



Small-Scale Variation in the Soundscapes of Coral Reefs

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Contents

Introduction	2
Methods	3
Acoustic Analyses	5
Results	5
Horizontal Environment	5
Vertical Profiles	8
Spatial Variation in Motion Across a Reef: The Drifter	8
Discussion	11
References	13

Abstract

Coral reefs are complex habitats that emanate an array of sounds. These acoustic cues are integral to animal behaviors and are increasingly leveraged to discern ecological information. Reef soundscapes are often measured with an overarching view to characterize broad differences between reef sites. Further, there is a

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limited understanding of soundscape variation within particular reefs. Here, three acoustic recording methods (benthic recorders, vertical arrays, drifters) were used to address if and how soundscapes vary across coral reefs. Research took place at eight sites in the highly protected region of Jardines de la Reina, Cuba. Sound levels and frequency composition varied across small horizontal and vertical spatial scales. Horizontal differences were notable within reefs over meters, particularly when comparing recordings from adjacent dead and live massive coral. Vertically, sound levels and variation changed with distance from the benthos, with greater variation at lower frequencies. The drifter revealed sound levels that varied substantially relative to bottom type and nearby biota. Overall, the coral reef soundscape, like its biodiversity, was not uniform in distribution. Acoustic patterns varied substantially in ways that likely offer fine-scale acoustic cues to fishes and invertebrates. Moreover, this chapter highlights that small-scale spatial variation must be considered when implementing broad scale eco-acoustic monitoring of coral reef habitats.

Keywords

Acoustic environment · Acoustic ecology · Noise · Biodiversity · Bioacoustics · Recruitment · Cuba · Caribbean · Fish · Coral disease

Introduction

Marine animals move through a sea of chemical, visual, and acoustic cues as they select habitats, avoid predators, forage, and enact other vital behaviors. While some of these cues have long been studied, there is a growing understanding of the ecological importance of underwater acoustic cues and signals. Sounds can provide habitat and situational information to a diverse and increasingly realized number of animal taxa including many invertebrates, fish with and without auditory specializations, seabirds, and marine mammals (Buxton et al. 2017; Ellison et al. 2012; Fay 2009; Myrberg 1986). Soundscape data are increasingly being measured for the potential to discern broad-scale differences between habitats such as coral reefs of different quality or health, reefs of different coral cover, or reefs versus adjacent sandy and seagrass habitats (Kaplan et al. 2015; Radford et al. 2014). Yet most reef and coastal animals enact behaviors that likely require sensory information on smaller scales. For example, acoustic communication in fishes is generally considered to be limited to several body lengths or several meters (Coombs et al. 1992; Myrberg 1997; Zeddies et al. 2012). Coral and fish larvae must use vertical water column cues to address depth, vertical distance from a reef, and whether the reef is a proper location to settle (Leis and Carson-Ewart 1999; Leis 2004). Cues in the horizontal plane may offer information such as predator presence, distance of a predator, conspecific territoriality distance, and location of attractive mates (Hanlon and Budelmann 1987; Sweatman 1983). Temporally varying choruses may offer information regarding spawning, help induce physiological or behavioral responses,

coordinate activities, and provide cues to potential settlement locations (Kaplan and Mooney 2016; Mann and Grothues 2009; Parsons et al. 2016).

Despite these ecological benefits, there is limited information regarding the spatial or temporal variation of acoustic cues on smaller scales that likely more relevant to a particular animal. However, initial work suggests such variation exists. An acoustic hydrophone array deployed in the Northwest Hawaiian Islands found sound pressure directionality and hotspots of snapping shrimp sound levels (Freeman et al. 2015). Multiple recorders deployed on reefs in the US Virgin Islands showed small, but significant differences between sites within reefs (Kaplan et al. 2015). The biological relevance or importance of these differences was not considered. Surface drifting hydrophones have detected significant changes in soundscape characteristics across meters within a reefscape, related to benthic habitat structure differences (Lillis et al. 2018). Further, modeled water columns around reefs reflect what are likely distinct vertical gradients of sound, based on frequency and propagation conditions from the reef (Salas et al. 2022). Given this growing suggestive evidence, there is a need to collect empirical data addressing the prevalence of these acoustic hotspots (or cue spaces), and evaluations of their biological relevance.

