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Soundscapes as heard by invertebrates and fishes: Particle motion measurements on coral reefs[a)]

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ABSTRACT:

Coral reef soundscapes are increasingly studied for their ecological uses by invertebrates and fishes, for monitoring habitat quality, and to investigate effects of anthropogenic noise pollution. Few examinations of aquatic soundscapes have reported particle motion levels and variability, despite their relevance to invertebrates and fishes. In this study, ambient particle acceleration was quantified from orthogonal hydrophone arrays over several months at four coral reef sites, which varied in benthic habitat and fish communities. Time-averaged particle acceleration magnitudes were similar across axes, within 3 dB. Temporal trends of particle acceleration corresponded with those of sound pressure, and the strength of diel trends in both metrics significantly correlated with percent coral cover. Higher magnitude particle accelerations diverged further from pressure values, potentially representing sounds recorded in the near field. Particle acceleration levels were also reported for boat and example fish sounds. Comparisons with particle acceleration derived audiograms suggest the greatest capacity of invertebrates and fishes to detect soundscape components below 100 Hz, and poorer detectability of soundscapes by invertebrates compared to fishes. Based on these results, research foci are discussed for which reporting of particle motion is essential, versus those for which sound pressure may suffice. © *2022 Acoustical Society of America*. https://doi.org/10.1121/10.0012579

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I. INTRODUCTION

Coral reefs are biodiverse habitats with complex soundscapes consisting of biological, geophysical, and anthropogenic sounds. Passive acoustic monitoring of these soundscapes is essential for understanding acoustic ecology of coral reefs, and can be applied to assess and monitor local biodiversity (Mooney *et al.*, 2020). As a growing number of studies describe marine soundscapes, the ecological importance of natural soundscape cues to invertebrates and fishes has been increasingly realized (Popper and Hawkins, 2018; Putland *et al.*, 2019). Reef soundscapes may aid pelagic larvae and juveniles of fishes and corals navigating toward reefs (Gordon *et al.*, 2018; Lillis *et al.*, 2016; Lillis *et al.*, 2018; Parmentier *et al.*, 2015; Radford *et al.*, 2011; Suca *et al.*, 2020). Soundscapes cues may be utilized by sound-sensitive taxa for communication in competitive or reproductive contexts, as demonstrated in many reef fishes (Lobel *et al.*, 2010; Tricas and Boyle, 2014) and in crustaceans (Buscaino *et al.*, 2015; Jézéquel *et al.*, 2020; Lillis *et al.*, 2017; Popper *et al.*, 2001). More basally, animals may listen to soundscape cues to orient themselves, navigate, and locate sound-producing organisms in their habitat (Fay, 2009).

Underwater soundscapes have almost exclusively been reported in sound pressure, despite a growing appreciation of particle motion's relevance to invertebrate and fish hearing. Few studies have reported particle motion of soundscapes, typically quantified as particle acceleration (dB re 1 μm s^{-2}) which is considered the relevant transduction stimulus for hearing organs of invertebrates and fishes (Popper and Hawkins, 2018). These studies examined ambient particle motion in diverse habitats, from coral reefs in the Pacific (Horch and Salmon, 1973; Kaplan and Mooney, 2016), to a sandy tropical bay in Brazil (Jesus *et al.*, 2020), to freshwater rivers and streams (Lugli and Fine, 2007; Lumsdon *et al.*, 2018), and coastal waters in the North Sea (Rogers *et al.*, 2021). Some have addressed particle motion of vessel noise (Magnhagen *et al.*, 2017; McCormick *et al.*, 2018; Nedelec *et al.*, 2014; Picciulin *et al.*, 2010; Wahlberg *et al.*, 2008), seismic surveys (McCauley *et al.*, 2021; Rogers *et al.*, 2021), pile driving (Ceraulo *et al.*, 2016), and wind turbine noise (Sigray and Andersson, 2011; Wahlberg and Westerberg, 2005). These evaluations reported particle motion levels for short time periods (less than 1 week), thus temporal variability (a key parameter, at least for pressure) of particle motion soundscapes remains poorly understood (Mooney *et al.*, 2020). Further, particle motion levels of specific soundscape components, such as fish calls, are rarely described.

Fishes and invertebrates primarily detect particle motion at frequencies below 1000 Hz, and many detect infrasound, i.e., below 20 Hz (Ladich and Fay, 2013; Packard *et al.*, 1990; Popper and Hawkins, 2018; Sand

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et al., 2000; Wilson *et al.*, 2018). On coral reefs, commonly occurring sounds within this frequency range include abiotic sounds from wind and wave motion, and sounds produced by fishes (Montgomery *et al.*, 2006; Tricas and Boyle, 2014). Anthropogenic boat noise is also in this frequency range, and is present daily at many coral reefs and other nearshore habitats (Butler *et al.*, 2021; Dinh *et al.*, 2018). Broadband choruses of snapping shrimp snaps are omnipresent in many coral reef soundscapes, and usually have peak frequencies at or above 2000 Hz (Au and Banks, 1998; Lillis and Mooney, 2018).

Measurements of particle motion are useful when studying coral reef soundscapes for several reasons. First, it may not always be assumed *a priori* that particle motion levels scale directly with sound pressure levels, as they do for a plane wave in the "free-field". Many coral reefs are relatively shallow and have rugose benthos; in such environments, the actual (empirical) particle motion is more likely to deviate from that predicted by theory for a plane wave, especially for low frequencies, e.g., below 100 Hz (Gray *et al.*, 2016; Nedelec *et al.*, 2016). This necessitates either direct measurement of particle motion (e.g., with an accelerometer) or calculation from pressure differentials using a hydrophone array.

Second, by reporting magnitudes of particle motion, one can better estimate the detectability of soundscape cues for invertebrates or fishes. Particle motion may have different propagation losses and signal-to-noise ratios compared to those of pressure (Jesus *et al.*, 2020; Kalmijn, 1988). Comparisons of particle motion soundscape measurements with animals' particle motion detection thresholds are needed to address questions regarding the detectability and ecological functionality of natural soundscape cues for these taxa.

Further, particle motion is inherently directional at a given point, whereas sound pressure is not. This directionality likely plays important (though often poorly understood) roles in how invertebrates and fishes process acoustic cues to identify, localize, and behaviorally respond to sounds in their environment (Wilson *et al.*, 2018; Zeddies *et al.*, 2012). Directional particle motion data may help discern how reef animals use acoustic cues to enact fundamental processes, such as navigation, selection of settlement sites, avoidance of predators, and communication.

Anthropogenic sounds from recreational vessels and commercial shipping are frequent in many coastal habitats, including coral reefs (Bittencourt *et al.*, 2020; Dinh *et al.*, 2018; Kaplan and Mooney, 2015). Such sounds can have a multitude of adverse physiological and behavioral effects on invertebrates and fishes (Bruintjes *et al.*, 2016; Filiciotto *et al.*, 2016; Holles *et al.*, 2013; Magnhagen *et al.*, 2017; Mensinger *et al.*, 2018; Simpson *et al.*, 2016; Wale *et al.*, 2013), and can mask ecologically relevant cues (Pine *et al.*, 2016). Given that particle motion is a relevant stimulus for fishes and marine invertebrates, efforts to identify impacts of anthropogenic sounds and establish protective noise criteria for these taxa should consider particle motion levels of noise. There is an increasing trend to include particle motion measurements when assessing the impacts of anthropogenic sounds on non-mammal marine taxa (Wale *et al.*, 2021).

Quantification of underwater soundscapes is actively being pursued as an efficient and high temporal-resolution approach to monitor habitat health (Mooney *et al.*, 2020; Nedelec *et al.*, 2015). Trends of sound pressure levels on coral reefs, particularly those below 2 kHz, are often positively correlated with visually measured indicators of reef health, such as coral cover and fish biomass (Freeman and Freeman, 2016; Kaplan *et al.*, 2015; Staaterman *et al.*, 2017). Though temporal and spectral acoustic trends are site-specific (Radford *et al.*, 2014), soundscape analyses show promise as effective means for long-term monitoring of biodiversity (Mooney *et al.*, 2020). Yet, such associations between acoustic and non-acoustic indicators have not been addressed for particle motion.

