluctuations, particularly in cases where more complex time series analyses were not feasible due to limited temporal replication.

To ascertain a potential relationship between mean coral cover and mean ACI and SPL values, Pearson linear correlation analyses were conducted for the full, mid—range, and low—frequency bands. For these analyses, all data across space and time were combined. The coefficient of variation (CV) was calculated for each location to visually assess intraday variability at each site.

**TABLE 1.** *Summary of the models evaluated using Generalized Linear Mixed Models (GLMM) for Sound Pressure Levels (SPL) and Acoustic Complexity Index (ACI). The table lists model names, their parameter structures, and a brief description of what each model tests. All models include a random intercept for Sampling Date to account for variability across sampling dates.*

| Model | Parameters evaluated | Description |
|---|---|---|
| Full Model | ~ Hour * Site + (1 \| Sampling date) | Tests the main effects of Hour and Site and their interaction, accounting for random variation by Date. |
| Model 1 | ~ Hour + Substation + (1 \| Sampling date) | Tests additive effects of Hour and Site without Interaction, accounting for Date variability |
| Model 2 | ~ Hour + (1 \| Sampling date) | Tests effect of Hour alone, accounting for Date Variability. |
| Model 3 | ~ Substation + (1 \| Sampling date) | Tests effect of Site alone, accounting for Date Variability. |
| Null Model | ~ (1 \| Sampling date) | Null model with only random Date effect, no fixed predictors |

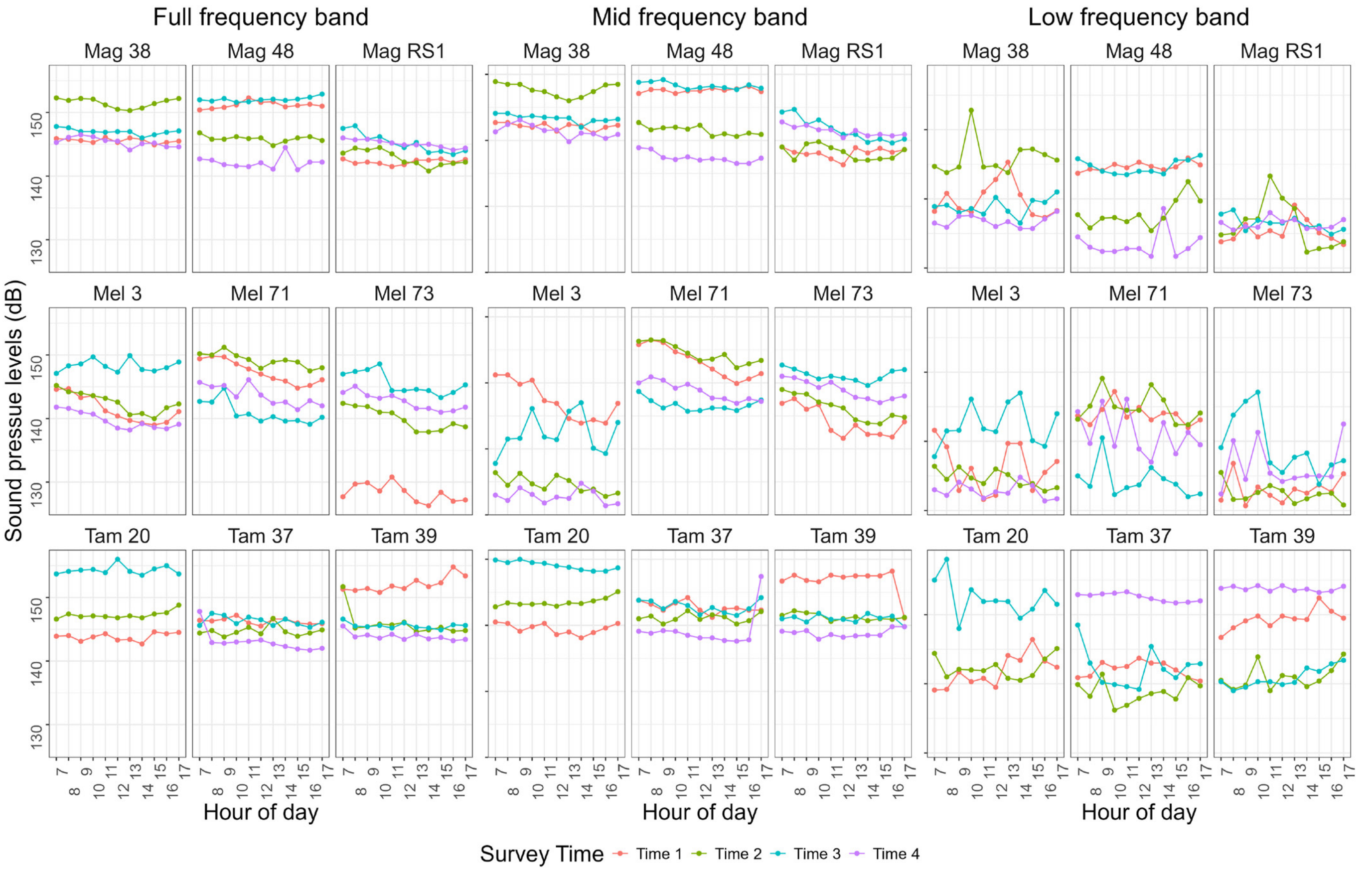

***Figure 2*** *Diurnal patterns in Sound Pressure Levels (SPL) across 3 acoustic frequency bands (Full, Mid, and Low) for 9 substations across 3 coral reef sites in Culebra, Puerto Rico. Each panel represents a specific substation and frequency band combination, with SPL values (in dB) on the y–axis and hour of day on the x–axis. Data are color–coded by survey time (Time 1 to Time 4), corresponding to different sampling days. Mag–Maguey; Mel–Melones; Tam–Tamarindo. For specific survey time (i.e., dates) see Supplemental Table S2.*

## RESULTS

### Study Site Coral Cover

At MEL, the percentage of coral cover varied between 3.66% and 6.67% (Supplemental Table S3), with *Porites porites* and *P. astreoides* identified as the most common species. Of the 3 substations within MEL, the substrate at Substation–71 (= Mel–71; rugosity index = 1.17, Supplemental Table S1) was mostly covered by dead coral, sand, and rocks. Substation –73 (=Mel–73; rugosity index = 1.24, Supplemental Table S1) and Substation–3 (= Mel–3; rugosity index = 1.19, Supplemental Table S1) were dominated by octocorals, primarily the sea fan coral *Gorgonia ventalina*. Across the 3 substations, *Dictyota* spp. and turf, composed of mixed filamentous algae and cyanobacteria, were the most common non–animal groups, though *Dictyota's* presence fluctuated over time (personal observation).

The TAM reef was characterized by a hardbottom habitat with a common presence of *Orbicella annularis* boulders and no adjacent seagrass or sand, at depths ranging from 5– 8 m. The benthic community was dominated by macroalgae, turf algae complex, *Ramicrusta* spp., and *Dictyota* spp. None of the 3 substations within TAM (TAM–20, TAM–37, TAM–39) exceeded 6.5% coral cover (Supplemental Table S3), with the most common species being the endangered star coral, *O. annularis*. The rugosity index was 1.53, 1.36, and 1.62 for TAM–20, TAM–37, TAM–39, respectively (Supplemental Table S1).

The MAG reef was characterized by a coral cover varying between 2.38% and 7.15% (Supplemental Table S3), with *P. astreoides* and *P. porites* being the most common species. Similar to TAM, the reef substrates at the 3 substations (MAG–38, MAG–48, MAG–RS1) were characterized by hardbottom habitat with several rocks and dead coral boulders. The rugosity index was 1.63, 1.48, and 1.49 for MAG–38, MAG–48, MAG–RS1, respectively (Supplemental Table S1). The substations were mostly covered by turf algae complex and *Ramicrusta* spp. Depths ranged from about 4–8 m.

### Sound Pressure Levels

The SPL measured across substations ranged from 126–156 dB in the full frequency band, with mid–range and low–frequency bands exhibiting slightly lower ranges of 120–150 dB. No consistent diurnal patterns were observed in any frequency band; rather, SPL peaks occurred at varying hours throughout the day without a clear trend (Figure 2). Substations at MEL reef exhibited the greatest diurnal variability across survey times, with its mean diurnal coefficient of variation (CV) being 2 to 2.5 times higher than that at MAG and TAM for the full frequency band, 2–3 times higher in the mid–range band, and 6–7 times higher in the low–frequency band (Figure 3). Substations at MEL reef also showed the greatest within–reef

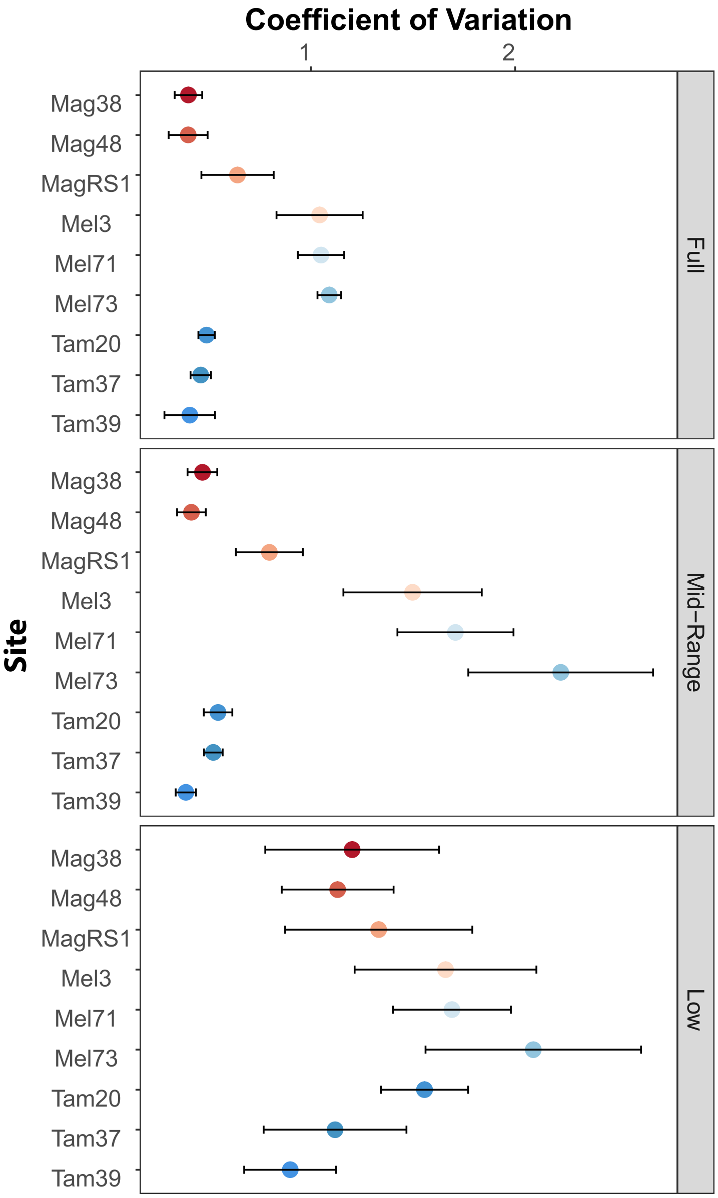

***Figure 3.*** *The coefficient of variation (CV, mean ± se) in Sound Pressure Levels (SPL) of 9 substations across 3 coral reef sites in Culebra, Puerto Rico, grouped by acoustic frequency band (Full, Mid–Range, and Low). The CV was calculated by combining data from all hours of the day and all survey times, capturing overall spatiotemporal variability in each site's soundscape, and is a standardized measure of variability (standard deviation divided by the mean). The x–axis lists the site names. MAG–Maguey; MEL–Melones; TAM–Tamarindo.*

heterogeneity in SPL intensity, followed by MAG and TAM, particularly in the mid– and low–frequency bands.