The reefs of Jardines de la Reina (“Gardens of the Queen”) Cuba are an ideal environment to examine soundscapes. The reefs host some of the highest coral cover and fish abundance in the Caribbean (González-Díaz et al. 2018; Navarro-Martínez et al. 2022). This high habitat quality is a result of many factors including their inclusion within one of the largest Caribbean marine protected areas, their large distance from shore, and their strong enforcement of no-take fishing areas. The Jardines de la Reina (JR) reefs are therefore a unique place to study Caribbean reef sounds due to the abundant and diverse reef life as well as limited exposures to boat noise, which can alter animal behaviors (Simpson et al. 2016).

A 2017 cruise of opportunity to the shallow forereefs in the Jardines de la Reina system was used to address fundamental questions in reef soundscapes. Are there within-reef acoustic hotspots? Are there habitat-scale differences within a reef? How do soundscape cues vary in space and time on a reef? The effort sought to more generally address whether there are potential acoustically mediated differences within a reef that may be relevant for fundamental behaviors such as communication, predator detection, settlement, and within-reef habitat selection.

Methods

Work was conducted from small boat operations based off the *M/V Alucia* scientific vessel. The research cruise took place from November 4–20, 2017. Measurements were made exclusively within Jardines de la Reina National Park, Cuba (permitting noted below). Observations were made opportunistically during the expedition with the overall goal of surveying the reef system using multiple acoustic platforms and examining multiple reefs across multiple days. Long-term deployments in a single location were not possible due to the cruise schedule.

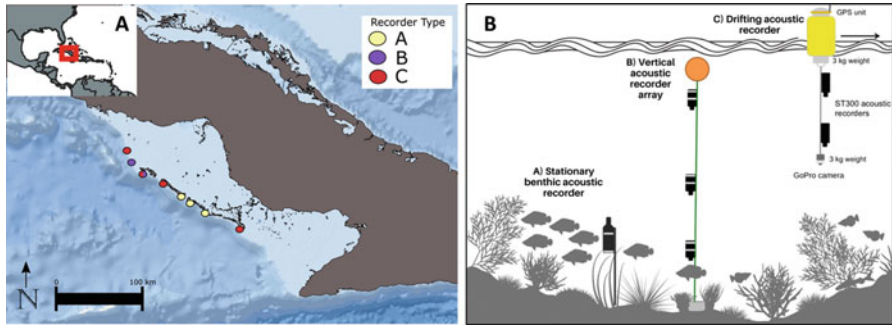


Fig. 1 (A) Map of the study sites off the south shore of Cuba. (B) Schematic depicting the three acoustic recorder configurations used to examine scales of soundscape variation on coral reefs

Passive acoustic work was conducted at eight reef sites across the archipelago (Fig. 1a). Data were collected using three complementary recorder configurations with the goal of investigating the small-scale soundscape variation within and above reef mosaics (Fig. 1b). Recorders utilized were either one-channel SoundTrap 300 s or 4-channel SoundTrap 4300 s [ST-300/4300; Ocean Instruments NZ (Ferguson et al. 2022)].

The first configuration consisted of stationary benthic recorders placed at multiple adjacent locations within a reef allowing for comparisons of simultaneous recordings across the horizontal plane of the reef, targeting small-scale differences (tens of meters) in habitat predicted to affect biological sound production (e.g., coral type, bathymetry, fish aggregation distribution). During the study, the set of recorders were able to be placed at three reef sites for 48–72-h periods, capturing 1-min recordings every 5 min.

Second, to examine small-scale depth variation in soundscapes above reef habitat we positioned acoustic recorders on a vertical array. The array was moored in one location and had a subsurface float and from that float, a surface buoy. The latter allowed the array to be sighted from the surface for retrieval while the subsurface float enabled the array to suspend vertically in the water column. On each vertical array, recorders were placed at 1, 5, and 10 m from the seafloor, and sites were selected where water depth was between 12 and 15 m. These systems were deployed at dusk for overnight recordings at 3 reef sites during the study period. Each deployment captured 3–12 h of continuous recording at 96 kHz.