The present study is the first to report particle motion levels of coral reef soundscapes over an extensive time period (several months). Sounds were recorded from reefs on the southern shore of St. John, U.S. Virgin Islands. The primary goals of this study were to describe particle motion magnitudes of coral reef sounds, how they correlate with sound pressure and non-acoustic indicators of habitat quality, and the extent to which soundscapes may be detectable by marine invertebrates and fishes. This study also aimed to describe how particle motion levels vary over time, with particular focus on diel trends, and how they vary directionally, i.e., between horizontal and vertical axes. Particle motion levels of example fish sounds and boat noise were described. Finally, a discussion is presented on soundscape-focused research questions that would necessitate particle motion measurement, and those that may only require descriptions of sound pressure.

II. METHODS

A. Study sites and visual surveys

Study sites were along the southern shore of St. John, U.S. Virgin Islands (18.31' N, 64.74' W), within the Virgin Islands National Park [Fig. 1(a)]. Four reef sites that represent a range of habitat quality were selected for this study: Tektite, Yawzi, Ram Head, and Cocoloba. Visual surveys of benthic cover and fish presence were conducted by scuba divers from July 17–24, 2017. For detailed methods of visual surveys, see Dinh *et al.* (2018) and Kaplan *et al.* (2015). Briefly, benthic point surveys were conducted along six 10 m transects at 10 cm increments to quantify benthic cover type including hard and soft corals, macroalgae, sponges, sand, and rock. The present study focused on coral cover as a benthic habitat quality indicator. The number of points identified as hard and soft coral were totaled and divided by the total number of points surveyed at a site ($n = 600$), and reported as percent coral cover. Fish surveys consisted of three 30 m video transects per site. Transects started at the location of the acoustic array, and were swum straight along haphazardly selected bearings. Tektite and

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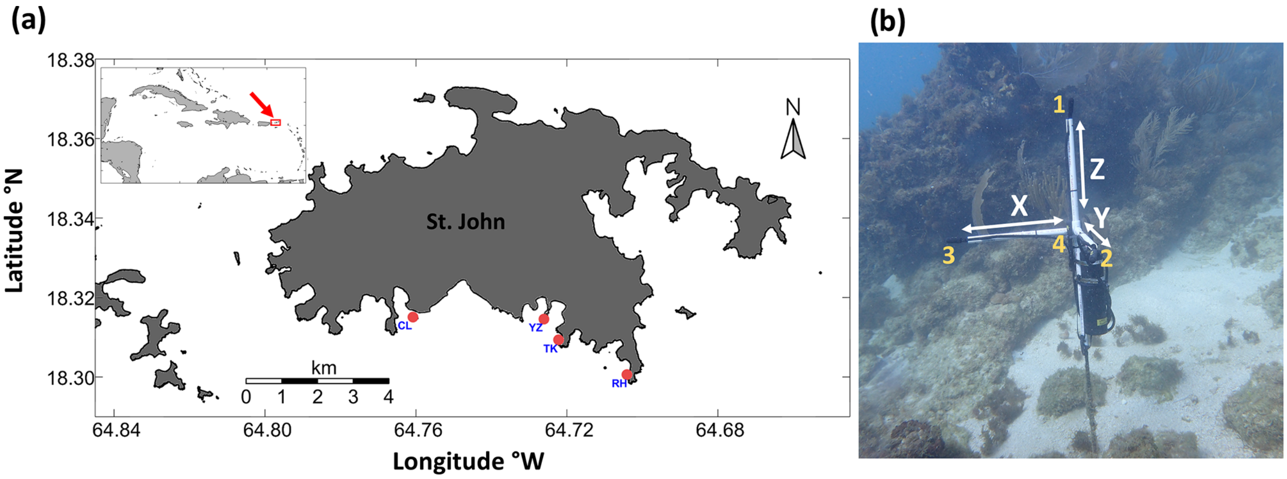

FIG. 1. (Color online) (a) Map of St. John with reef sites marked. CL = Cocoloba, YZ = Yawzi, TK = Tektite, RH = Ram Head. The map inset shows the location of the U.S. Virgin Islands within the Caribbean. (b) Image of the hydrophone array at Cocoloba. Numbers mark locations of the four hydrophones and arrows with letters indicate the three orthogonal axes along which particle acceleration was calculated.

Yawzi had higher percent coral cover and greater fish abundance than Ram Head and Cocoloba (Table I). Coral cover was significantly greater at Tektite compared to Ram Head and to Cocoloba ($p = 0.009$ and $p < 0.001$, respectively) and at Yawzi compared to Cocoloba ($p = 0.014$; t-tests). Fish abundance was significantly greater at Yawzi compared to Cocoloba ($p = 0.025$; t-test). Tektite also had the highest species richness (number of different fish species) whereas Cocoloba had the lowest species richness. Overall, surveys indicated Tektite and Yawzi were healthier reefs (i.e., with more coral cover and supporting more fish or higher biodiversity) during the study period compared to Ram Head and Cocoloba. Benthic cover was not expected to have changed throughout the acoustic recording period (March–November 2017), as visual surveys conducted in November 2017 recorded coral cover within 0.5% (Tektite, Ram Head, Cocoloba) or 6% (Tektite) of that recorded in July 2017, and within standard deviations of July 2017 data. Fish surveys for Tektite and Cocoloba in November 2017 (not conducted for Yawzi or Ram Head that month) recorded fish abundance within standard deviations of July data (November mean abundances of 104 and 78, respectively) and similar species richness (33 and 25, respectively).

TABLE I. Visual survey data from July 2017 for each reef site. Percent coral cover and fish abundance are shown as mean ± standard deviation across transects. Percent coral cover includes hard and soft corals. Fish abundance is the count of individual fish, and fish species richness is the total number of species found among three transects.

Reef Site	% Coral cover	Fish abundance	Fish species richness
Tektite	28 ± 5.2	165.7 ± 132.0	36
Yawzi	23 ± 7.1	161 ± 46.1	24
Ram Head	16.2 ± 7.3	99.7 ± 24.8	27
Cocoloba	11.7 ± 6.1	51 ± 29.2	21

B. Passive acoustic array configuration

At each reef, a four-channel array was deployed on a rebar stake, 1 m above the substrate; this was considered far enough above the water-substrate interface to have negligible influence from potential sources of seabed vibration that can lead to higher particle motion levels at and directly above the seabed (Hawkins *et al.*, 2021; Hazelwood and Macey, 2021). The recorders were at the following depths: Tektite: 10.6 m, Yawzi: 9.1 m, Ram Head: 8.5 m, Cocoloba: 7 m. Arrays consisted of four hydrophones (HTI-96-MIN/3V/Low Noise; High Tech Inc., Long Beach, MS; nominal sensitivity: –165 dB re 1 V/μPa; frequency response: 2 Hz to 30 kHz) secured to a PVC frame and spaced 0.38 m apart in an orthogonal arrangement [Fig. 1(b)]. Arrays were placed above small sandy patches within reefs. Compass headings of X and Y axes (measured outward from the center hydrophone) varied across sites (Tektite: X = 135°, Y = 45°; Yawzi: X = 75°, Y = 345°; Ram Head: X = 125°, Y = 35°; Cocoloba: X = 345°, Y = 255°). Hydrophones were connected to a SoundTrap ST4300 (Ocean Instruments, Auckland, New Zealand), which synced recordings across channels, applied a 4 dB gain, and digitized each channel at a 48 kHz sample rate and 16 bit sampling depth.