Model selection using AICc revealed that spatial variation (i.e., substations) was the strongest predictor of SPL across all frequency bands (Table 2A, B, C). For the full frequency band, the model including only Substation received overwhelming support (AICc weight = 0.99), with all other models, including those with temporal predictors (Hour or Substation × Hour interaction), showing less support (ΔAICc > 10). Similarly, for the mid– and low–frequency bands, Substation–only models were favored (AICc weights 0.99 and 1.00, respectively). These results indicate that spatial differences among Substations were primarily structured SPL patterns, while the factor Hour had minimal influence. However, no single substations consistently exhibited significantly higher or lower SPL values across sampling dates, suggesting that while substations strongly influence SPL, temporal variability within them may be high and inconsistent (Figure 2).

Of the 51 pairwise correlations tested in the full frequency band, 10 comparisons (19.6%, Supplemental Table S4) were positive and significant at $p < 0.05$, indicating that only a minority of the substations exhibited consistent SPL patterns throughout the daylight hours (0700–1700, Figure 4). Based on correlation strength and significance, the substations can be grouped into 3 general clusters. That most locations either lacked daylight structure or showed erratic acoustic fluctuations, suggests that full–band SPL values do not show diurnal periodicity.

*Full–frequency band cluster 1.* High diurnal coherence in which MEL–3 and MEL–71 exhibited multiple strong and statistically significant correlations, suggesting strong diurnal coherence in SPL values (Supplemental Table S4). For instance, MEL–3 showed high correlations between 11 September 2022 and 24 September 2022 ($\rho = 0.945$, $p = 0.0001$), 11 September 2022 and 24 January 2023 ($\rho = 0.800$, $p = 0.0124$), and between 24 September 2022 and 24 January 2023 ($\rho = 0.855$, $p = 0.0040$). Similarly, MEL–71 exhibited significant correlations among most pairs of sampling dates. At this site, only when comparing 24 September 2022 vs. 24 January 2023 ($\rho = 0.610$ $p = 0.0730$) and 4 November 2022 vs. 24 January 2023 ($\rho = 0.633$, $p = 0.0730$) the correlations were not significant.

*Full–frequency band cluster 2.* Isolated significance in which MAG–RS1 and MEL–73 displayed a combination of strong and weak correlations, with a few significant results (Supplemental Table S4). MAG–RS1 showed significant correlations between 12 September 2022 and 28 September 2022 ($\rho = 0.870$, $p = 0.0030$) and 28 September 2022 and 25 January 2023 ($\rho = 0.829$, $p = 0.0080$). Correlations at MEL–73 included a strong significant correlation between 24 September 2022 and 24 January 2023 ($\rho = 0.874$, $p = 0.0026$), with other moderately high but non–significant values likely affected by multiple comparison correction.

*Full–frequency band cluster 3.* Lack of coherence in which Substations MAG–38, MAG–48, TAM–20, TAM–37, and TAM–39 showed weak, non–significant, or negative correlations between sampling dates (Supplemental Table S4). In some cases, correlations were near zero (e.g., MAG–48: 26 July 2022 vs. 28 September 2022, $\rho = -0.073$, $p = 1.00$). In the case of TAM–20 (27 July 2022 vs. 14 September 2022, $\rho = 0.678$, $p = 0.0654$) and TAM–39 (27 July 2022 vs. 14 September 2022, $\rho = -0.715$, $p = 0.0801$) moderately strong correlations were observed, but none reached statistical significance. Overall, these results indicate high variability and a lack of predictable diurnal patterns at these substations.

When considering SPL values in the mid frequency band, 7 comparisons (13.7%, Supplemental Table S5) were positive and statistically significant at $p < 0.05$, indicating that only

**TABLE 2**. *Summary of the results of the Generalized Linear Mixed Model (GLMM) model selection for Sound Pressure Levels (SPL) across frequency bands using key model selection metrics. AICc is the corrected Akaike Information Criterion, which penalizes model complexity to avoid overfitting. Delta AICc represents the difference in AICc between each model and the best-performing one. AICcWt indicates the relative likelihood of each model being the best among the set, while Cum. Wt shows the cumulative weight across models. LL refers to the log-likelihood, with higher values indicating better model fit. A. Full Frequency Band. B. Mid frequency band. C. Low frequency band.*

**A. Full Frequency Band**

| Model | Parameters evaluated | AICc | Delta_AICc | AICcWt | Cum.Wt | LL |
|---|---|---|---|---|---|---|
| Model 3 | ~ Substation | 2098.51 | 0.00 | 0.99 | 0.99 | -1037.90 |
| Model 1 | ~ Substation + Hour | 2108.74 | 10.23 | 0.01 | 1.00 | -1032.10 |
| Null | ~ (1 \| Sampling date) | 2256.63 | 158.13 | 0.00 | 1.00 | -1125.29 |
| Model 2 | ~ Hour | 2270.25 | 171.74 | 0.00 | 1.00 | -1121.63 |
| Full Model | ~ Hour * Site | 2338.70 | 240.19 | 0.00 | 1.00 | -1031.95 |

**B. Mid Frequency Band**

| Model | Parameters evaluated | AICc | Delta_AICc | AICcWt | Cum.Wt | LL |
|---|---|---|---|---|---|---|
| Model 3 | ~ Substation | 2155.02 | 0.00 | 0.99 | 0.99 | -1066.15 |
| Model 1 | ~ Substation + Hour | 2164.10 | 9.08 | 0.01 | 1.00 | -1059.78 |
| Full Model | ~ Hour * Site | 2392.95 | 237.93 | 0.00 | 1.00 | -1059.07 |
| Null | ~ (1 \| Sampling date) | 2446.08 | 291.07 | 0.00 | 1.00 | -1220.01 |
| Model 2 | ~ Hour | 2461.36 | 306.35 | 0.00 | 1.00 | -1217.19 |

**C. Low Frequency Band**

| Model | Parameters evaluated | AICc | Delta_AICc | AICcWt | Cum.Wt | LL |
|---|---|---|---|---|---|---|
| Model 3 | ~ Substation | 2284.21 | 0.00 | 1 | 1 | -1130.75 |
| Model 1 | ~ Substation + Hour | 2303.64 | 19.43 | 0 | 1 | -1129.55 |
| Null | ~ (1 \| Sampling date) | 2468.63 | 184.42 | 0 | 1 | -1231.28 |
| Model 2 | ~ Hour | 2488.13 | 203.92 | 0 | 1 | -1230.58 |
| Full | ~ Hour * Site | 2495.02 | 210.81 | 0 | 1 | -1110.11 |

a minority of substations exhibited consistent SPL patterns throughout the daylight hours (Figure 4). Following the description above, the substations can likewise be grouped into 3 general clusters. The results indicate that when considering SPL in the mid frequency band, there is no consistent diurnal pattern in SPL. Instead, temporal coherence in reef soundscapes was highly site—specific, and often limited to isolated time events.

*Mid—frequency band cluster 1.* High diurnal coherence. Substations MEL—71 and MEL—73 exhibited relatively strong and, in several cases, statistically significant correlations between multiple sampling dates pairs (Supplemental Table S5). For example, MEL—71 showed significant correlations between 11 September 2022 and 24 September 2022 ($\rho = 0.929$, $p = 0.0002$), 11 September 2022 and 24 January 2025 ($\rho = 0.961$, $p = 0.0000$), and 23 September 2022 and 24 January 2025($\rho = 0.913$, $p = 0.0003$), indicating a more consistent temporal coherence in SPL than the other sites. Substation MEL—73 also demonstrated significant coherence when comparing between 11 September 2022 and 24 January 2025 ($\rho = 0.742$, $p = 0.0447$) and 24 Septemberm2022 and 24 January 2025 ($\rho = 0.952$, $p = 0.0000$), with several other comparisons nearing significance.

*Mid—frequency band cluster 2.* Isolated significance; MAG—RS1 and TAM—37 showed mostly weak or non—significant correlations, but each had one strong and statistically significant comparison (Supplemental Table S5). MAG—RS1 exhibited a significant positive correlation between 28 September 2022 and 25 January 2023 ($\rho = 0.832$, $p = 0.0089$), while TAM—37 showed a significant correlation for the same time pair ($\rho = 0.773$, $p = 0.0314$). Substation TAM—20 showed a single significant negative correlation (14 September 2022 vs. 25 September 2022: $\rho = -0.708$, $p = 0.0443$). The rest of the comparisons at these sites were relatively weak and, in some instances, negative.

*Mid—frequency band cluster 3.* Lack of coherence. Despite occasionally strong correlations in MAG—38 and MEL—3, which were not statistically significant, the majority of correlations across these two substations, as well as at MAG—48, TAM—3, and TAM—39, were weak, non—significant, or even negative across time pairs (Supplemental Table S5), highlighting the overall lack of coherent temporal patterns. Substation TAM—20 showed a single significant correlation, but it was negative (14 September 2022 vs. 25 September 2022: $\rho = -0.708$, $p = 0.0443$).

When considering SPL values in the low frequency band, only one comparison (1.96%, Supplemental Table S6) was positive and significant at $p < 0.05$, indicating a very limited presence of consistent low frequency SPL patterns throughout the day (Figure 4). Thus, only 2 substation clusters were evident. The results suggest that temporal coherence in the low—frequency component of reef soundscapes was largely absent or highly variable across sites. The lack of significant correlations in most locations, combined with the presence of negative or near—zero coefficients, indicates that a clear or consistent diurnal pattern in low—frequency SPL was generally not evident.

*Low—frequency band cluster 1.* Isolated significant coherence at MEL—73, the only site that showed a significant correlation, with a strong positive relationship between 11 September 2022 and 24 January 2023 ($\rho = 0.765$, $p = 0.0363$; Supplemental Table S6), suggesting a potential diurnal signal at this site. However, the remaining correlations at MEL—73 were weak, negative, or non—significant, indicating that this coherence was not sustained throughout the daylight hours.