The third recording configuration utilized a drifting hydrophone setup described previously (Lillis et al. 2018). Briefly, a GPS-outfitted surface buoy relayed location to a handheld GPS unit allowing the recording system to be deployed and left to drift on its own, facilitating later retrieval. Below the float was a line with a 3 kg weight at the bottom, and two acoustic recorders were attached vertically along the line. The recorders were located 1 and 2 m from the surface. A GoPro camera facing downwards recorded the benthic composition during the drift track. The drifter allowed for mobile recordings while minimizing the interfering noise of autonomous

vehicles. Surface current and wind direction were visually observed just before deployment to facilitate predicting a general drift direction. The drifter was then typically deployed “up reef” (windward side) and allowed to drift over the reef and observation area, and later retrieved via the GPS location. Drift trajectories, distance, and length depended on currents, wind, and conditions, and were typically 1–2 h in duration, and covered ~0.5–1 km distance. This sampling was conducted at 4 JR reefs, with 2–4 drifts achieved at each site.

Acoustic Analyses

Acoustic data were analyzed in MATLAB using custom-written code. The files were initially examined for potential transient or anthropogenic (e.g., boat, diver) noise and any such files were removed. Comparisons were then made using acoustic power spectra. Sound pressure levels (in rms – root-mean-squared) were calculated for low (0.1–2 kHz) and high (2–23 to 48 kHz) frequency bands which generally constitute the frequency ranges of fish and snapping shrimp sounds, respectively (Au and Banks 1998; Urick 1983). Where appropriate, the median and interquartile range of spectrum and sound pressure levels were calculated from the analysis of non-overlapping 1-s duration windows spanning the 1-min recordings, which could then be used for plotting and further statistical analysis where appropriate.

Results

Approximately 16,000 1-min audio files were successfully recorded between the different configurations applied across 8 reef sites in the Jardines de la Reina (Fig. 1) during the research cruise. Below are results describing findings that exemplify the types of small-scale soundscape variation observed using this dataset.

Horizontal Environment

At site JR10, a relatively high number of large, endangered pillar coral (*Dendrogyra cylindrus*) colonies were observed, of varying size and condition. As these large corals are known to create distinct three-dimensional structure and provide habitat hotspots for reef diversity, the distinct reef features were targeted for acoustic sampling and provide an ideal example for the examination of within-reef soundscape patterns related to coral type and health. Three SoundTrap 300 (ST-300) acoustic recorders were placed at *D. cylindrus* pillar coral towers, and three in nearby soft coral patches for a 72-h period. Recorders were all deployed within a small study area ~100 m × 20 m reef segment. The colonies denoted as DCYL 1 and 2 were live, but the DCYL 3 structure was dead coral skeleton with minimal living tissue (Fig. 2). The spectra of all three sites can roughly be divided into two

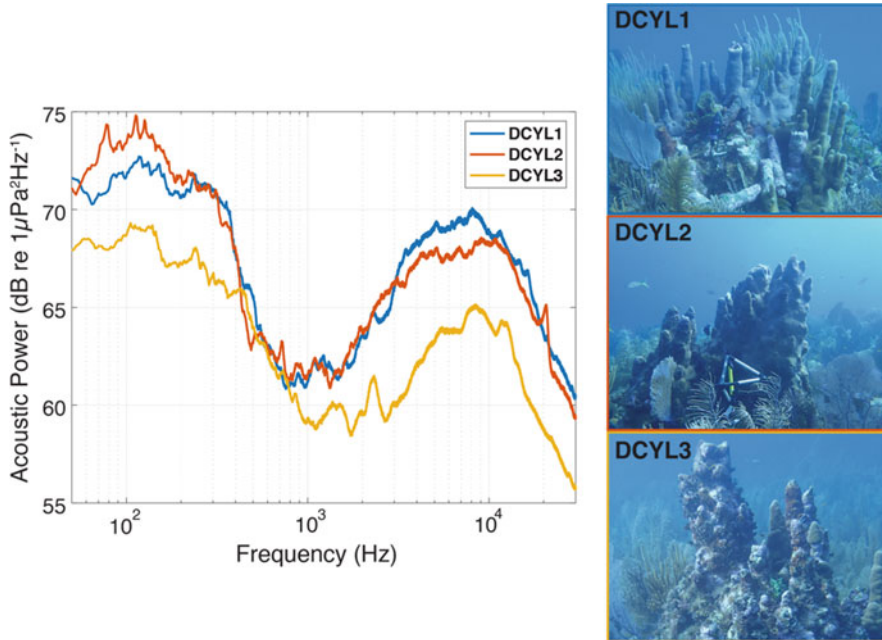


Fig. 2 Full band acoustic power at two healthy (DCYL1 and 2) and one dead (DCYL3) *Dendrogyra cylindrus* colonies. Note the overall lower sound levels at DCYL3 suggesting a diminished community of soniferous fish and invertebrates