C. Recording schedule

Recordings were collected between March 19 and November 21, 2017, an 8-month period spanning when many fishes are reproductively active and produce courtship sounds (Johannes, 1978), including species observed in visual surveys, for example, bicolor damselfish (*Stegastes partitus*) (Myrberg *et al.*, 1986), yellowtail hamlet (*Hypoplectrus unicolor*), and striped parrotfish (*Scarus iserti*) (Lobel, 1992). SoundTraps were set to a duty cycle of 63 s per 10 min. Each file had a 3 s "ramp-up" (a direct current offset caused by the SoundTrap) which was omitted from analyses, leaving 60 s available for each recording. Hurricanes Irma and Maria made landfall at St. John on

September 6 and September 20, respectively, causing data loss between August and November for Yawzi and Ram Head. Acoustic arrays at Tektite and Cocoloba survived; however, they were thrown off their rebar stakes, likely during Hurricanes Irma and Maria, respectively. Upon recovery in November, these two arrays were found lying on their side on the sand 10–20 m away from their original locations. Although recovered long-term data are shown for the full deployments in Fig. 2, due to array displacement and consequently a lack of comparability of post-hurricane recordings with earlier recordings, subsequent analyses for all sites were limited to March through August 2017.

D. Acoustic analyses

Acoustic data analyses were conducted in MATLAB (Mathworks Inc., Natick, MA) versions 2016b and 2020a. A random 3 s sample within each 60 s recording was used to calculate all metrics. This 3 s integration time was considered representative of individual biological signals (which can vary in duration but are relatively short) and of how these taxa might perceptually integrate sounds, compared to a 60 s integration (Radford *et al.*, 2014; Wysocki and Ladich, 2003), and also incorporates some of the natural temporal variability of pulsed sounds on reefs. Particle acceleration was calculated using the finite difference approximation:

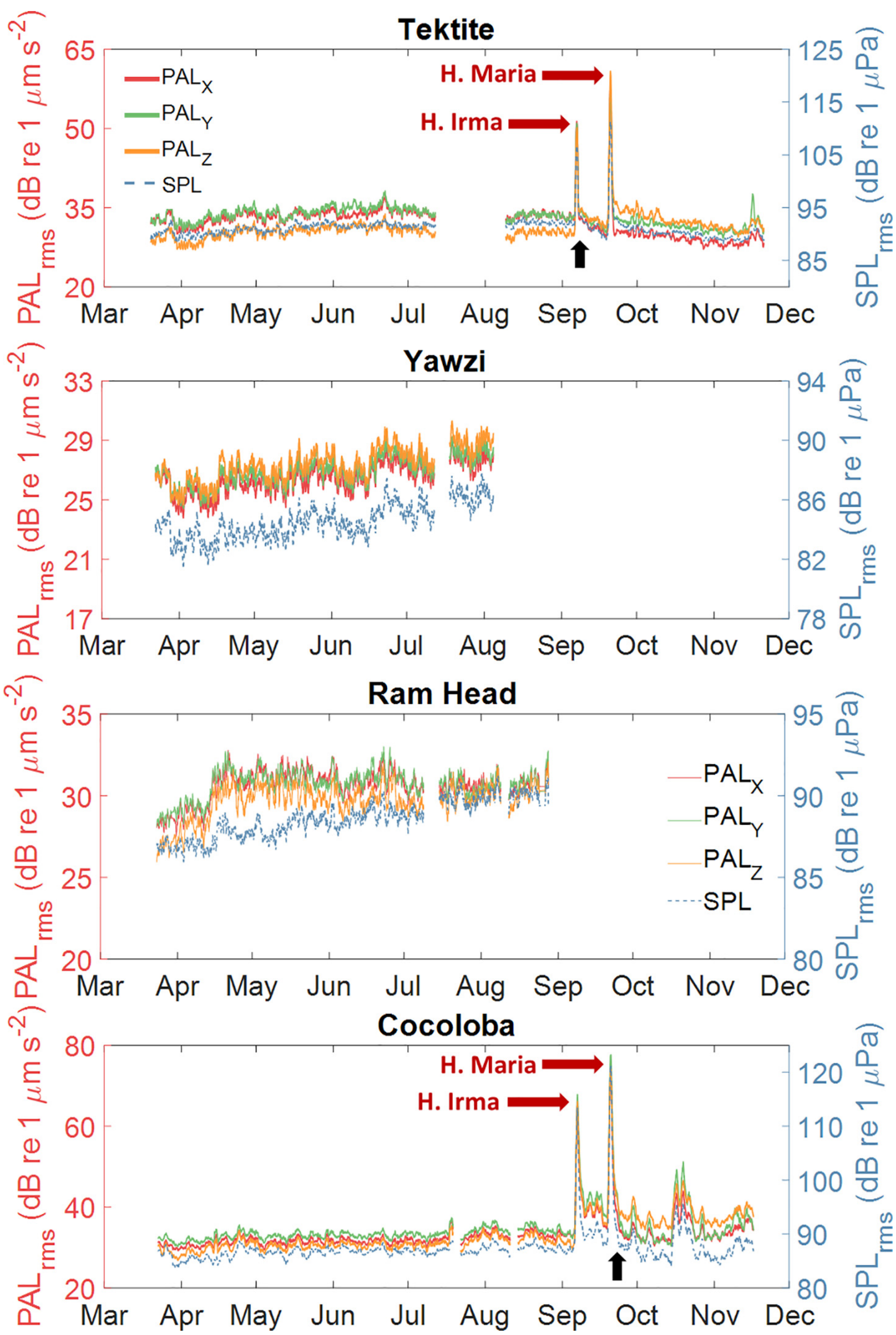

FIG. 2. (Color online) Sliding daily averages of root mean square particle acceleration (PAL_{rms}) along each axis (X, Y, Z) and sound pressure level (SPL_{rms}), of recordings subsampled to 3 s time windows and bandpass filtered to 100–1000 Hz. Peaks labeled with horizontal arrows correspond to abiotic noise from hurricanes Irma and Maria. Upward-facing arrows point to times where the relative PAL_{rms} of individual axes shifted, likely due to the array being moved by hurricanes.

$$a_{21}(t) = -\frac{(p_2(t) - p_1(t))}{\rho d}, \qquad (1)$$

where $p_1(t)$ and $p_2(t)$ are the pressures (Pa), at two hydrophones at time point t, ρ is the seawater density (1022 kg m^{-3}; average of CTD (Conductivity, Temperature, Depth) casts at all sites during summer 2017), d is the distance (0.38 m) between hydrophones, and a is the particle acceleration (m s^{-2}) along the axis of the two hydrophones. Particle acceleration was calculated along three axes, including two horizontal (X, Y) axes and one vertical (Z) axis [Fig. 1(b)]. To report sound pressure metrics from each acoustic array, the average of the pressure time series of the four hydrophones was taken.

Root-mean square (rms) levels were calculated for pressure and particle acceleration in a 100–1000 Hz frequency band after zero-phase filtering of data with an 8th order Butterworth filter. These levels are hereafter referred to as SPL_{rms} (rms sound pressure level) and PAL_{rms} (rms particle acceleration level). The 100–1000 Hz band was selected because it covers much of the hearing ranges of invertebrates and fish, while limiting errors of calculated particle acceleration inherent in the array setup (signal to instrument-noise ratio, calibration and spacing uncertainty error), which were expected to be greater outside of this frequency range (Fig. S1)[1] (Gray *et al.*, 2016). Sliding daily averages of PAL_{rms} and SPL_{rms} were calculated to observe long term trends over the entire deployment at each site.

To investigate diel cycles of soundscape data, dusk periods were defined from sunset to 90 min after sunset, and dawn periods were defined from 75 min before sunrise to sunrise, reflecting astronomical twilight periods year-round. Periodograms were plotted to visualize the relative strength of diel periodicity, using Welch's method with a sample rate of 144 samples per day (corresponding to the recorder's duty cycle), a FFT size of 2880 samples, a window length of 20 days, and 50% overlap of time windows.

All data were manually scanned for the presence of boat noise by looking at pressure spectrograms generated for each audio file, following Dinh *et al.* (2018) and Kaplan and Mooney (2015). Except where otherwise noted, results reported are from recordings without boat noise, representing natural sound sources on the reefs.