*Low—frequency band cluster 2.* Generally weak and non—significant patterns. Most sites, including MAG—38, MAG—48, MAG—RS1, MEL—3, MEL—71, TAM—20, TAM—37, and TAM—39, displayed predominantly weak, negative, or non—significant correlations across sampling date pairs (Supplemental Table S6). For instance, all 6 comparisons at MAG—38 were

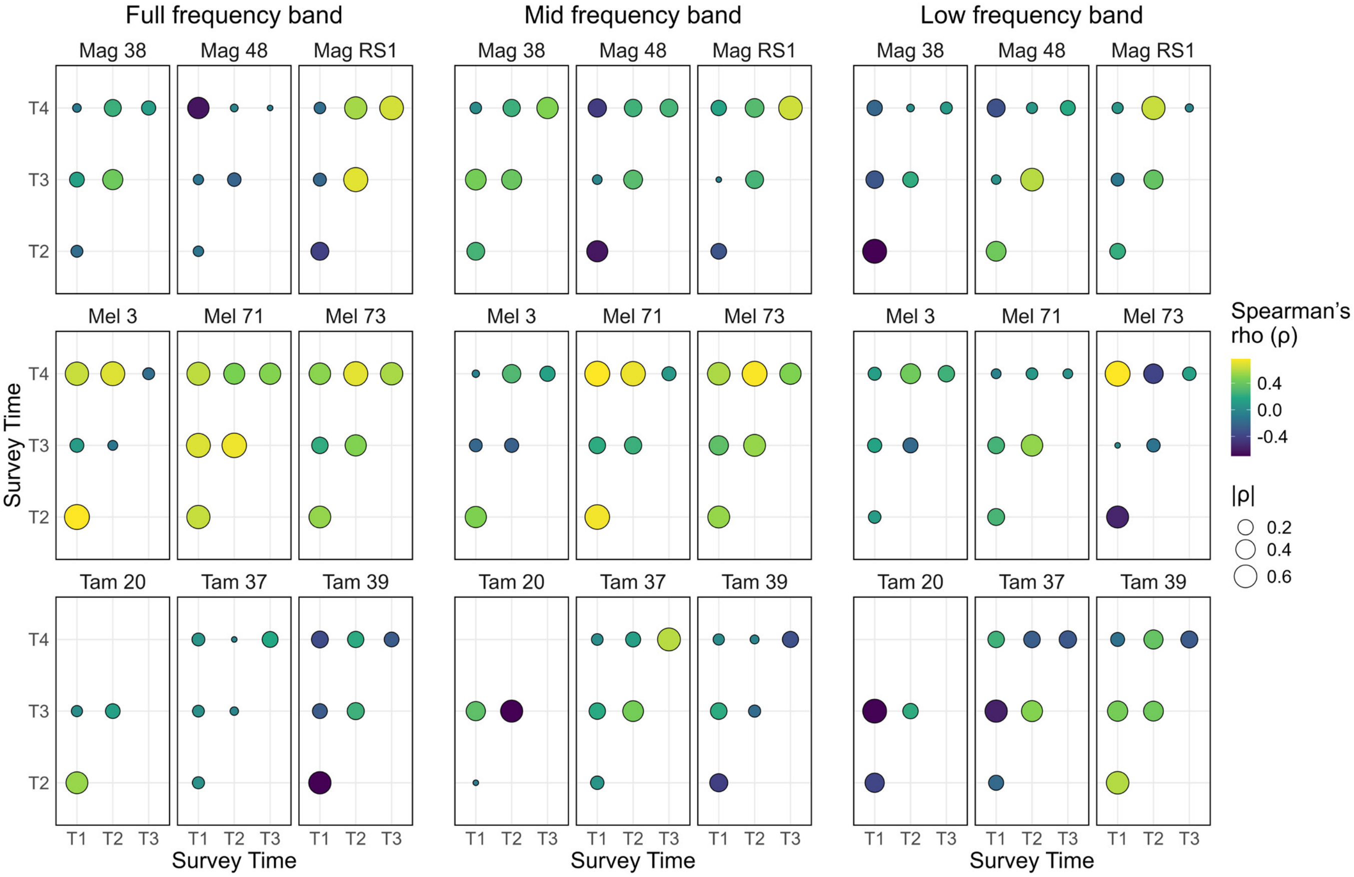

***Figure 4.*** *Pairwise Spearman's rank correlations (ρ) of Sound Pressure Level (SPL) between survey times for each of the 9 study substations across 3 coral reef sites in Culebra, Puerto Rico, separated by frequency bands (Full, Mid, and Low). Each subplot represents one substation within a frequency band. Axes show pairwise comparisons between Survey Times (T1–T4). Circle color indicates the direction and strength of correlation. Green–positive correlation; Purple–negative correlation. Circle size indicates the magnitude of correlation (|ρ|), with larger circles reflecting stronger associations. MAG–Maguey; MEL–Melones; TAM–Tamarindo. For specific survey time (i.e., dates) see Supplemental Table S2.*

non–significant, including several negative values (e.g., 26 July 2022 and 12 September 2022: ρ = –0.694, p = 0.1069). Similarly, MEL–3 and MEL–71 had uniformly low correlation coefficients with no discernible temporal coherence. Substations TAM–20 and TAM–37 exhibited several moderate–to–strong negative correlations (e.g., TAM–20: 27 July 2022 and 25 September 2023: ρ = –0.688, p = 0.0579), but none were statistically significant.

### Acoustic Complexity Index

The ACI varied markedly across frequency bands, with values ranging from 191–244 for the full spectrum, 20–48 in the mid–frequency range, and 3–9 in the low–frequency band (Figure 5). In general, ACI did not follow a consistent daylight pattern across all substations, as peak values occurred at different hours of the day and fluctuated within sampling dates. However, some substations showed higher diurnal variability than others. For instance, substations within the MEL reef exhibited the highest hourly fluctuations (all sampling dates and hours combined) in ACI for the full–band signal, with mean CV 1.17–1.25 times greater than those observed at MAG and TAM, respectively (Figure 6). In the mid–frequency band, no consistent diurnal trends were observed across sites; rather, variability appeared to be specific to individual substation. For example, MAG–RS1 and TAM–39 showed the lowest CVs (~2.2), while MAG–38 and TAM–37 were among the highest (CV ~2.7). A similar substation–specific pattern was observed in the low–frequency band, where MAG–RS1 showed the greatest diurnal variability (CV = 5.0), followed by MEL–71 (CV = 4.9) and TAM–20 (CV = 4.6), whereas MAG–48 (CV = 3.2) and MEL–73 (CV = 3.6) had the lowest.

Model selection based on AICc supported these observations and revealed distinct acoustic patterns across frequency bands. For the full frequency band, the additive model including both Substation and Hour had the strongest support (AICcWt = 0.96; Table 3A), indicating independent contributions of spatial and temporal factors to ACI. In the mid–frequency band, the model including only Substation was best supported (AICcWt = 1.00; Table 3B), suggesting that spatial differences among reefs drove most of the acoustic variation, with minimal diurnal influence. In contrast, in the low–frequency band, the model with Substation × Hour interaction had the highest support (combined AICcWt = 0.98; Table 3C), reflecting that diurnal ACI patterns were site–dependent. These results confirm that diurnal variability in ACI exists.

**TABLE 3.** *Summary of the results of the Generalized Linear Mixed Model (GLMM) model selection for Acoustic complexity Index (ACI) across frequency bands using key model selection metrics. AICc is the corrected Akaike Information Criterion, which penalizes model complexity to avoid overfitting. Delta AICc represents the difference in AICc between each model and the best-performing one. AICcWt indicates the relative likelihood of each model being the best among the set, while Cum. Wt shows the cumulative weight across models. LL refers to the log-likelihood, with higher values indicating better model fit. A. Full frequency band. B. Mid frequency band. C. Low frequency band.*

**A. Full Frequency Band**

| Model | Parameters evaluated | AICc | Delta_AICc | AICcWt | Cum.Wt | LL |
|---|---|---|---|---|---|---|
| Model 1 | ~ Substation + Hour | 2503.86 | 0.0 | 0.96 | 0.96 | -1229.66 |
| Model 3 | ~ Substation | 2510.42 | 6.57 | 0.04 | 1.0 | -1243.86 |
| Full | ~ Hour * Site | 2674.69 | 170.83 | 0.0 | 1.0 | -1199.94 |
| Null | ~ (1 \| Sampling date) | 3031.63 | 527.78 | 0.0 | 1.0 | -1512.79 |
| Model 2 | ~ Hour | 3046.02 | 542.16 | 0.0 | 1.0 | -1509.52 |

**B. Mid Frequency Band**

| Model | Parameters evaluated | AICc | Delta_AICc | AICcWt | Cum.Wt | LL |
|---|---|---|---|---|---|---|
| Model 3 | ~ Substation | 2200.23 | 0.0 | 1.0 | 1.0 | -1088.76 |
| Model 1 | ~ Substation + Hour | 2221.65 | 21.42 | 0.0 | 1.0 | -1088.55 |
| Null | ~ (1 \| Sampling date) | 2361.67 | 161.44 | 0.0 | 1.0 | -1177.8 |
| Model 2 | ~ Hour | 2382.32 | 182.1 | 0.0 | 1.0 | -1177.67 |
| Full | ~ Hour * Site | 2615.66 | 415.44 | 0.0 | 1.0 | -1170.43 |

**C. Low Frequency Band**

| Model | Parameters evaluated | AICc | Delta_AICc | AICcWt | Cum.Wt | LL |
|---|---|---|---|---|---|---|
| Full | ~ Hour * Site | 805.73 | 0.0 | 0.49 | 0.49 | -265.46 |
| Model 3 | ~ Substation | 812.67 | 6.94 | 0.02 | 1.0 | -394.98 |
| Model 1 | ~ Substation + Hour | 832.52 | 26.8 | 0.0 | 1.0 | -393.99 |
| Null | ~ (1 \| Sampling date) | 918.4 | 112.67 | 0.0 | 1.0 | -456.17 |
| Model 2 | ~ Hour | 937.88 | 132.15 | 0.0 | 1.0 | -455.45 |

Of the pairwise correlation tests performed when considering ACI values in the full band, 6 comparisons (11.7%, Supplemental Table S7) were positive and statistically significant at $p < 0.05$, indicating that only a small proportion of the substations exhibited consistent diurnal patterns in ACI values (Figure 5). Three clusters were evident. Taken together, the results suggest that no consistent diurnal trend in ACI values was observed across sites and time when considering the full band.

*Full—frequency band cluster 1.* High hourly—scale coherence where MAG—48 exhibited consistently strong and statistically significant correlations across all sampling dates, including very strong correlations between 12 September 2022 and 28 September 2022 ($\rho = 0.945$, $p = 0.0001$, Supplemental Table S7) as well as 28 September 2022 and 25 January 2023 ($\rho = 0.864$, $p = 0.0031$). All other comparisons at this substation were significant, although less strong. This suggests a relatively stable diurnal coherence in ACI dynamics at MAG—48 in the full—band frequency.

*Full—frequency band cluster 2.* Isolated significance at MEL—73 which showed a significant, but a negative correlation between 24 September 2022 and 24 January 2023 ($\rho = -0.818$, $p = 0.0125$).

*Full—frequency band cluster 3.* Except for MAG—48 (all pairs) and MEL—73, which showed one instance of a significant correlation, all other substations displayed weak, non—significant, and sometimes negative correlations (Supplemental Table S7). For example, at MEL—3, 5 of the 6 pairwise comparisons were negative (e.g., 11 September 2022 vs. 24 January 2023, $p = -0.427$). Only 2 correlations in this cluster were strong and marginally significant: MAG—38 when comparing 26 July 2022 with 28 September 2022 ($\rho = 0.727$, $p = 0.0672$), and MEL—3 when comparing 24 September 2022 with 4 November 2022 ($\rho = 0.718$, $p = 0.0768$); indicating that these 2 sites may exhibit partial or intermittent diurnal structure, but the evidence remains inconsistent.