components, below 1500 Hz and above 2000 Hz. Fish sounds are generally found in the former, low-frequency band, while snapping shrimp sounds are typically higher in frequency (>2000 Hz) (Kaplan et al. 2015). All three DCYL spectra showed peaks in the low and high frequency bands, near 100–200 Hz in the low frequency and 7–9 kHz in the high frequency. The sites differed in the amplitude of these peaks; DCYL 1 and 2 were similar in spectral characteristics, and while the spectral shape of DCYL 3 followed the same pattern, median power was ~ 4 –7 dB lower in both the low and high-frequency ranges compared to the healthy DCYLs (Figs. 2 and 3). In comparing the median SPLs by site for the two frequency bands, significant differences existed among nearly all recording sites (Fig. 3b; Kruskal-Wallis test: low frequency $\chi^2 = 977$, $p < 0.001$, high frequency $\chi^2 = 2414$, $p < 0.001$) underscoring the high small-scale inter-reef variability in soundscape. Low frequency sound levels were significantly lower at DCYL 3 compared to DCYL 1 and 2; however, it is important to note that one of the octocoral sites exhibited similar SPL levels to the healthy DCYL in the low frequency band (OCTO 2; Fig. 3b(i)).

Spectrograms demonstrate the influence of time of day on these within-reef soundscape patterns and highlight differences among the nearby recording sites (Fig. 3a). At lower frequencies (<2 kHz), diel rhythms were notable at all recording sites with a consistent peak in SPL just after sunset each night (Fig. 3a). DCYL 1 and