Spectral analyses encompassed frequencies from 5–2000 Hz to allow a wider range to compare soundscape data with particle-motion detection thresholds of fishes and invertebrates. Power spectral density (PSD) was calculated using Welch's method, in 1 Hz bins and over 1 s time windows with 50% overlap. For each recording, peak PSD and frequency were extracted for comparison with audiograms. One octave band levels were calculated at center frequencies of 16, 32, 63, 125, 250, 500, and 1000 Hz, *via* octave smoothing of PSD data using the poctave function from MATLAB's Signal Processing Toolbox. Spectrograms were also plotted for 1 min examples of boat noise and 4–30 s examples of fish sounds (selected from files within the 90th[h] percentile of PAL_{rms}), in 8 Hz bins and 125 ms time windows with 80% overlap. Table II gives a summary of metrics reported, including reference units (ISO 18405, 2017).

The rms and PSD metrics were calculated for each particle acceleration axis (X, Y, Z). They were also calculated as a vector (Euclidean) norm to report an overall 3D (three-dimensional) magnitude, as follows:

$$a_{Tot} = \sqrt{{a_x}^2 + {a_y}^2 + {a_z}^2}, \qquad (2)$$

where a_i represents either the rms or PSD value of particle acceleration obtained for an individual axis i. The mean pressure of all four hydrophones was taken when comparing pressure with 3D particle acceleration.

The PSD of 3D particle acceleration obtained from Eq. (2) was also compared with PSD of theoretical particle acceleration predicted for a plane wave in the far field, calculated as follows:

$$a_{pw} = \frac{2\pi f * \sqrt{P_{PSD}}}{\rho c}, \qquad (3)$$

where f is the frequency (Hz), P_{PSD} is the mean PSD (for each 1 Hz bin) of all four hydrophones (Pa^2 Hz^{-1}), ρ is the seawater density (kg m^{-3}), c is the sound speed (1543 m s^{-1}; as measured *via* CTD data), and a_{pw} is the particle acceleration for a plane wave in the far field (m s^{-2}). The a_{pw} was then converted to PSD. Three-dimensional particle acceleration from Eq. (2) close to or below that from Eq. (3) can be approximated as a plane wave, whereas higher acceleration levels from Eq. (2) indicate sounds propagating as different wave types, such as point sources, or sounds recorded in the near field (Gray *et al.*, 2016; Rogers and Cox, 1988).

To place soundscape levels in the context of animal hearing abilities, as done in previous studies (Amoser and Ladich, 2005; Mooney *et al.*, 2018), previously published hearing thresholds of several fish and invertebrate species were compared with soundscape data in the present study,

TABLE II Definitions of acoustic metrics. p = sound pressure (μPa), a = particle acceleration (μm s^{-2}), t = time window (3 s), f = frequency bin (1 Hz).

Metric	Sound pressure equation	Sound pressure units	Particle acceleration equation[a]	Particle acceleration units
Root mean square level	$SPL_{rms} = 20 * \log_{10}\left(\sqrt{\overline{p_t^2}}\right)$	dB re 1 μPa	$PAL_{rms} = 20 * \log_{10}\left(\sqrt{\overline{a_t^2}}\right)$	dB re 1 μm s^{-2}
Power spectral density level	$PSD = 10 * \log_{10}\left(p_f^2\right)$	dB re 1 μPa^2/Hz	$PSD = 10 * \log_{10}\left(a_f^2\right)$	dB re (1 μm s^{-2})^2/Hz

[a]For a single axis, X, Y, or Z.

including PSD levels (1 Hz bins) and 1 octave bands, with the latter approximating hypothesized auditory frequency filtering by marine fishes, such as cod (Hawkins and Chapman, 1975; Stanley *et al.*, 2017); no such auditory filter estimates have been made for aquatic invertebrates. Few studies report thresholds of fish species that inhabit Caribbean coral reefs (Anderson and Mann, 2011; Casper and Mann, 2006), and none report those of Caribbean invertebrates; thus, species from other habitats and regions were included to give a general indication of these animals' abilities to detect the soundscape.

E. Statistical analyses

Correlations between wideband (100–1000 Hz) SPL_{rms} and 3D PAL_{rms} were analyzed with ordinary least squares regression and Spearman's Rho. To assess the influence of boat noise on particle motion levels, Mann–Whitney U tests were performed to test differences in the distribution of PAL_{rms} between files with and without boat noise at each reef site ($\alpha = 0.05$). To quantify the strength of diel particle motion trends, medians across each time of day were found for the whole analysis period (March through August) for each site. Then, the maximum of the median levels during dawn or dusk periods (where medians were highest throughout a 24 h period) was subtracted by the minimum median level during the night (where medians were lowest throughout a 24 h period). These dawn–night and dusk–night differences were regressed against percent coral cover and fish abundance data for each site, and Pearson correlation coefficients were reported ($\alpha = 0.05$).

III. RESULTS

A. Long-term trends in particle acceleration and pressure

At all sites, daily averages of one-dimensional PAL_{rms} and SPL_{rms} gradually increased from April to August by ca. 3 dB (Fig. 2). On this temporal scale, trends of the three particle acceleration axes and sound pressure closely matched each other. Strong PAL_{rms} and SPL_{rms} peaks of abiotic sounds (wind, wave motion, and rain) occurred in September when hurricanes Irma and Maria made landfall at St. John. Peaks occurred at Cocoloba from October 14–25. These sounds were likely due to fallen hydrophones brushing against the benthos or animals brushing against the hydrophones repeatedly, leading to noise artifacts. Prior to the hurricanes, at all sites but Yawzi, the Z axis was 1–3 dB lower compared to the horizontal axes, whereas the horizontal axes were within 1 dB of each other. At Yawzi, PAL_{rms} of the three axes were within 1 dB of each other, though the Z axis was consistently higher than X and Y.

Including all recordings from March through August, 3D PAL_{rms} showed a stronger correlation with SPL_{rms} at Tektite and Yawzi ($R^2 = 0.74$ and 0.76, respectively), and weaker correlation with SPL_{rms} at Ram Head and Cocoloba ($R^2 = 0.50$ and 0.60, respectively, Fig. 3). All correlations were statistically significant ($p < 0.001$). At each site, there were two overlapping clusters; 3D PAL_{rms} above 45 dB and SPL_{rms} above 100 dB appeared to cluster around a steeper slope than that below these values (Fig. 3). These clusters were also distinguished in residual plots (Fig. S2)[1] that

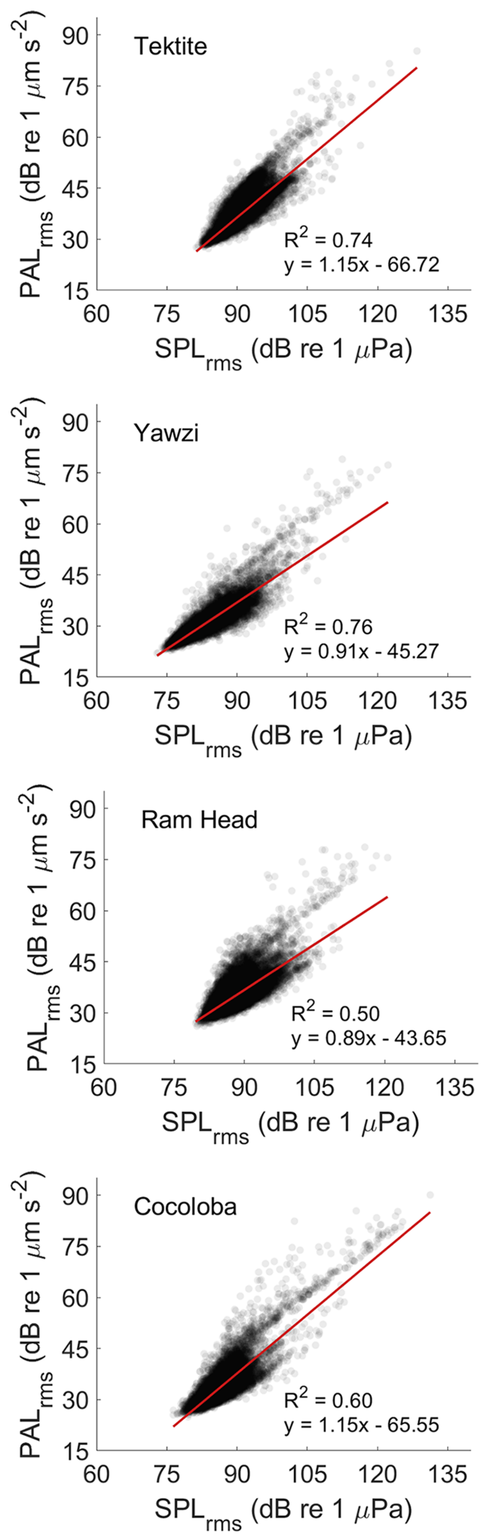

FIG. 3. (Color online) Scatterplots of 3D root mean square particle acceleration (PAL_{rms}) versus sound pressure (SPL_{rms}) for 3 s samples of all recordings from March–August 2017, for each reef site. Lines of best fit, regression equations, and Spearman's rho correlation coefficients (R^2) are shown.