Of the pairwise correlation tests performed when considering ACI values in the mid—frequency band, 3 comparisons (5.9%) were positive and statistically significant at $p < 0.05$, indicating that only a small proportion of sites exhibited consistent diurnal patterns in mid—range ACI values (Figure 5). Based on these significant relationships, 3 main substation—level clusters were evident. Taken together, the results indicate that significant mid—range hourly—scale ACI coherence was highly restricted both temporally (i.e., Sampling—date) and spatially (i.e., Substation), with only isolated cases of consistent acoustic structure observed across the surveyed reef sites.

*Mid—frequency band cluster 1.* High hourly—scale coherence was observed exclusively at MAG—48, which exhibited two significant and strong correlations (Supplemental Table S8), between 12 September 2022 and 28 September 2022 ($\rho = 0.791$, $p = 0.0187$) and 28 September 2022 and 25 January 2023 ($\rho = 0.891$, $p = 0.0014$).

*Mid—frequency band cluster 2.* Isolated positive significant coherence included only TAM—20 (Supplemental Table S8), where a single significant positive correlation was observed between 14 September 2022 and 25 September 2022 ($\rho = 0.736$, $p= 0.0293$), indicating localized or short—duration diurnal structure in ACI dynamics at TAM reef. Substation MEL—73 could also be included in this cluster as it showed a strong and significant correlation between 24 September 2022 and 24 January 2023 although the relationship was negative ($\rho = -0.845$, $p = 0.0063$, Supplemental Table S8).

*Mid—frequency band cluster 3.* Generally weak and non—significant patterns as all other substations (Supplemental Table S8) did not exhibit any significant correlations. These substations likely reflect high variability or lack of structured diurnal patterns in mid—frequency acoustic complexity.

When considering ACI values in the low frequency band,

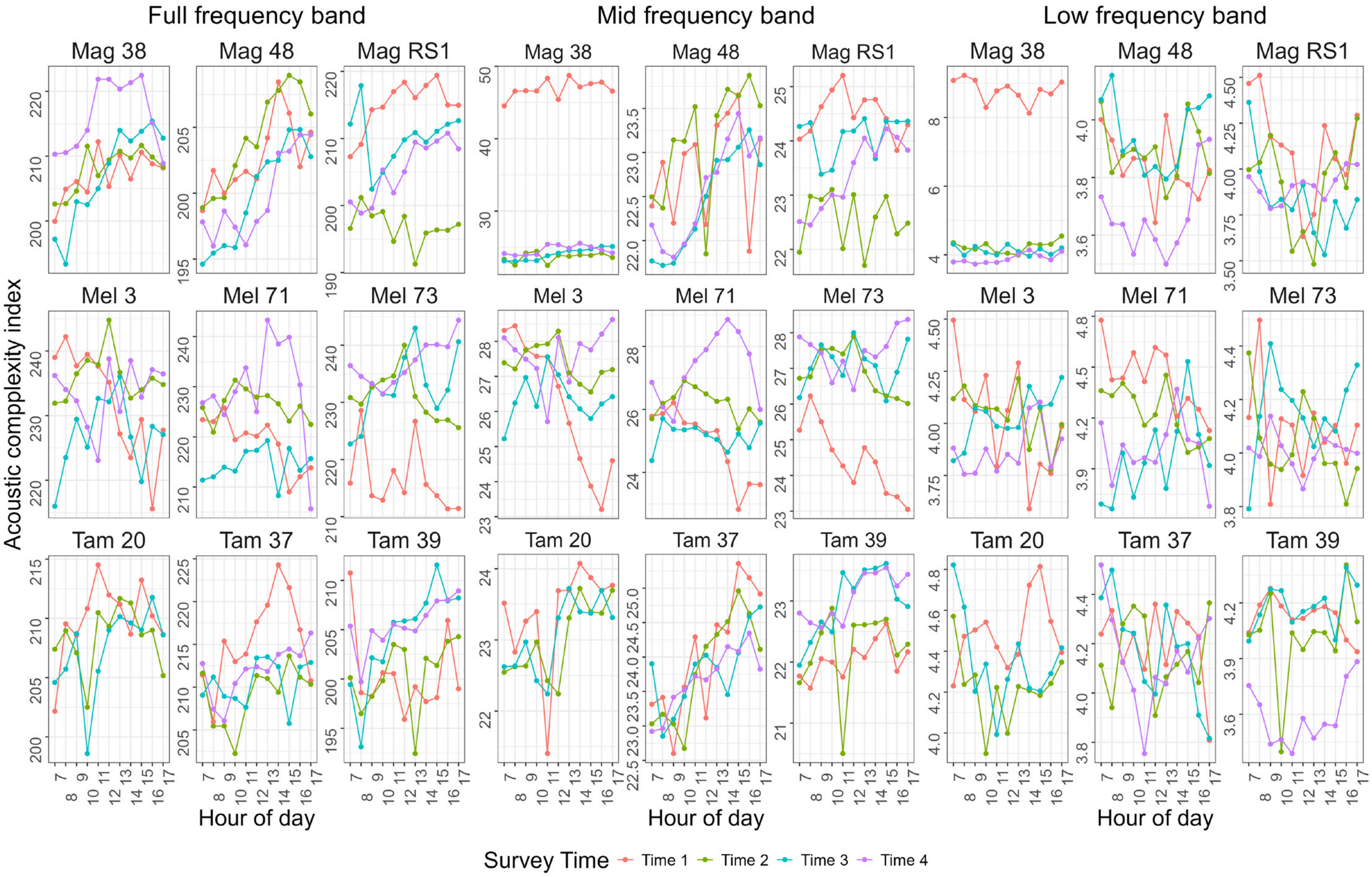

***Figure 5.*** *Diurnal patterns in Acoustic Complexity Index (ACI) across 3 acoustic frequency bands (Full, Mid, and Low) for 9 substations across 3 coral reef sites in Culebra, Puerto Rico. Each panel represents a specific substation and frequency band combination, with SPL values (in dB) on the y–axis and hour of day on the x–axis. Data are color–coded by survey time (Time 1 to Time 4), corresponding to different sampling days. MAG–Maguey; MEL–Melones; TAM–Tamarindo.*

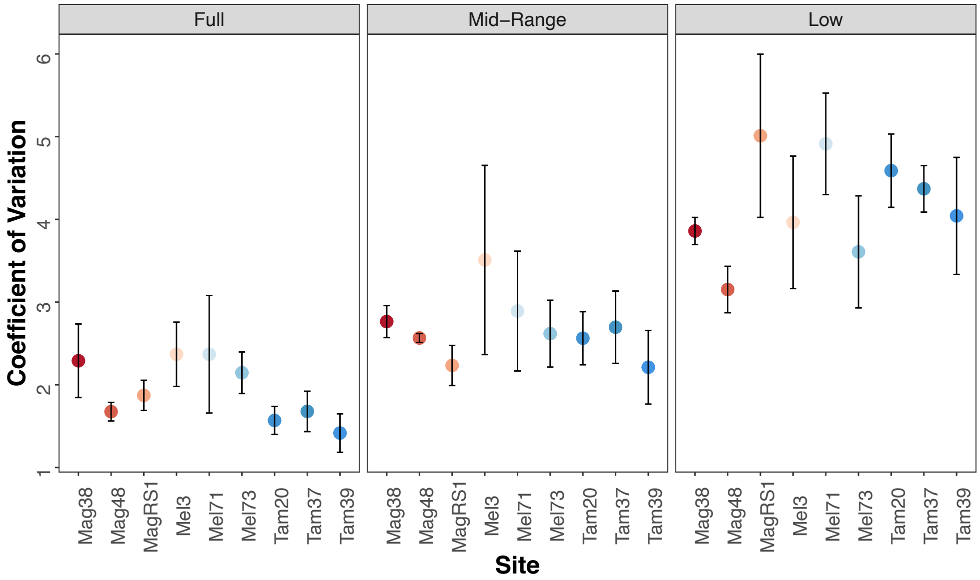

***Figure 6.*** *The coefficient of variation (CV; mean ± se) in Acoustic Complexity Index (ACI) of 9 substations across 3 coral reef sites in Culebra, Puerto Rico, grouped by acoustic frequency band (Full, Mid–Range, and Low). The CV was calculated by combining data from all hours of the day and all survey times, capturing overall spatiotemporal variability in each site's soundscape, and is a standardized measure of variability (standard deviation divided by the mean). The x–axis lists the site names. MAG–Maguey; MEL–Melones; TAM–Tamarindo.*

only one comparison (1.96%) was positive and significant at $p < 0.05$, indicating very limited diurnal consistency in ACI Low values (Figure 5). Thus, only 2 substation clusters were evident.

*Low–frequency band cluster 1*: Isolated positive significant coherence. Substation MEL—3 was the only site to exhibit a positive significant intraday correlation (Supplemental Table S9): 11 September 2022 and 24 September 2022 ($\rho = 0.773$, $p = 0.0318$). Interestingly, when relating 11 September 20221 vs. 4 November 2022 there was a significant correlation but in the opposite direction ($\rho = -0.745$, $p = 0.0423$, Supplemental Table

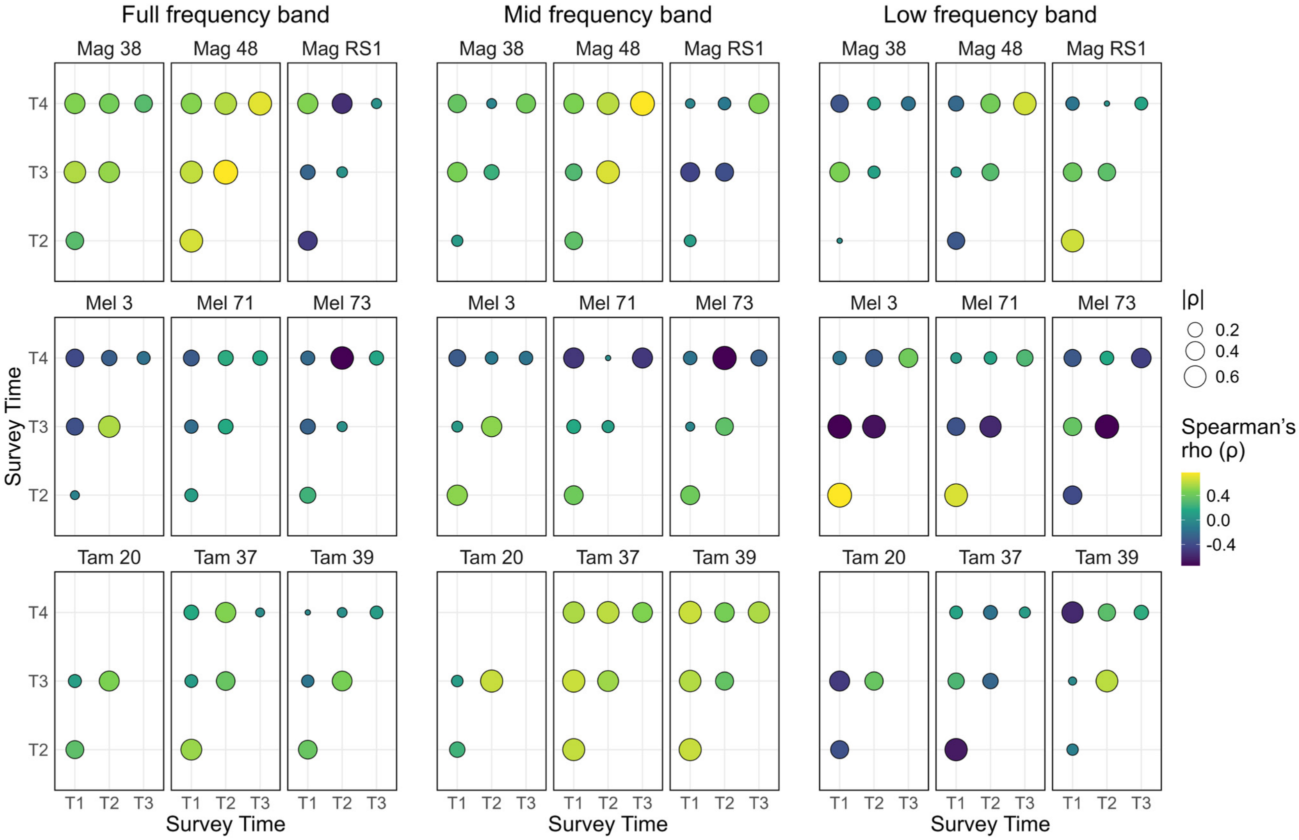

***Figure 7:*** *Pairwise Spearman's rank correlations (ρ) of Acoustic Complexity Index (ACI) between survey times for each of the 9 study substations, separated by frequency bands (Full, Mid, and Low). Each subplot represents one substation within a frequency band. Axes show pairwise comparisons between Survey Times (T1 –T4). Circle color indicates the direction and strength of correlation. Green—positive correlation; Purple—negative correlation. Circle size indicates the magnitude of correlation (|ρ|), with larger circles reflecting stronger associations.*