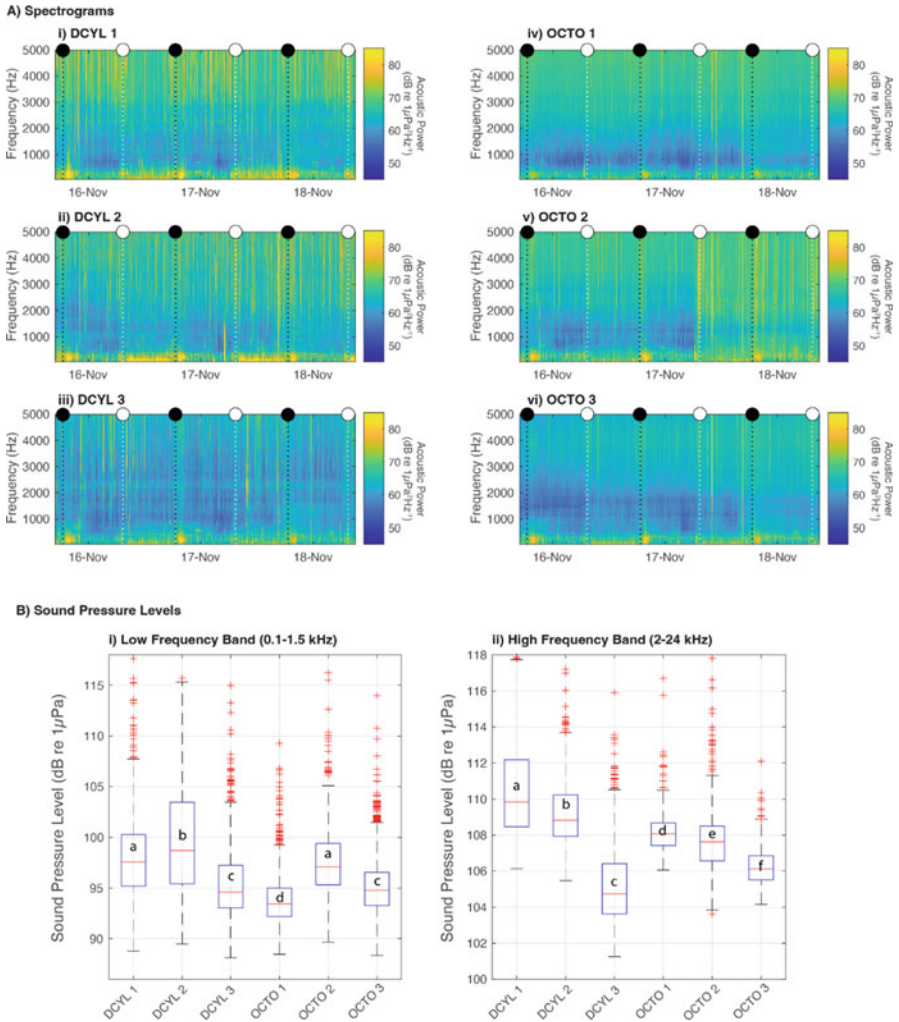


Fig. 3 (A) Spectrograms showing frequency specific patterns for recordings made adjacent to the endangered *Dendrogyra cylindrus* (i–iii) and octocorals (iv–vi). Black and white circles denote sunset and sunrise, respectively. (B) Boxplots depicting medians and interquartile ranges for (i) Low frequency (0.1–1.5 kHz) and (ii) High frequency (2–24 kHz) bandwidths. Letters signify statistically significant differences between sites, based on a non-parametric multiple comparison post-hoc test

2 showed stronger dusk increases in low frequency SPL and had more acoustic activity during daytime hours compared to DCYL 3 (Fig. 3a(i–iii)). The day-night low frequency difference is less evident at DCYL 3 and the OCTO sites. Subtle diel patterns were also observed in the snapping shrimp-driven high-frequency band, with modest increases in snapping at night observed across sites (Fig. 3).

Vertical Profiles

There was a clear vertical gradient of acoustic energy at sampled reefs (Figs. 4 and 5). At JR3, where 2-h continuous recordings were collected, sound pressure levels were greatest near the reef/benthos (10 m) and decreased when measured at 5 and 1 m from the sea surface (Fig. 4a, b). At 1 m depth, median SPL was ca. 6–7 dB lower, or about half the acoustic energy, than the bottom recorder. Variation was similarly lower at 1 m depth, compared to the deeper positions. However, these changes were not equally spread across frequencies. The benthic and mid-water positions showed greater, but variable, acoustic power in the low frequencies (Fig. 4).

For site JR3, at low frequencies (<400 Hz), acoustic power was ca. 5–8 dB higher closer to the reef, but frequency specific variability was relatively large (Fig. 4). At higher frequencies (>1000 Hz) dominated by snapping shrimp, acoustic power was ca. 3 dB lower near the benthos and similar at the mid-water and surface stations. There was also less variability between sites. Between ca. 500 and 1000 Hz, the surface generally showed higher sound levels, and variably was high, perhaps reflecting the effects of noise attenuating from the surface.

Conversely, Fig. 5 shows the results of vertical array recordings made at JR4 for a 12-h period. In this dataset, the mid-water recorder displayed the highest sound levels (Fig. 5b). Upon further inspection, it was determined that the ship thrusters contributed to this low frequency signal elevation, received most strongly at the 5 m depth hydrophone. The higher frequency bandwidth sound levels were relatively consistent with depth for this vertical array (Fig. 4b).

Spatial Variation in Motion Across a Reef: The Drifter

The drifter spectrogram provides a unique ability to assess how a reef area soundscape varies spatially [(Lillis et al. 2018), Fig. 6]. Over the course of an hour, the

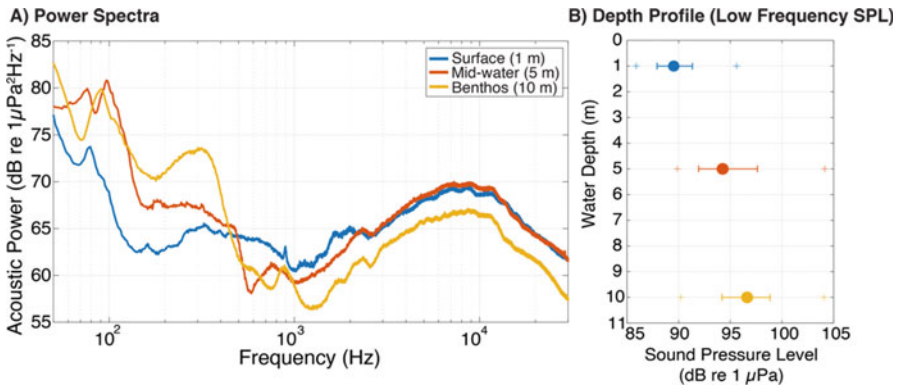


Fig. 4 (A) Power spectra and (B) low frequency sound pressure level variation with depth measured at JR3 over 2 h of recording from the stationary vertical array