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showed residuals within ± 10 dB at lower SPL_{rms} but strong divergence of PAL_{rms} (residuals $> +15$ dB) from the regression line at SPL_{rms} of 95–100 dB and higher. This could indicate the presence of several types of acoustic fields (see Sec. IV).

Quantiles (25th–99th) of empirical 3D particle acceleration PSD [Eq. (2)] were compared to PSD for theoretical particle acceleration for a far-field plane wave [Eq. (3)]. Above 100 Hz, empirical PSD levels at most of these quantiles closely approximated those of a plane wave (Fig. S3).[1] The 99th percentile empirical curve for Tektite was at least 6 dB greater than the respective plane wave curve from 100–300 Hz, peaking at 10 dB greater at 300 Hz. From 2–100 Hz, empirical acceleration PSD remained relatively flat whereas theoretical acceleration logarithmically increased with increasing frequency; theoretical plane wave acceleration was as much as 40 dB re 1 $(\mu m\ s^{-2})^2$/Hz lower than empirical acceleration. Thus, the plane wave approximation greatly under-predicted true particle acceleration of the soundscape in this low frequency range. Examples of these comparisons for Ram Head and Tektite are shown in Fig. S3.[1]

B. Diel patterns and diversity of reef sounds

All sites had similar diel periodicity, with higher 3D PAL_{rms} levels during the day than at night, and peaks during dawn and dusk (Fig. 4; examples shown for Tektite and Cocoloba). This pattern was also true for the one-dimensional axes (3 axes) of particle acceleration and for pressure (Fig. S4).[1] Periodograms also indicated diel periodicity, peaking at one and two cycles per day. Diel cycles were strongest at Tektite, followed by Yawzi, Ram Head, and weakest at Cocoloba. These diel patterns primarily reflect fish sounds, with higher amplitude tonal chorusing of multiple individuals detected in crepuscular periods, as observed previously (Kaplan and Mooney, 2015). Compared to other sites, at Tektite, quantiles of PAL_{rms} were more variable between adjacent times of day, especially the 90th percentile. The peak shortly after dawn in the 90th percentile curve for Cocoloba was due to broadband fish sounds like those shown in Fig. 5(a) (from Tektite); these sounds occurred at other times of day as well.

Recordings from Tektite and Cocoloba that had 3D PAL_{rms} within the 90th percentile were sampled, and among

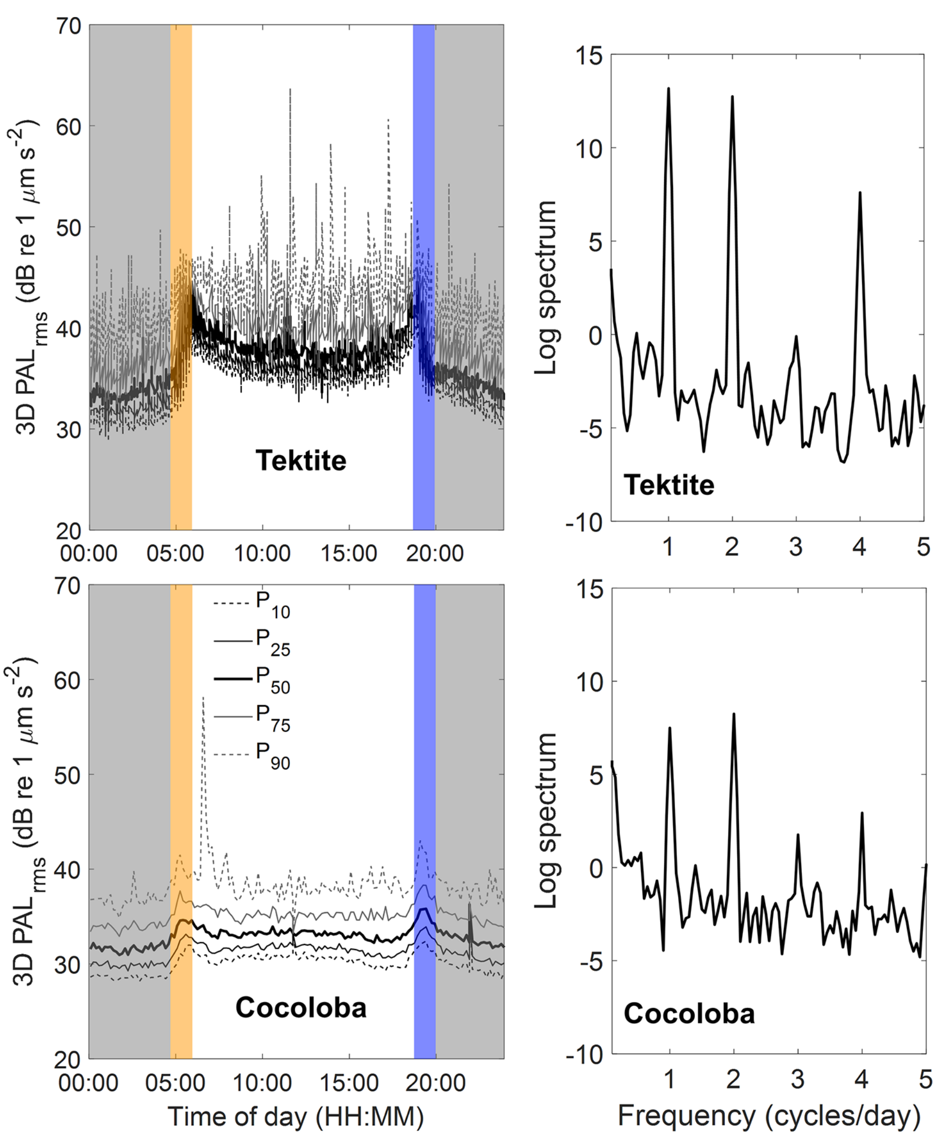

FIG. 4. (Color online) Diel patterns and periodicity of 3D PAL_{rms} for Tektite (top row) and Cocoloba (bottom row) expressed as time-of-day quantiles (10th, 25th, 50th, 75th, and 90th percentiles) on the left and periodograms on the right. For quantile plots, the lightest background indicates day, darkest shaded background indicates night, and dawn and dusk periods (around 0:50 and 19:00, respectively) are shaded.