S9), suggesting a possible shift in acoustic activity through the daylight hours. Additionally, MEL—73 showed a marginally significant negative correlation between 24 September 2022 and 4 November 2022 (ρ = –0.745, p = 0.0507, (Supplemental Table S9), which may reflect irregular fluctuations rather than a consistent diurnal trend.

*Low—frequency band cluster 2*: The remaining substations showed mostly weak or non—significant correlations, and in many cases, correlations were close to zero or negative. These results suggest that ACI in the low frequency band did not exhibit strong or predictable diurnal patterns across reef sites or survey times.

### Methodological Constraints

It is important to note that several pairwise correlations showed relatively high correlation coefficients but did not reach statistical significance after correcting for multiple comparisons. This pattern likely reflects the limited sample size and the strict correction methods applied to reduced statistical errors. Consequently, significant relationships may have been masked, despite their apparent strength (i.e., relatively high ρ). However, the fact that many substations showed weak, non—significant, or even negative correlations suggests that, beyond methodological constraints, there is an overall lack of a clear and consistent diurnal pattern in both SPL and ACI across sites and survey times. While methodological constraints such as limited sample size and multiple comparison corrections may have reduced statistical power, the overall pattern points to considerable variability or a lack of pronounced diurnal acoustic signals across the studied reefs.

### Relationship Between Coral Cover and Acoustic Indexes

The results of the correlation analyses indicate that SPL was not correlated with coral cover when considering the full bandwidth or low—frequency band. However, a weak negative

**TABLE 4**. *Results of the correlation analyses between coral cover and acoustic metrics (Sound Pressure Level (SPL) and Acoustic Complexity Index (ACI)) by frequency band. The r value represents the correlation coefficient, which measures the strength and direction of the linear relationship between the 2 variables. p < 0.05 indicates significance (in bold).*

| | Full | Mid | Low |
|---|---|---|---|
| SPL | r = -0.27<br>p = 0.69 | r = -0.38<br>p = 0.14 | r = 0.075<br>**p = 0.036** |
| ACI | r = 0.57<br>**p < 0.001** | r = 0.57<br>**p < 0.001** | r = 0.36<br>**p = 0.048** |

correlation was found when considering frequencies between 2000 and 7000 Hz (mid—range frequency band; Table 4). The ACI was positively correlated with coral cover across the 3 band frequencies considered, but in the case of the low frequency, the relationship was weak and barely significant (Table 4).

## Discussion

Outplanting nursery—reared coral colonies into deteriorated coral reefs is widely recognized as a potential tool for facilitating ecological recovery (Bowden—Kerby 2001, Hernández—Delgado et al. 2014). In this context, various metrics have been employed to evaluate the success of restoration initiatives, with post—restoration changes in biodiversity being a potential indicator (Calle—Triviño et al. 2020, Goergen et al. 2020). Given the integral role of biophony in the ecological functions of coral reef habitats, assessing spatiotemporal variations in soundscape dynamics could complement traditional visual surveys and video censuses to evaluate the efficacy of restoration actions in enhancing reef biodiversity. However, before it is widely adopted as a reliable monitoring tool, it is imperative to recognize the strengths and weaknesses of passive acoustic monitoring. Indeed, there is ongoing debate regarding the efficacy of the distinct acoustics parameters to accurately reflect reef biodiversity (Nedelec et al. 2015, Carriço et al. 2020, Dimoff et al. 2021, Raick et al. 2023).

We used the Acoustic Complexity Index (ACI) and Sound Pressure Level (SPL) not to validate acoustical signals against *in-situ* biodiversity observations, but rather to determine whether reef soundscapes exhibited notable diurnal patterns across different locations (i.e., reefs and reef—substations) as previously found in Florida and Australia (Locascio and Mann 2008, McWilliams et al. 2017). If the soundscape shows consistent diurnal biophony patterns, acoustic monitoring on restored coral can be more effective. Fieldwork, for instance, can be scheduled for those times of day that show the highest acoustic diversity. In this context, our GLMM results indicate that “Hour” does not exert a statistically significant effect on ACI or SPL when modeled across all substations and survey periods as a random factor. However, this should not be interpreted as evidence of a lack of diurnal variability. Instead, the absence of a fixed effect suggests that diurnal acoustic patterns are not consistent, they vary idiosyncratically depending on substations and survey period. This interpretation is strongly supported by visual inspection of raw acoustic data, which reveals that peaks in acoustic activity shift across the daylight hours of the day and differ markedly between reefs, substations, and sampling dates and by the correlation analyses which statistically highlighted that diurnal acoustic periodicity were mostly absent. It is possible that diurnal patterns may exist, but they may not be predictable or uniform. Thus, limiting acoustic sampling to a single time risks missing important ecological patterns and may reduce the reliability of ACI and SPL as indicators of reef biodiversity.

The lack of consistent patterns in the timing of ACI peaks contrasts with the observations of Bertucci et al. (2016) in Moorea, French Polynesia and Pieretti et al. (2017) in the Adriatic Sea, who reported higher ACI values either during the day or night in coral reef ecosystems. It is important to note that in these studies, the authors grouped hours into day or night, potentially obscuring diurnal variability. An alternative explanation lies in the categorization of sound frequencies. Pieretti et al. (2017) classified frequencies below 250 Hz as low—frequency sounds and those from 620–3500 Hz as high—frequency sounds. In contrast, our study defined the low—frequency band from 20–1000 Hz and the mid—range—frequency band from 2000–7000 Hz, in alignment with Nedelec et al. (2015) and Lamont et al. (2022). The broader frequency range defined for the low—frequency band in our study may have captured sounds produced by snapping shrimp and other benthic invertebrates. Previous studies have shown that snapping shrimp produce sounds across a wide frequency range, typically from 2000–20,000 Hz (Pieretti et al. 2017, Lillis and Mooney 2018), and that their acoustic activity can vary significantly over hour—long intervals (Pieretti et al. 2017). This temporal variability may have contributed to the patterns observed in our results. The discrepancy in the resulting acoustic patterns when employing distinct frequencies underscores the necessity of standardizing the frequency bands when employing ACI to describe underwater soundscapes (Carriço et al. 2020, Dimoff et al. 2021). Indeed, several authors have recommended caution when using ACI to characterize the acoustic environment of coral reefs due to many discrepancies in the daily periodicity (Bohnenstiehl et al. 2018, Bolgan et al. 2018, Carriço et al. 2020, Dimoff et al. 2021).

Compared to more dynamic indices like ACI, SPL has been regarded as a more stable and site—specific metric in coral reef bioacoustics, with values that tend to reflect persistent environmental features such as reef structure or fish biomass. This perceived consistency has led some researchers to recommend SPL as a preferred tool for assessing reef soundscapes (Bertucci et al. 2016, Kaplan et al. 2018). However, our findings caution against overreliance on this recommendation. Like ACI, SPL values also varied considerably throughout daylight hours, especially in the mid—range and low frequencies, generally lacking regularity in their occurrence throughout daily intervals. The SPL values also varied among coral reefs and across substation within coral reef, which agrees with the results of La Manna et al. (2021) in a study during July 2020, at Capo Caccia—Isola Piana Marine Protected Area (Italy, Western Mediterranean Sea). These findings suggest that while SPL can be useful for describing broad acoustic trends, it may not consistently reflect short—term biological dynamics and should be interpreted alongside complementary indices such as ACI to fully characterize reef soundscapes.

Since SPL provides a general assessment of soundscape amplitude (i.e., loudness), it may be more influenced by constant biological factors (e.g., fish abundance, Kaplan et al. 2018, Carriço et al. 2020). Indeed, studies have shown that SPL is positively correlated with the abundance of soniferous fish and snapping shrimp (Kaplan et al. 2018). If this were true for our study locations (i.e., substations), one would anticipate higher SPLs at substations with greater fish abundance. Interestingly, our results did not meet this expectation. For instance, fish abundance, biomass, and diversity are significantly higher at TAM—20 compared to TAM—35 and TAM—39 (Hernández—Delgado et al. 2025). The same is true when comparing MAG—48, with higher fish diversity than MAG—38 (Hernández—Delgado et al. 2025). Given that recordings within substations at each reef location were conducted simultaneously and under comparable environmental conditions (e.g., reef structure, depth, and benthic composition), these discrepancies likely reflect the limitations of SPL as a proxy for biological richness.

The SPL captures overall sound intensity but does not differentiate between sound sources or account for the acoustic behavior of specific taxa, which may vary independently of abundance, diversity, or biomass. Nonetheless, we acknowledge that behavioral rhythms, such as feeding aggregations, can vary even within short spatiotemporal scales and may not be fully captured by our sampling approach. Thus, it remains unclear why reef substations with higher fish diversity, abundance, and biomass did not consistently exhibit a higher SPL. A plausible explanation may lie in the assertion by Carriço et al. (2020) that SPL may not be a reliable metric when fish abundance is low. However, determining what constitutes low or high fish abundance within the context of reef biophony remains an open question, warranting further investigation.

The findings that biophony (i.e., low—frequency band) presents distinct diurnal patterns within sites (i.e., intra—site sampling substations) on the same sampling date underscore the complexity and variability inherent in coral reef acoustics. While such small—scale spatial variability could suggest the presence of localized acoustic or biodiversity “hotspots,” our findings do not support this as a consistent pattern. Higher ACI and SPL values were not repeatedly associated with any single substation; instead, peak values shifted across substation and sampling dates. This suggests that, rather than being driven by stable substation—level biological variables such as coral cover, or physical characteristics such as depth and reef topography, the acoustic environment may be more strongly influenced by transient local factors, such as the temporary presence of vocalizing species or day (and site)—specific hydrodynamic conditions. For instance, wave—induced water movement has the capability to modify fish trajectory across the seascape (Webb et al. 2010). In this context, it is reasonable to consider each substation as acoustically independent.