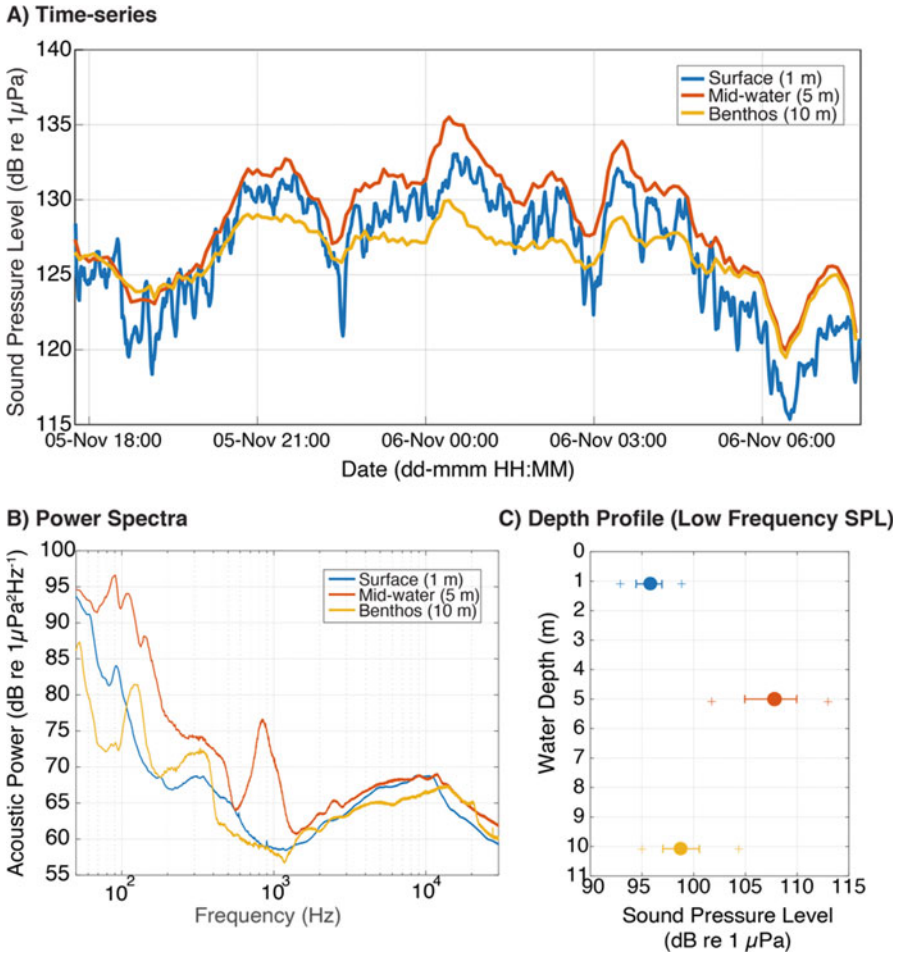


Fig. 5 (A) Time-series, (B) power spectra, and (C) depth variation in low frequency sound pressure level measured overnight at JR4 from the stationary vertical array

drifter started on the coral reef but drifted off and away to areas of mixed benthic structures. High frequency energy was clearly elevated over the reef and this greatly influenced the full bandwidth analysis. Around 16:50 local time, the drifter approached an area of small patch reefs and subsequently the higher frequency snapping shrimp sound levels increased. Notably, just off the reef, around 16:22 and 16:28 schools of small jacks approached the drifter. At these times, low frequency SPLs peaked (Fig. 6a, b-ii), reflecting sounds produced by these schools. Otherwise, the low frequency fish sounds were generally consistent for the first 20–30 min, and then decreased substantially just off the reef (ca. 16:40), but slowly began to increase as the drifter approached the patch reef.