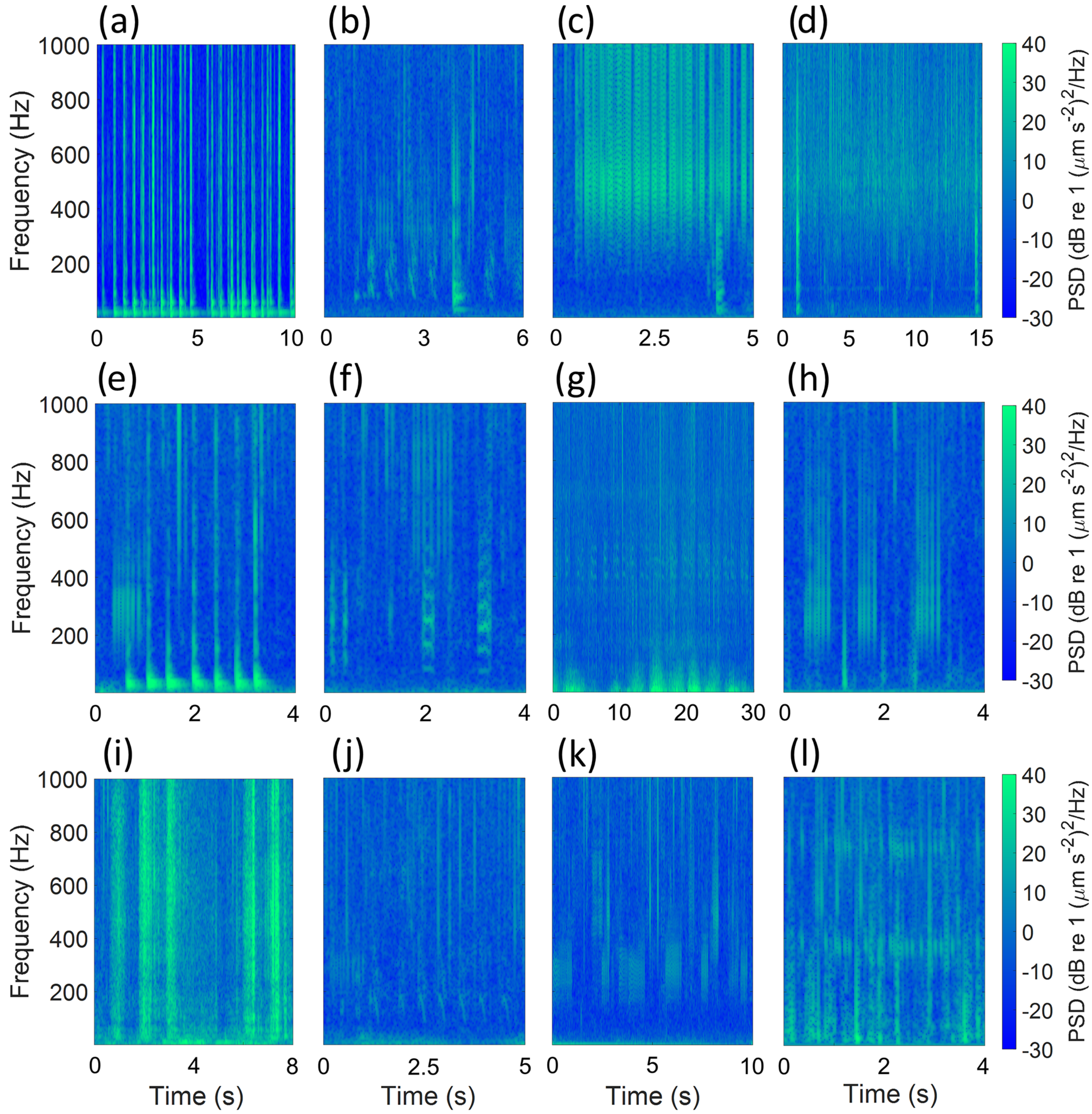

FIG. 5. (Color online) Example spectrograms of fish sounds from files within the 90th percentile of 3D PAL_{rms} levels at Tektite (a)–(d) and Cocoloba (e)–(l). Note that all *y* axes have the same frequency range but *x* axes have different time ranges. Colorbars show PSD of 3D particle acceleration.

these, a diversity of pulsed, broadband, and tonal fish sounds were found (Fig. 5). This study aimed to provide an overview of particle motion of different fish sounds, rather than identify sounds to specific taxa. Currently, there is no comprehensive database of Caribbean reef fish sounds (Parsons *et al.*, 2022), nor synced visual and audio data that would allow accurate identification of sound producers. The highest acceleration peaks in the 90th percentile in Fig. 4 (>55 dB PAL_{rms}) were from broadband, "grinding" pulses at short (<1 s) intervals, which may be stridulatory or feeding sounds from unidentified fishes [Fig. 5(a)]. Other fish sound types included trains of frequency down-sweeps from 200–100 Hz [Figs. 5(b) and 5(j)], rapid broadband pulses with peak frequencies around 500 Hz [Fig. 5(c)], short broadband pulses with peak frequencies between 200 and 400 Hz [Figs. 5(e) and 5(h)], pulsed calls peaking around 50 Hz with a broadband component at the beginning of the pulse [Fig. 5(e)], short (<0.5 s) tonal "groans" with a fundamental frequency near 100 Hz [Fig. 5(f)], a crepuscular chorus of tonal 1 s duration calls between 400 and 500 Hz [Fig. 5(g), shown during dusk], broadband calls with more diffuse energy across time and frequencies [Fig. 5(i)], and rapidly pulsed calls with harmonics at 400 and 800 Hz [Fig. 5(l)]. Examples of dusk choruses with multiple types of these calls together are shown in Figs. 5(d) and 5(k).

Visual surveys identified a variety of fish belonging to known soniferous taxa (Amorim, 2006; Kaschner, 2012; Tricas and Boyle, 2014) that may contribute to these sounds, including but not limited to *Caranx* spp. (jacks), *Haemulon* spp. (grunts), Holocentridae (squirrelfish and soldierfish), *Lutjanus apodus* (schoolmaster snapper), *Ocyurus chrysurus* (yellowtail snapper), Pomacentridae (damselfish), Scaridae (parrotfishes), Sciaenidae (drums/croakers), and Serranidae (groupers).

C. Boat noise

Median 3D PAL_{rms} levels were significantly higher for files with boat noise than without boat noise, at each reef site [$p < 0.001$, Mann–Whitney U tests, Fig. 6(a)]. Example 3D particle acceleration spectrograms of individual boat passes are shown from Tektite [Fig. 6(b)] and Yawzi [Fig. 6(c)]. Spectrograms of individual boat passes were similar in sound pressure and 3D particle acceleration. Those of individual particle acceleration axes could vary slightly across time; these differences likely were due to boats' changing direction of travel relative to the hydrophone array (Fig. S5).[1]

D. Particle motion of reef soundscapes relative to fish and invertebrate hearing thresholds

Peak PSD clustered around distinct frequency bands corresponding to different soundscape components (Fig. 7). Above 1000 Hz, peaks primarily are from snapping shrimp. Peak PSD around 400–800 Hz likely indicates various fish sounds, such as those seen in Figs. 5(g), 5(i), and 5(l), whereas the cluster around 300 Hz may correspond to fish sounds seen in Figs. 5(f) and 5(h). Peaks below 100 Hz likely correspond to broadband fish sounds with low-frequency peaks [Figs. 5(a) and 5(e)], as well as abiotic noise [as seen in Fig. 5(g)].

Peak particle acceleration PSD levels were compared with previously published particle acceleration audiograms of several invertebrate [Fig. 7(a)] and fish species [Fig. 7(b)]. One of the invertebrate species shown inhabits reefs in Australia and New Zealand (*Alpheus richardsoni*, Richardson's snapping shrimp). Of the fish species shown, two inhabit Caribbean coral reefs (*Ginglymostoma cirratum*, nurse shark; *Hippocampus erectus*, lined seahorse), and one inhabits Indo-Pacific coral reefs (*Chiloscyllium plagiosum*, white-spotted bamboo shark). Species were also selected from other habitats to cover a range of sensitivities, and give a comparative view to broadly investigate detectability of ambient coral reef particle motion by these taxa. At 100 Hz and above, even the highest particle acceleration PSD levels were below hearing thresholds of invertebrates, and only a few data points were above thresholds of fishes, including *Sciaena umbra* (brown meagre), *Micropogonias unduluatus* (Atlantic croaker), *Pempheris adspersa* (New Zealand bigeye), and the white-spotted bamboo shark.