Given that substations can be considered acoustically independent, accounting for fine—scale spatial variability is critical to improving reef soundscape assessments. This highlights the importance of increasing spatial resolution in acoustic monitoring and designing studies that account for fine—scale ecological variability. Specifically, increasing the number of hydrophones within a site is essential for better describing the site—specific dynamics of coral reef soundscapes. Determining the appropriate number and spatial arrangement of hydrophones to accurately characterize reef soundscapes, however, remains a major challenge in the field. This difficulty stems from the inherent spatial heterogeneity of reef habitats and the variability of biological sound sources, which makes a universal solution unlikely. By emphasizing the importance of spatial resolution, our study contributes to ongoing efforts to refine acoustic monitoring methodologies and supports the development of standardized, high—resolution frameworks for reef soundscape assessments.

Reefs with high coral cover promote biodiversity through complex framework structures that reduce competitive interactions and predation risk (Almany 2004, Grabowski 2004). Accordingly, it could be expected that, when compared to coral—depleted reef zones, reef areas with a high percentage of coral cover would show higher ACI and SPL. Such a contention is supported by various authors who have found a relationship between these acoustic metrics and coral cover (Kaplan et al. 2015, Bertucci et al., 2016, 2020). However, the relationship between coral cover and soundscapes remains far from being solved. Kaplan et al. (2018) found that mid—range—frequency SPL, but not low—frequency SPL, could be related to coral cover. Our results contribute to the ongoing uncertainty surrounding the relationship between coral cover and soundscape metrics. For instance, we did find a significant correlation between the mid—range SPL and coral cover, but such a relationship was weak and in the opposite direction (i.e., negative). One possible explanation for the unexpected mid—frequency pattern is the contribution of snapping shrimp, which are known to produce prominent mid—frequency sounds and are often associated with non—coral benthic organisms such as sponges (Ríos and Duffy 2007, Butler et al. 2017). While we recognize this possibility, sponges comprised only a small fraction of the benthic assemblage at our study sites. Therefore, we consider it unlikely that sponge—related shrimp activity played a dominant role in shaping the observed acoustic patterns. In contrast, and consistent with Kaplan et al. (2018), no relationship between coral cover and SPL in the low and full—frequency bands was found.

In the case of ACI, this study identified a positive and significant correlation with coral cover in the full, mid—range, and low ranges, although in the latter frequency the relationship was weak and marginally significant. These results diverge from those of Bertucci et al. (2016), who did not find a relationship between the ACI and coral cover in 8 coral reefs on Moorea Island, South Pacific. These contrasting results raise questions regarding the applicability of ACI and SPL as metrics of the overall health (i.e., coral cover and biodiversity) of shallow—water coral reef ecosystems as previously argued by Raick et al. (2023). An important aspect to consider when comparing these results with previous studies is the coral cover range. Culebra’s coral reefs are categorized as “poor” since coral cover does not exceed 10%, whereas in other studies, coral cover was as high as > 80% (Kaplan et al. 2018, Lamont et al. 2022). Notably, previous studies have shown, in disagreement with our findings, that acoustic metrics (e.g., ACI and SPL) exhibit less variability in reefs with low coral cover (< 15%) compared to those with a high percentage of coral cover (Elise et al. 2019). This disparity between coral soundscape research underscores the importance of considering specific coral cover ranges when interpreting acoustic metrics in the context of coral reef health assessments. It also cautions against directly extrapolating soundscape patterns from high—cover Pacific reefs to degraded Caribbean sites. Instead, interpreting acoustic data must be grounded in the local ecological context, particularly coral cover, to ensure accurate assessments of reef condition.

We acknowledge several important limitations that should be considered when interpreting our findings. First, acoustic data were collected only during daylight hours. As a result, our recordings do not capture crepuscular (dawn and dusk) or nocturnal acoustic activity, periods during which many reef organisms are most vocally active (Nedelec et al. 2015, Ferguson et al. 2022, Lillis et al. 2023). This limitation has likely led to the underrepresentation of certain species and behaviors in our dataset. However, our focus on daylight hours still provides valuable insights into the bioacoustics dynamics of restored coral reefs. Diurnal acoustic activity, though often overlooked in bioacoustic studies, reflects important ecological processes such as herbivory, invertebrate foraging, predator—prey interactions, competition, reproductive dynamics, and changes in animal behavior due to human disturbances (e.g., boat traffic) (Remage—Healey et al. 2006, Kennedy et al. 2010). These daytime activities contribute meaningfully to reef soundscapes and may exhibit distinct spatiotemporal signatures that need to be described to fully comprehend site—specific soundscape dynamics.

Second, each site was sampled on a single day per sampling time, as we were unable to conduct consecutive—day recordings. This limited our ability to account for short—term (between days) temporal variability. We also acknowledge that averaging acoustic metrics over several consecutive days would likely reduce the influence of between days variability and provide a more robust characterization of each site's soundscape. The way we collected our data, however, is consistent with several previously published studies in reef bioacoustics. For example, Pieretti et al. (2017) recorded only twice, with an 8—week interval between deployments; Bertucci et al. (2016) sampled 3 times between March and June 2015 at different locations, with 3—week intervals; and Kaplan et al. (2015) conducted 2 sampling events separated by 3 months. These examples demonstrate that monthly sampling remains a common practice in the field, especially in studies constrained by logistical or environmental challenges. Therefore, although limited, our approach aligns with established methodologies in the literature.

We fully recognize that long—term and higher—frequency acoustic monitoring efforts are essential for capturing temporal variability more comprehensively and improving our understanding of reef soundscape dynamics over time. While the limitations of our study may have contributed to the variability observed, we believe that the absence of nocturnal data or multi—day sampling does not undermine our main conclusion: bioacoustic signals (ACI and SPL) recorded during daylight hours exhibit considerably variations within sites (i.e., substations), across sites (i.e., coral reefs), and sampling days. First, our primary objective was not to characterize complete diel biodiversity patterns or to validate acoustical signals against *in—situ* biodiversity observations, but rather to evaluate whether soundscapes exhibit consistent diurnal patterns during daylight hours. Identifying predictable periods of elevated acoustic activity or complexity during daylight could inform the design of cost—effective monitoring strategies, particularly in situations where continuous or overnight recordings are not feasible, a limitation commonly faced by scientists working in underfunded regions. In this context, focusing on daylight hours may offer a practical and ecologically meaningful approach to reef monitoring and habitat assessment. Second, even if acoustic patterns were more consistent at night or across consecutive days, the observed daytime fluctuations alone raise concerns about the reliability of these metrics as standalone indicators of reef condition or biodiversity. The variability highlights the need for cautious interpretation and supports the use of bioacoustic metrics in combination with other ecological monitoring tools.

## CONCLUSIONS

The ecological restoration of degraded coral reefs, that is, coral outplanting, requires significant human and financial resources. Therefore, determining the potential success of coral restoration projects to promote coral reef recovery is crucial for securing continuous financial support. Various monitoring—based metrics have been developed for this purpose, including coral outplant demographic performance (Mercado—Molina et al. 2015), coral recruitment rates (Montoya—Maya et al. 2016, Mercado—Molina and Suleimán—Ramos 2023), and changes in fish biodiversity (Calle—Triviño et al. 2020, Goergen et al. 2020). However, monitoring itself is resource intensive. Passive acoustic monitoring using underwater hydrophones has been suggested as a potentially cost—effective tool; however, its utility remains debatable. Our results indicate that patterns of ACI and SPL values can vary considerably throughout the day, among sites, within sites, and across sampling dates at the same site. This variability led us to align with previous studies that cautioned against its sole use for monitoring coral reef health. Instead, ACI and SPL can serve as complementary tools alongside visual and video census methods.

Our results and conclusion may be challenged by the argument that the spatiotemporal variability we documented in ACI and SPL is to be expected, given the inherent ecological complexity of coral reef systems. However, our study was guided by the expectation that reef—associated soniferous organisms typically exhibit regular and predictable diel acoustic behaviors, as supported by previous work (e.g., Staaterman et al. 2017, Kaplan et al. 2018). In fact, this expectation is foundational to the use of passive acoustic monitoring: if acoustic activity were inherently erratic and unpredictable across time and space, the ecological utility of soundscape metrics such as ACI and SPL would be fundamentally undermined. That we observed inconsistent diurnal patterns within reefs, as well as across reefs and months calls into question the general stability of these metrics, particularly in degraded or actively restored habitats.

We, however, recognized that coral reef bioacoustics is still a relatively young field and that we are in a steep learning phase regarding the proper application and interpretation of the proposed indexes. Continued research is essential to better understand how ACI, SPL, and other indices can reliably reflect reef biodiversity across temporal and spatial scales. For instance, identifying reef fish sounds as types or per species and related phonic richness to variations in AIC and SPL are vital. In this context, emerging AI—based tools that enable species—level detection and classification of reef—associated sounds offer a promising complement to existing indices. Although still in early development, such technologies could significantly improve the ecological resolution of acoustic monitoring in coral reefs. In the case of SPL, it is important to note that our analysis focused on the root—mean—square (RMS), computed by the PAM—Guide algorithm, which is a metric that represents an average over multiple short time windows within the recording period. This averaging process, while useful for summarizing overall sound levels, may mask important short—term acoustic variability. Such variability often reflects ecologically meaningful phenomena, including transient biological sounds (e.g., fish calls, snapping shrimp bursts) and anthropogenic noise events, which could provide insights into reef health, biodiversity, or organism behavior. Future studies would benefit from incorporating additional acoustic metrics that capture variability (i.e., standard deviation, coefficient of variation, or SPL percentiles) to better resolve these finer—scale temporal dynamics. Incorporating these measures may improve the detection of ecological patterns that mean SPL alone cannot fully reveal.

We also acknowledge that future research should explicitly examine the environmental and ecological drivers of spatio-temporal variability in reef soundscapes to refine the utility of bioacoustics as a monitoring tool. Geophonic sources such as tidal movements, wave action, and sea state can substantially influence soundscape metrics, particularly in shallow reef systems. Thus, variation in SPL and ACI across sampling periods may also reflect changes in these physical drivers. Future monitoring programs should therefore incorporate concurrent measurements of tidal conditions, current direction, and weather to better disentangle biological from geophysical contributions to reef soundscapes.

In addition to physical drivers such as tides and sea state, biological rhythms also contribute to temporal variability in reef soundscapes. Seasonal changes in fish and invertebrate behavior can influence acoustic activity, as many species exhibit distinct reproductive, foraging, or territorial patterns that vary across months, even in tropical systems. We acknowledge that shifts in community behavior across seasons likely contribute to the observed acoustic variability. Incorporating known behavioral cycles of key sound—producing taxa into future analyses would improve interpretation of acoustic indices and enhance the ecological resolution of long—term monitoring programs.

While our understanding of the utility of bioacoustics for monitoring reef health continues to evolve, we recommend caution in interpreting metrics such as ACI and SPL. In cases where the ACI and SPL are chosen, we recommend deploying multiple hydrophones within the same reef and conducting repeated deployments. As the methodology becomes standardized, we recognize that PAM can evolve into a valuable tool for monitoring coral reefs. This study aims to contribute to these ongoing efforts.