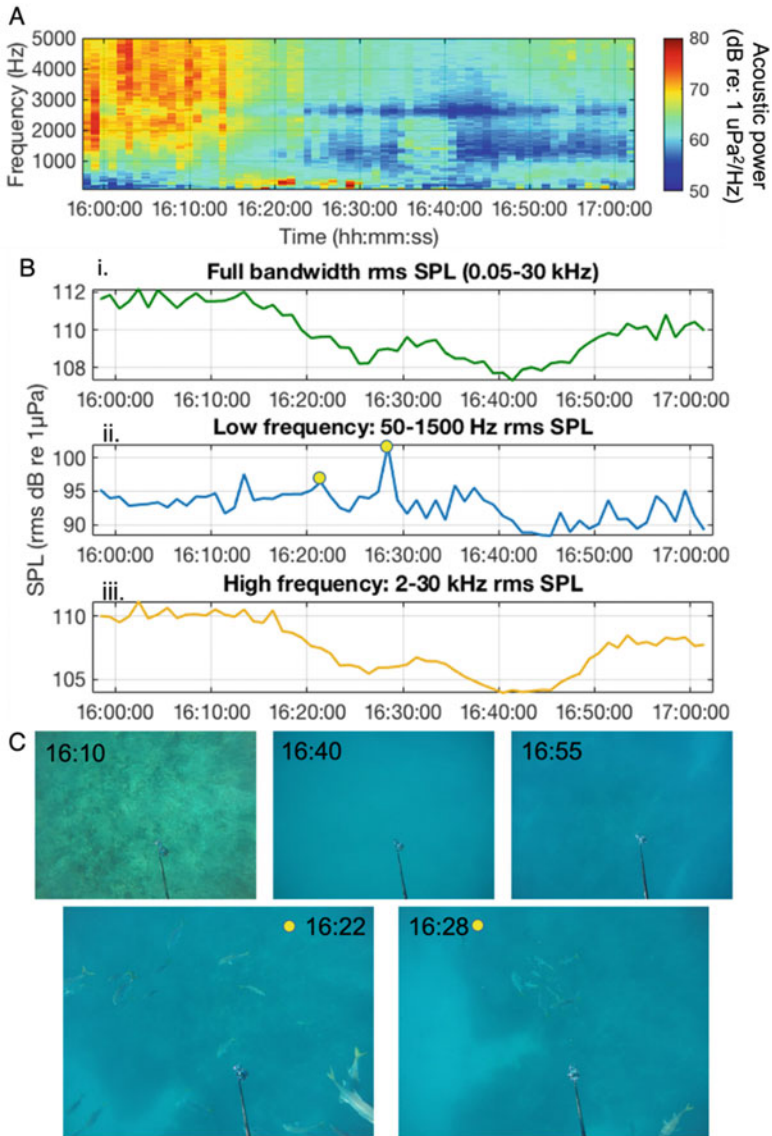


Fig. 6 (A) Spectrogram of the drift; (B) i–iii corresponding spectra in the full, low, and high frequency bands, and (C) downward facing images at five timepoints during the drift. Note the increased high-frequency and overall sound levels over the initial reef habitat (16:10), reflective of an increase in snapping shrimp. There was increase in sound levels over reef areas, and particularly notable low frequency signals (highlighted by the yellow dots) when fish schools passed by

Discussion

The goal of this research was to address spatial soundscape variation within a coral reef environment, particularly to establish if substantial variation exists that impacts passive acoustic monitoring, and to provide ecological context for the data collected. The results show evidence of substantial small-scale horizontal acoustic variation using complementary recording configurations: recorders deployed via benthic mooring in close proximity and via a low-noise drifter buoy. Multi-depth vertical arrays revealed that sound levels and frequencies also changed over small depth changes, with substantial particularly at lower frequencies (below ca. 1000 Hz). The suite of configurations was applied to holistically sample the reef environment, rather than focus on fewer locations for a longer period. This allowed us to make inferences regarding the reef soundscape over scales not typically monitored with PAM and emphasizes the importance of careful site selection when initiating an acoustic reef monitoring effort.

The soundscape of the dead pillar coral colony (DCYL 3) differed from the other two living colonies likely because a dead colony does not attract the same soniferous animal community. The structure of large *Dendrogyra* pillar coral is a unique community hub on the reef, providing habitat for fishes, which create nutrient hotspots and in turn increased coral cover additional fish local habitat (Shantz et al. 2015). Together, it is not surprising that these micro-habitats associated with the live *Dendrogyra* would foster a distinct soundscape with high levels of acoustic activity reflecting the community hub this structure provides. Reef soundscapes are expected to change concomitantly with deteriorating reef conditions caused by bleaching, diseases, and loss of corals (Lamont et al. 2022). However, it is important to note that in this chapter our measurements of adjacent soft coral areas also displayed unique and complex soundscape parameters, overlapping with the *Dendrogyra* SPLs and frequency patterns. It is clear that careful application of broad acoustic metrics and cautious interpretation of crude differences associated with reef variation is required. Nonetheless, the insights gained into loss of acoustic activity at a dead *Dendrogyra* colony has implications for broad, community-scale impacts of stony coral tissue loss disease (SCTLD), which has rapidly spread throughout the Caribbean causing nearly complete mortality of *Dendrogyra* corals (Neely et al. 2021). These results support the need for advanced acoustic analyses (e.g., machine learning) and sound libraries (Parsons et al. 2022) to enhance our ability to identify the drivers and understand the ecological relevance underpinning small-scale acoustic variation.