Most fish species were only tested for particle motion thresholds at frequencies as low as 100 Hz; however, thresholds of the white-spotted bamboo shark were measured at lower frequencies. Below 80 Hz, peak soundscape PSD levels were up to 60 dB higher than this shark's thresholds, suggesting hearing of these cues was likely. Comparing sound pressure-derived audiograms of fishes that detect sound pressure, the highest outliers of the soundscape between 100 and 600 Hz reached or exceeded hearing thresholds [Fig. 7(c)]. Yet, the majority of peak PSD pressure values were at least 10 dB below the pressure hearing thresholds, suggesting hearing of these pressure cues may be limited as well.

Another way to compare soundscape data with hearing data is to report soundscape data in frequency bands approximating auditory filters of species of interest, which is appropriate when estimating the detectability of signals (e.g., fish calls) in the midst of ambient noise (Stanley *et al.*, 2017). The bandwidth of auditory filters has not been determined for any marine invertebrate, though 1 octave bands

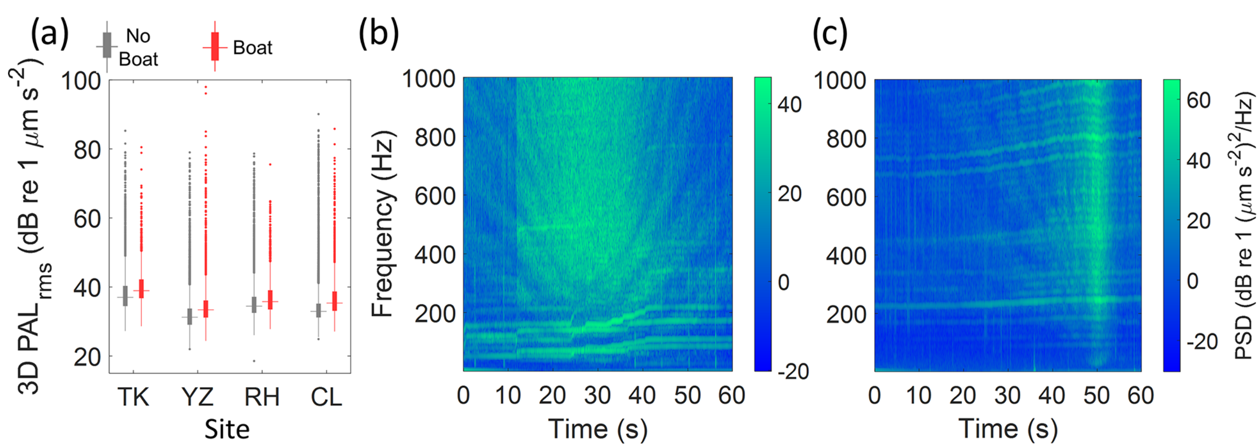

FIG. 6. (Color online) (a) Boxplots showing the distribution of 3D PAL_{rms} for files without and with boat noise, for each reef site. Horizontal lines indicate medians, and boxes extend from the 25th–75th percentile. Whiskers extend down to $q_1-1.5*(q_3-q_1)$ and up to $q_3+1.5*(q_3-q_1)$, where q_1 and q_3 are the 25th and 75th percentiles, respectively. Outliers are indicated by dots. TK = Tektite, YZ = Yawzi, RH = Ram Head, CL = Cocoloba. (b) Example boat noise from June 22 at Tektite. (c) Example boat noise from June 16 at Yawzi. Colorbars for (b) and (c) show power–spectral–density (PSD) of 3D particle acceleration [dB re (1 μm s^{-2})^2 Hz^{-1}]. Both boat noise examples were within the 99th percentile of 3D particle acceleration levels.

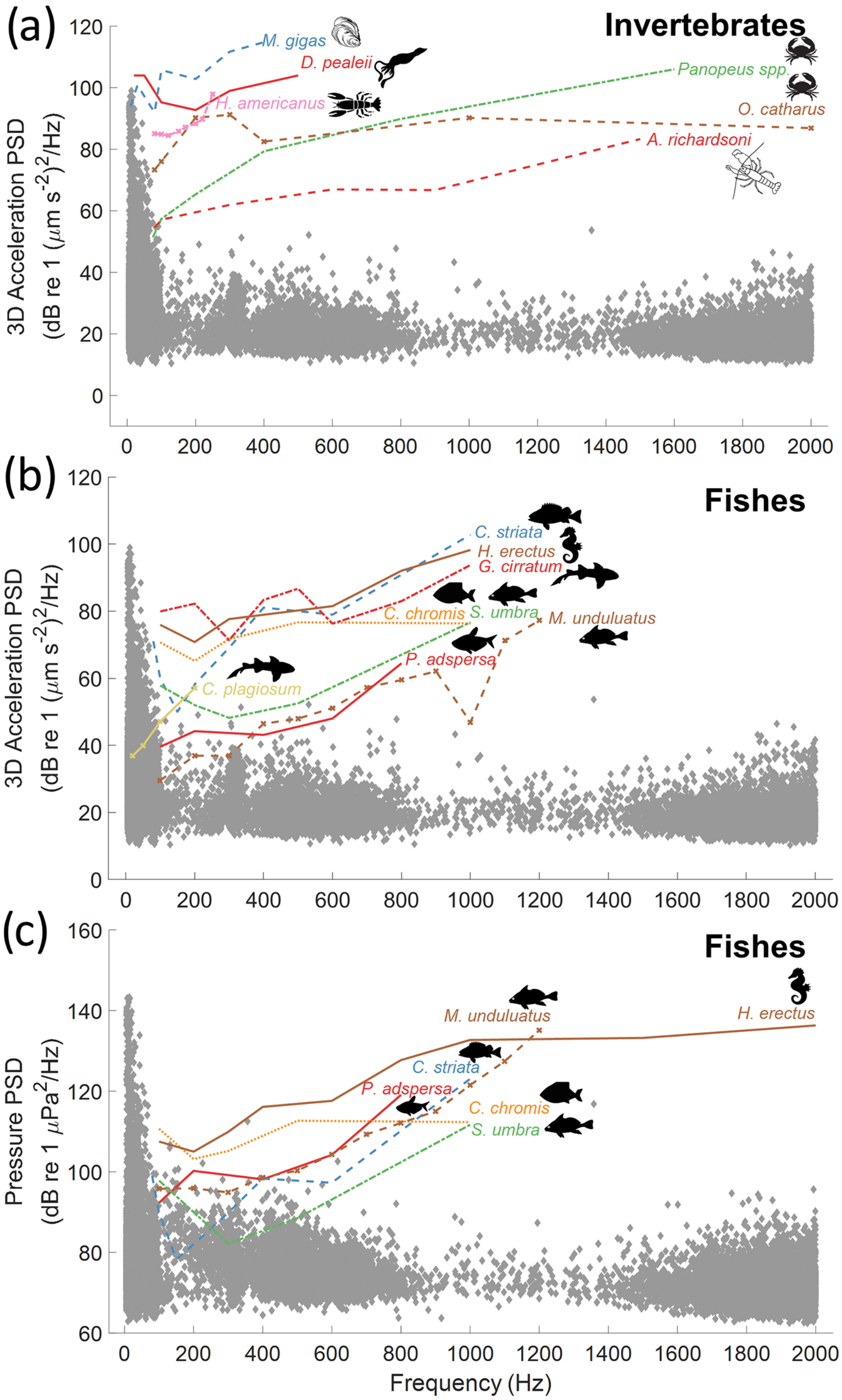

FIG. 7. (Color online) Peak PSD of 3D particle acceleration from Tektite compared with selected published audiograms of (a) invertebrates and (b) fishes. (c) Audiograms of pressure-sensitive fishes in (b) compared with peak PSD of pressure from Tektite. Each point (diamond) represents the peak amplitude and frequency for a 3 s recording. Invertebrates: *Magallana gigas* (Pacific oyster; Charifi *et al.*, 2017), *Doryteuthis pealeii* (longfin squid; Mooney *et al.*, 2010); *Homarus americanus* (American lobster; Jézéquel *et al.*, 2021); *Panopeus* spp. (mud crab; Hughes *et al.*, 2014); *Ovalipes catharus* (paddle crab; Radford *et al.*, 2016); *Alpheus richardsoni* (snapping shrimp; Dinh and Radford, 2021). Fishes: *Centropristis striata* (black sea bass; Stanley *et al.*, 2020); *Hippocampus erectus* (lined seahorse; Anderson and Mann, 2011); *Ginglymostoma cirratum* (nurse shark; Casper and Mann, 2006); *Chromis chromis* (damselfish; Wysocki *et al.*, 2009); *Sciaena umbra* (brown meagre; Wysocki *et al.*, 2009); *Micropogonias unduluatus* (Atlantic croaker; Horodysky *et al.*, 2008); *Pempheris adspersa* (bigeye; Radford *et al.*, 2012); *Chiloscyllium plagiosum* (white-spotted bamboo shark; Casper and Mann, 2007). All thresholds were measured with auditory evoked potentials, except for *M. gigas* which is a behavioral threshold based on valve closure. Thresholds for *D. pealeii* and *C. plagiosum* were obtained using a shaker table; a speaker was used to present stimuli for all other species.