## ACKNOWLEDGMENTS

This project was partially funded by the National Fish & Wildlife Foundation Award #66113, National Oceanographic and Atmospheric Administration Award #NA20NMF4630303, and the US Department of Education Award #P120A200019. The study was performed under the Research Protocol Number UAGM: R03—010—23 and under the permit # 0—VS—PVS15—SJ—01188—1203—2021 granted by the Puerto Rico Department of Natural and Environmental Resources to Sociedad Ambiente Marino (SAM). SAM provided logistical and fieldwork support. We thank I. Calderon for her invaluable assistance in collecting field data and editing the manuscript. Thanks to R. Martínez and L. Fernández for their help in data processing, analysis, and visualization. Our special appreciation to S. Alvarado—Soto and M. Velázquez—Rivera for their unconditional support. This article is based in part on the J. Velazquez—Alvarado M.Sc. thesis titled "**Characterization of Coral Reefs Soundscape in Culebra, Puerto Rico**", submitted to the Ana G. Méndez University and available through ProQuest. We would like to sincerely thank the 3 reviewers and the editors of the Gulf and Caribbean Research for their thoughtful and constructive feedback. Your comments and suggestions greatly contributed to improving the clarity, rigor, and overall quality of the manuscript. We truly appreciate the time and care you dedicated to reviewing our work, and we are confident that the published version reflects these valuable contributions. During the preparation of this work, the authors used ChatGPT, EndNote, and Grammarly to assist with grammar checks, sentence structure, and synonym selection. After using these tools, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

## LITERATURE CITED

Almany, G.R. 2004. Does increased habitat complexity reduce predation and competition in coral reef fish assemblages? Oikos 106:275–284. https://doi.org/10.1111/j.0030—1299.2004.13193.x

Bertucci, F., A.S. Guerra, V. Sturny, E. Blin, G.T. Sang, and D. Lecchini. 2020. A preliminary acoustic evaluation of three sites in the lagoon of Bora Bora, French Polynesia. Environmental Biology of Fishes 103:891–902. https://doi.org/10.1007/s10641—021—01179—4

Bertucci, F., E. Parmentier, G. Lecellier, A.D. Hawkins, and D. Lecchini. 2016. Acoustic indices provide information on the status of coral reefs: An example from Moorea Island in the South Pacific. Scientific Reports 6:33326. https://doi.org/10.1038/srep33326

Bohnenstiehl, D.R., R.P. Lyon, O.N. Caretti, S.W. Ricci, and D.B. Eggleston. 2018. Investigating the utility of ecoacoustic metrics in marine soundscapes. Journal of Ecoacoustics 2:1156. https://doi.org/10.22261/JEA.R1156

Bolgan, M., M.C.P. Amorim, P.J. Fonseca, L. Di Iorio, and E. Parmentier. 2018. Acoustic complexity of vocal fish communities: A field and controlled validation. Scientific Reports 8:10559. https://doi.org/10.1038/s41598–018–28771–6

Bolker, B.M. 2015. Linear and generalized linear mixed models. In: G.A. Fox, S. Negrete–Yankelevich, and V.J. Sosa, eds. *Ecological Statistics: Contemporary Theory and Application.* Oxford University Press, Oxford, UK, p. 309–333. https://doi.org/10.1093/acprof:oso/9780199672547.003.0014

Bolker, B.M., M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H.H. Stevens, and J.S.S. White 2009. Generalized linear mixed models: A practical guide for ecology and evolution. Trends in Ecology and Evolution 24:127–135. https://doi.org/10.1016/j.tree.2008.10.008

Brooks, M.E., K. Kristensen, K.J. Van Benthem, A. Magnusson, C.W. Berg, A. Nielsen, H.J. Skaug, M. Mächler, and B.M. Bolker. 2017. glmmTMB balances speed and flexibility among packages for zero–inflated generalized linear mixed modeling. The RJournal 9:378–400. https://doi.org/10.32614/RJ–2017–066

Brooks, M, B. Bolker, K. Kristensen, M. Maechler, A. Magnusson, H. Skaug, A. Nielsen, C. Berg, and. van Bentham. 2025. Package 'glmmtmb'. R Package Version 0.2. 0, 25. https://doi.org/10.32614/CRAN.package.glmmTMB

Bowden–Kerby, A. 2001. Low–tech coral reef restoration methods modeled after natural fragmentation processes. Bulletin of Marine Science 69:915–931.

Browning, E., R. Gibb, P. Glover–Kapfer, and K.E. Jones. 2017. Passive acoustic monitoring in ecology and conservation. WWF Conservation Technology Series 1:1–75. https://doi.org/10.25607/OBP–876

Butler, J., J. Stanley, and M. Butler. 2016. Underwater soundscapes in near–shore tropical habitats and the effects of environmental degradation and habitat restoration. Journal of Experimental Marine Biology and Ecology 479:89–96. https://doi.org/10.1016/j.jembe.2016.03.006.

Calle–Triviño, J., R. Rivera–Madrid, M.G. León–Pech, C. Cortés–Useche, R.I. Sellares–Blasco, M. Aguilar–Espinosa, and J.E. Arias–González. 2020. Assessing and genotyping threatened staghorn coral *Acropora cervicornis* nurseries during restoration in southeast Dominican Republic. PeerJ 2020(4):8863. https://doi.org/10.7717/peerj.8863

Carriço, R., M.A. Silva, M. Vieira, P. Afonso, G.M. Menezes, P.J. Fonseca, and M.C.P. Amorim. 2020. The use of soundscapes to monitor fish communities: Meaningful graphical representations differ with acoustic environment. Acoustics 2:382–398. https://doi.org/10.3390/acoustics2020022

Dimoff, S.A., W.D. Halliday, M.K. Pine, K.L. Tietjen, F. Juanes, and J.K. Baum. 2021. The utility of different acoustic indicators to describe biological sounds of a coral reef soundscape. Ecological Indicators 124:107435. https://doi.org/10.1016/j.ecolind.2021.107435

Duarte, C.M., L. Chapuis, S.P. Collin, D.P. Costa, R.P. Devassy, V.M. Eguiluz, C. Erbe, T.A.C. Gordon, T.A.C., B.S. Halpern, H.R. Harding, M.N. Havlik, M. Meekan, N.D. Merchant, J.L. Miksis–Olds, M. Parsons, M. Predragovic, A.N. Radford, C.A. Radford, S.D. Simpson, H. Slabbekoorn, E. Staaterman, I.C. Van Opzeeland, J. Windern, X. Zhang, and F. Juanes. 2021. The soundscape of the Anthropocene ocean. Science 371:6529. https://doi.org/10.1126/science.aba4658

Eddy, T.D., V.W.Y. Lam, G. Reygondeau, A.M. Cisneros–Montemayor, K. Greer, M.L.D. Palomares, J.F. Bruno, Y. Ota, and W.W.L. Cheung. 2021. Global decline in capacity of coral reefs to provide ecosystem services. One Earth 4:1278–1285. https//doi.org/10.1016/j.oneear.2021.08.016

Elise, S., I. Urbina–Barreto, R. Pinel, V. Mahamadaly, S. Bureau, L. Penin, M. Adjeroud, M. Kulbicki, and J.H. Bruggemann. 2019. Assessing key ecosystem functions through soundscapes: A new perspective from coral reefs. Ecological Indicators 107:105623. https://doi.org/10.1016/j.ecolind.2019.105623

Ferguson, S.R., F.H. Jensen, M.D. Hyer, A. Noble, A. Apprill, and T.A. Mooney. 2022. Ground–truthing daily and lunar patterns of coral reef fish call rates on a US Virgin Island reef. Aquatic Biology 31:77–87. https://doi.org/10.3354/ab00755

Ferrier–Pagès, C., M.C. Leal, R. Calado, D.W. Schmid, F. Bertucci, D. Lecchini, and D. Allemand. 2021. Noise pollution on coral reefs? – A yet underestimated threat to coral reef communities. Marine Pollution Bulletin 165:112129. https://doi.org/10.1016/j.marpolbul.2021.112129

Freeman, L.A. and S.E. Freeman. 2016. Rapidly obtained ecosystem indicators from coral reef soundscapes. Marine Ecology Progress Series 561:69–82. https:// doi: 10.3354/meps11938

Goergen, E.A., S. Schopmeyer, A.L. Moulding, A. Moura, P. Kramer, and T.S. Viehman. 2020. Coral reef restoration monitoring guide: Methods to evaluate restoration success from local to ecosystem scales. NOAA Technical Memorandum Contract No.: NOS NCCOS 279. National Ocean Service, National Centers for Coastal Ocean Science, Washington, D.C., USA, 1–158 p. https://doi.org/10.25923/xndz–h538

Grabowski, J.H. 2004. Habitat complexity disrupts predator–prey interactions but not the trophic cascade on oyster reefs. Ecology 85:995–1004. https://doi.org/10.1890/03–0067

Hernández–Delgado, E.A., A.E. Mercado–Molina, P.J. Alejandro–Camis, F. Candelas–Sánchez, J.S. Fonseca–Miranda, C.M. González–Ramos, R. Guzmán–Rodríguez, P. Mège, A.A. Montañez–Acuña, I.O. Maldonado, A. Otaño–Cruz, and S.E. Suleimán–Ramos. 2014. Community–based coral reef rehabilitation in a changing climate: Lessons learned from hurricanes, extreme rainfall, and changing land use impacts. Open Journal of Ecology 4:918–944. https://doi.org/10.4236/oje.2014.414077

Hernández–Delgado, E.A., J.S. Fonseca–Miranda, A.E. Mercado–Molina, and S.E. Suleimán–Ramos. 2025. Integrating 3D–printed and natural staghorn coral (A*cropora cervicornis*) restoration enhances fish assemblages and their ecological functions. Diversity 17:445. https://doi.org/10.3390/d17070445

Kaplan, M.B., M.O. Lammers, E. Zang, and T.A. Mooney. 2018. Acoustic and biological trends on coral reefs off Maui, Hawaii. Coral Reefs 37:121–133. https://doi.org/10.1007/s00338–017–1638–x

Kaplan, M B., T.A. Mooney, J. Partan, and A.R. Solow. 2015. Coral reef species assemblages are associated with ambient soundscapes. Marine Ecology Progress Series 533:93–107. https://doi.org/10.3354/meps11382

Kennedy, E.V., M.W. Holderied, J.NM. Mair, H.M. Guzman, and S.D. Simpson. 2010. Spatial patterns in reef–generated noise relate to habitats and communities: Evidence from a Panamanian case study. Journal of Experimental Marine Biology and Ecology 395:85–92. https://doi.org/10.1016/j.jembe.2010.08.017.