The paired camera-acoustics of the drifter provided a valuable method to visually observe the animals likely making certain sounds. This allowed us to video-capture what appears to be horse-eye jacks (*Caranx latus*), a predator fish, swimming around the recording system and suggests these could be the cause of concurrent higher low-frequency sound levels. These sounds appear to be biological in origin, not animals bumping hydrophones. Carangidae are one of the families with sound production noted (Fine and Parmentier 2015) but its origin or function has not yet been well-described.

The vertical array provided a new assessment of the shallow coral reef environment demonstrating vertical differences in sound level and frequency at the scale of meters. These differences may be particularly important for understanding the depth distribution of acoustic cues for settling larvae. When near reefs, larvae can be at shallower depths (2–4 m) (Leis and Carson-Ewart 1999) but as they settle and move toward a reef (increasing depth), they may have more low-frequency sound cues available to them. Reef fishes select microhabitats such as species/morphotypes of corals and it is generally assumed that they need to be close to the reef to make such decisions (Sweatman 1983). The variation observed across a 10-m depth water column indicates that such vertical patterns are relevant to studies of the soundscape as an orientation cue and should be considered in measurement of salient larval cuescapes.

The recorded vertical variation of sound pressure level should be addressed further. These measurements were certainly in the acoustic near-field for the low frequencies, yet this is the reality for fish larvae as they swim over a reef. The variability was likely due, at least in part, to the unpredictability of sounds in the near-field (Kalmijn 1988). Indeed, closer to the reef and its sound sources, where soniferous fish and invertebrates are in higher abundance, variability was higher (Fig. 4c). The decrease of variability as shallower depths may be explained because the near-field variability effects would be limited to only the lower frequencies. Although there are few data of in situ swimming behavior of settling fish larvae, they appear to maintain a relatively stable (often relatively shallow) depth although this “stable” depth can vary by ca. ± 0.5 m or more (Irissou et al. 2010). This movement would allow them to potentially “sample” this variable acoustic environment to better assess the reef below. Such a mechanism would be quite valuable for fish settling at night.

To our knowledge, this is the first passive acoustic examination of coral reefs in Cuban waters. This environment was particularly compelling to document acoustically as the Jardines de la Reina reef system is relatively healthy, compared to many other Caribbean coral reefs. The region and some reefs within it have higher coral cover than other areas of the Caribbean and are also relatively abundant with large fishes and sharks (Ferguson et al. 2022). The sound dataset collected in Jardines de La Reina offers a starting point for further comparisons with other impacted and declining Caribbean reefs. It also offers an important baseline to this hub of biodiversity as it faces, as other Cuban reefs, ongoing impacts by chronic stressors and stochastic events (Caballero-Aragón et al. 2022).

Importantly, this study demonstrates that the soundscape of a single coral reef is not uniform in distribution. Rather, acoustic cuescapes vary horizontally across the reef and vertically with distance from the seafloor. Given the importance of sounds to reef fishes and invertebrates, these differences likely offer acoustic cues as animals seek to settle, find mates, or establish territories. The shelter that large corals provide to soniferous animals may support acoustic hotspots, given the increased density of fishes and invertebrates at these microhabitats and the potential interactions with the confined space that the coral-shelter may provide. Understanding the variation in reef soundscape is also important as we seek to leverage these patterns for assessing

reef communities. Thus, it is key to determine the diversity and structure of these sound-producer communities associated with reef microhabitats and the ecological function that they provide. Finally, understanding the spatiotemporal distribution of reef microhabitats should be a consideration and caveat to valuations from snapshot acoustic measurements. Indeed, this supports the need for longer-duration measurements as we seek to understand coral reef soundscapes and the communities they represent.

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