Kohler, K.E., and S.M. Gill. 2006. Coral point count with Excel extensions (CPCe): A Visual Basic program for the determination of coral and substrate coverage using random point count methodology. Computers & Geosciences 32:1259–1269. https://doi.org/10.1016/j.cageo.2005.11.009

La Manna, G., M. Picciulin, A. Crobu, F. Perretti, F. Ronchetti, M. Manghi, A. Ruiu, and G. Ceccherelli. 2021. Marine soundscape and fish biophony of a Mediterranean marine protected area. PeerJ 9:12551. https://doi.org/10.7717/peerj.12551

Lamont, T.A.C., B. Williams, L. Chapuis, M.E. Prasetya, M.J. Seraphim, H.R. Harding, E.B. May, N. Janetski, J. Jompa, D.J. Smith, A.N. Radford, and S.D. Simpson. 2022. The sound of recovery: Coral reef restoration success is detectable in the soundscape. Journal of Applied Ecology 59:742–756. https://doi.org/10.1111/1365–2664.14089

Lillis, A. and T.A. Mooney. 2018. Snapping shrimp sound production patterns on Caribbean coral reefs: Relationships with celestial cycles and environmental variables. Coral Reefs 37:597–607. https://doi.org/10.1007/s00338–018–1684–z

Lillis, A., A. Apprill, M. Armenteros, and T.A. Mooney. 2023. Small–scale variation in the soundscapes of coral reefs. In: A.N. Popper, J. Sisneros, A.D. Hawkins and F. Thomsen, eds. *The Effects of Noise on Aquatic Life: Principles and Practical Considerations*. Cham, Switzerland: Springer International Publishing, p. 1–15. https://doi.org/10.1007/978–3–031–10417–6_114–1

Lin, T.H., T. Akamatsu, F. Sinniger, and S. Harii. 2021. Exploring coral reef biodiversity via underwater soundscapes. Biological Conservation 253:108901. https://doi.org/10.1016/j.biocon.2020.108901

Lindseth, A.V. and P. Lobel. 2018. Underwater soundscape monitoring and fish bioacoustics: A review. Fishes 3:3030036. https://doi.org/10.3390/fishes3030036

Lobel, P.S. 1992. Sounds produced by spawning fishes. Environmental Biology of Fishes 33:351–358. https://doi.org/10.1007/BF00010947

Locascio, J.V. and D.A. Mann. 2008. Diel periodicity of fish sound production in Charlotte Harbor, Florida. Transactions of the American Fisheries Society 137:606–615. https://doi.org/10.1577/T06–069.1

Mazerolle, M.J. 2017. "Package 'AICcmodavg'." R package 281:1–220. https://doi.org/10.32614/CRAN.package.AICcmodavg

McWilliam, J.N., R.D. McCauley, C. Erbe, and M.J. Parsons. 2017. Patterns of biophonic periodicity on coral reefs in the Great Barrier Reef. Scientific Reports 7:17459. https://doi.org/10.1038/s41598–017–15838–z

Mercado–Molina, A.E., C.P. Ruiz–Diaz, M.E. Pérez, R. Rodríguez–Barreras, and A.M. Sabat. 2015. Demography of the threatened coral *Acropora cervicornis*: Implications for its management and conservation. Coral Reefs 34:1113–1124. https://doi.org/10.1007/s00338–015–1341–8

Mercado–Molina, A. E. and S.E. Suleimán–Ramos. 2023. Outplants of the threatened coral *Acropora cervicornis* promote coral recruitment in a shallow–water coral reef, Culebra, Puerto Rico. Sustainability 15(24):16548. https://doi.org/10.3390/su152416548

Merchant, N.D., K.M. Fristrup, M.P. Johnson, P.L. Tyack, M.J. Witt, P. Blondel, and S.E. Parks. 2015. Measuring acoustic habitats. Methods in Ecology and Evolution 6:257–265. https://doi.org/10.1111/2041–210X.12330

Mooney, T.A., L. Di Iorio, M. Lammers, T.H. Lin, S.L. Nedelec, M. Parsons, C. Radford, E. Urban, and J. Stanley. 2020. Listening forward: Approaching marine biodiversity assessments using acoustic methods.. Royal Society Open Science 7(8):201287. https://doi.org/10.1098/rsos.201287

Montoya–Maya, P.H., K.P. Smit, A.J. Burt, and S. Frias–Torres. 2016. Large–scale coral reef restoration could assist natural recovery in Seychelles, Indian Ocean. Nature Conservation 16:8604. https://doi.org/10.3897/natureconservation.16.8604

Nedelec, S.L., S.D. Simpson, M. Holderied, A.N. Radford, G. Lecellier, C. Radford, and D. Lecchini. 2015. Soundscapes and living communities in coral reefs: Temporal and spatial variation. Marine Ecology Progress Series 524:125–135. https://doi.org/10.3354/meps11175

Parks, S.E., J.L. Miksis–Olds, and S.L. Denes. 2014. Assessing marine ecosystem acoustic diversity across ocean basins. Ecological Informatics 21:81–88. https://doi.org/10.1016/j.ecoinf.2013.11.003

Piercy, J.J.B., E.A. Codling, A.J. Hill, D.J. Smith, D.J., and S.D. Simpson. 2014. Habitat quality affects sound production and likely distance of detection on coral reefs. Marine Ecology Progress Series 516:35–47. https://doi: 10.3354/meps10986

Pieretti, N. and R. Danovaro. 2020. Acoustic indexes for marine biodiversity trends and ecosystem health: Acoustic indexes in marine environments. Philosophical Transactions of the Royal Society B: Biological Sciences 375:1814. https://doi.org/10.1098/rstb.2019.0447

Pieretti, N., M. Lo Martire, A. Farina, and R. Danovaro. 2017. Marine soundscape as an additional biodiversity monitoring tool: A case study from the Adriatic Sea (Mediterranean Sea). Ecological Indicators 83:13–20. https://doi.org/10.1016/j.ecolind.2017.07.011

Popper, A.N., C. Amorim, M.L. Fine, D.M. Higgs, A.F. Mensinger, and J.A. Sisneros. 2024. Introduction to the special issue on fish bioacoustics: Hearing and sound communication. The Journal of the Acoustical Society of America 155:2385–2391. https://doi.org/10.1121/10.0025553

Radford, C.A. and J.A. Stanley. 2023. Sound detection and production mechanisms in aquatic decapod and stomatopod crustaceans. Journal of Experimental Biology 226(10):243537. https://doi.org/10.1242/jeb.243537

Radford, C.A., J.A. Stanley, S.D. Simpson, and A.G. Jeffs. 2011. Juvenile coral reef fish use sound to locate habitats. Coral Reefs 30:295–305. https://doi.org.10.1007/s00338–010–0710–6

Raick, X., L. Di Iorio, D. Lecchini, M. Bolgan, and E. Parmentier. 2023. To be, or not to be: Critical assessment of the use of α–acoustic diversity indices to evaluate the richness and abundance of coastal marine fish sounds. Journal of Ecoacoustics 7:7010001. https://doi.org/10.35995/jea7010001

Remage–Healey, L., D. Nowacek, and A. Bass. 2006. Dolphin foraging sounds suppress calling and elevate stress hormone levels in a prey species, the Gulf toadfish. The Journal of Experimental Biology 209:4444–51. https://doi.org/ 10.1242/jeb.02525

Ríos, R. and J.E. Duffy. 2007. A review of the sponge-dwelling snapping shrimp from Carrie Bow Cay, Belize, with description of Zuzalpheus, new genus, and six new species (Crustacea: Decapoda: Alpheidae). Zootaxa 1602(1):1602. https://doi.org/10.11646/zootaxa.1602.1.1

Santiago–Padua, P., J. Velázquez–Alvarado,A.D.M López–Pérez, J. Nevárez–Mélendez, L.E. Díaz–Druet, S.E. Suleimán–Ramos, and A. Mercado–Molina. 2023. Demographic and population response of the threatened coral *Acropora cervicornis* (Scleractinia, Acroporidae) to fireworm corallivory. Revista de Biología Tropical 71(S1):e54912. https://doi.org/10.15517/rev.biol.trop..v71iS1.54912

Schärer, M.T., M.I. Nemeth, T.J. Rowell, T. J., and R.S. Appeldoorn. 2014. Sounds associated with the reproductive behavior of the black grouper (*Mycteroperca bonaci*). Marine Biology 161:141–147. https://doi.org/10.1007/s00227–013–2324–3

Simpson, S.D., M.G. Meekan, A. Jeffs, J.C. Montgomery, and R.D. McCauley. 2008. Settlement–stage coral reef fish prefer the higher–frequency invertebrate–generated audible component of reef noise. Animal Behaviour 75:1861–1868. https://doi.org/10.1016/j.anbehav.2007.11.004

Simpson, S.D., A.N. Radford, S.L. Nedelec, M.C.O. Ferrari, D.P. Chivers, M.I. McCormick, and M.G. Meekan. 2016. Anthropogenic noise increases fish mortality by predation. Nature Communications 7:10544. https://doi.org/10.1038/ncomms10544

Staaterman, E., A.M. Rice, D.A. Mann, and C.B. Paris. 2013. Soundscapes from a tropical Eastern Pacific reef and a Caribbean Sea reef. Coral Reefs 32:553–557. https://doi.org/10.1007/s00338–012–1007–8

Staaterman, E., M.B. Ogburn, A.H. Altieri, S.J. Brandl, R. Whippo, J. Seemann, M. Goodison, and J.E. Duffy. 2017. Bioacoustic measurements complement visual biodiversity surveys: Preliminary evidence from four shallow marine habitats. Marine Ecology Progress Series 575:207–215. https://doi.org/10.3354/meps12188

Sueur, J., T. Aubi, and C. Simonis. 2008. Seewave, a free modular tool for sound analysis and synthesis. Bioacoustics–the International Journal of Animal Sound and Its Recording 18:213–226. https://doi.org/10.1080/09524622.2008.9753600

Tellechea, J.S., S. Izquierdo, W. Perez, and W. Norbis. 2022. Sound variation by hypertrophy and atrophy sonic muscle in the male southern black drum (*Pogonias courbina*). The Journal of the Acoustical Society of America 152:429–436. https://doi.org/10.1121/10.0012690

Tolimieri, N., O. Haine, J.C. Montgomery, and A. Jeffs. 2002. Ambient sound as a navigational cue for larval reef fish. Bioacoustics 12:214–217. https://doi.org/10.1080/09524622.2002.9753700

Tricas, T.C. and K.S. Boyle. 2014. Acoustic behaviors in Hawaiian coral reef fish communities. Marine Ecology Progress Series 511:1–16. https://doi.org/doi: 10.3354/meps10930

Tyack, P.L. 2008. Implications for marine mammals of large–scale changes in the marine acoustic environment. Journal of Mammalogy 89:549–558. https://doi.org/10.1644/07-MAMM-S-307R.1

Vermeij, M.J.A., K.L. Marhaver, C.M. Huijbers, I. Nagelkerken and S.D. Simpson. 2010. Coral larvae move toward reef sounds. PLoS ONE 5(5):e10660 https://doi.org/10.1371/journal.pone.0010660

Villanueva–Rivera, L.J. and B.C. Pijanowski. 2018. Soundecology: Soundscape ecology. R package version 1(3):3 https://CRAN.R–project.org/package=soundecology.

Williams, B., T.A.C. Lamont, L. Chapuis, H.R. Harding, E.B. May, M.E. Prasetya, M.J. Seraphim, J. Jompa, D.J. Smith, N. Janetski, A.N. Radford, and S.D. Simpson. 2022. Enhancing automated analysis of marine soundscapes using ecoacoustic indices and machine learning. Ecological Indicators 140:108986. https://doi.org/10.1016/j.ecolind.2022.108986

Webb, P.W., A. Cotel, L.A. Meadows, P. Domenici, and B.G. Kapoor. 2010. Waves and eddies: Effects on fish behavior and habitat distribution. In: P. Domenici and B.G. Kapoor, eds. *Fish locomotion: An Eco–Ethological Perspective*. Science Publishers, Enfield, NH, USA, p. 1–39. https://doi.org/10.1201/b10190