have been used to approximate those of fishes (Hawkins and Chapman, 1975; Stanley *et al.*, 2017). Percentiles of 1 octave levels during dawn at Tektite (these percentiles were nearly identical for dusk), and examples of fish and boat noise in the 99th percentile at Tektite were compared with audiograms (Fig. 8). The 90th and 99th percentiles of natural ambient levels, and 99th percentiles of fish sounds and boat noise reached or exceeded particle acceleration thresholds of two of the most particle motion-sensitive fish species shown in Fig. 7(b). These thresholds were still above median ambient octave band levels.

E. Particle motion trends as indicators of habitat quality

Strength of the diel 3D PAL_{rms} trend (ratio of dawn or dusk level to night level) was significantly correlated with percent coral cover ($p < 0.05$, Fig. 9), but was not significantly correlated with fish species richness and fish abundance.

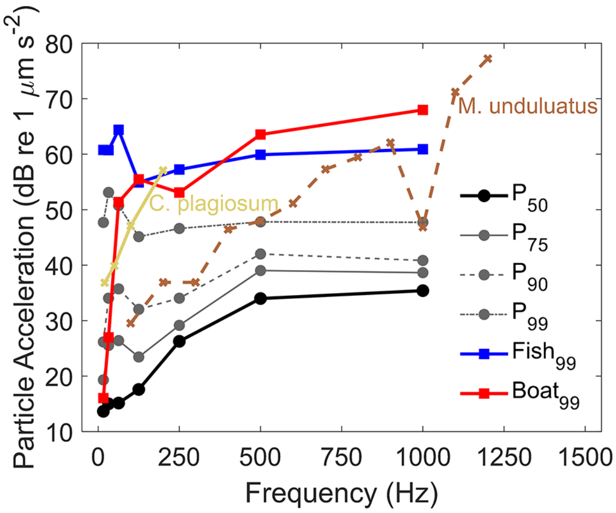

FIG. 8. (Color online) One octave smoothing of 3D particle acceleration PSD data, as percentiles (P_{50} = median, P_{75} = 75th percentile, etc.) during dawn at Tektite, across the March–August analysis period. Also shown are 1 octave band levels of an example fish sound [from Fig. 5(a)] and boat noise [from Fig. 6(b)] at Tektite, which were within the 99th percentile. Audiograms are shown for two fishes in Fig. 7(b) with low particle acceleration thresholds: *Micropogonias unduluatus* (Atlantic croaker; Horodysky *et al.*, 2008); *Chiloscyllium plagiosum* (white-spotted bamboo shark; Casper and Mann, 2007).

Regression coefficients indicated moderate-to-strong correlation for all metrics (R^2 range: 0.72–0.93). Diel strength of SPL_{rms} showed a significant correlation with percent coral cover ($p < 0.05$, dawn $R^2 = 0.96$, dusk $R^2 = 0.98$) and fish abundance ($p < 0.05$ for dawn only, $R^2 = 0.98$), and weaker correlation with fish species richness ($R^2 = 0.58$–0.82, Fig. S6).[1] For each site, 3D PAL_{rms} and SPL_{rms} diel trend strength (Fig. S6)[1] were similar, within 2 dB of each other.

IV. DISCUSSION

This dataset demonstrated key relationships between particle acceleration and pressure at shallow coral reefs. Parameters were found at which these metrics led to similar results, and at which empirical acceleration diverged from common theoretical approximations. Ambient particle acceleration levels, and even those of outlier (high amplitude) fish and boat sounds, were often below particle acceleration detection thresholds reported for invertebrates and for many fish, suggesting limited detectability of reef sounds by these taxa or an overestimate of detection thresholds. Last, the strength of diel trends in particle acceleration and pressure significantly correlated with visual habitat quality indicators, such as coral cover, indicating both of these soundscape quantities may potentially be utilized to monitor and predict changes in reef health.

A. Particle acceleration relationships with sound pressure

As seen in the regression plots (Fig. 3; Fig. S2), root mean square particle acceleration levels positively correlated with sound pressure levels, although these data appeared to have two overlapping clusters around slightly different slopes. The lower amplitude cluster ($PAL_{rms} < 45$ dB; $SPL_{rms} < 100$ dB) likely included sounds more closely approximating plane wave propagation in the acoustic far field. The higher amplitude cluster ($PAL_{rms} > 45$ dB; $SPL_{rms} > 100$ dB) might include more sounds recorded in the near field, for example, fish vocalizing within a few meters of the array, where a higher ratio of particle motion to pressure is expected (Gray *et al.*, 2016; Rogers and Cox, 1988). Relative magnitudes of particle motion (velocity or acceleration) over distance in the near field depend on the type of acoustic field (e.g., monopole, dipole, multipole) and its frequency content (Kalmijn, 1988; Popper and Hawkins, 2018). Such "near field effects" may have contributed to higher particle acceleration than predicted for far field plane waves, as seen for higher amplitude sounds (>45 dB re 1 μm s^{-2}, Fig. 3) and at lower frequencies (<100 Hz, Fig. S3).[1] Plane wave propagation is also limited by depth. A cutoff frequency exists below which sounds do not propagate as plane waves, and this cutoff is higher for shallower depths with a given substrate (Ainslie, 2010; Nedelec *et al.*, 2016). The acoustic recorders in the present study were over sandy patches within a reef. Using typical density (2140 kg m^{-3}) and sound speed (1797 m s^{-1}) values for sandy substrate (Merchant *et al.*, 2015), the cutoff frequencies were below 100 Hz for each site (as low as 47 Hz for Tektite and as high as 71 Hz for Cocoloba, depending on site depth). Below these cutoff frequencies empirical particle acceleration was much greater than that predicted for plane waves. Thus, the relatively shallow depths of the reef sites (<11 m) may have also contributed to higher particle motion to pressure ratios than those predicted for plane waves; the highest of these ratios was at the two shallower sites, Ram Head and Cocoloba (Fig. S2).[1] Differences between empirical and theoretically estimated particle motion may also arise from the directional nature of many fish and other natural sounds, which tend to propagate as dipoles or higher-moment (multipole) fields with variable magnitudes of particle motion along different spatial axes (Kalmijn, 1988). Notably, the directionality of these sounds also presents challenges in detecting and identifying soniferous species when vocalizations are directed away from stationary recorders, or reach recorders *via* indirect paths. Overall, the soundscape data show that using the plane wave approximation (e.g., from single pressure measurements) will underestimate particle motion magnitudes of many sounds present on coral reefs.

Studies correlating empirically measured particle motion and pressure in the field are rare. Similar to the present study, a 2 day study in a shallow (8 m deep) bay in Brazil found that dawn and dusk chorus patterns were present in particle velocity and pressure data; however, near crepuscular periods, particle velocity and acceleration data had low-frequency (<120 Hz) peaks not present in pressure data (Jesus *et al.*, 2020). Similarly, in shallow streams (<1 m depth), particle velocity to pressure ratios were greater than those expected for plane waves at sites with relatively high ambient noise, from 50–100 Hz (Lugli and Fine, 2007). These results are

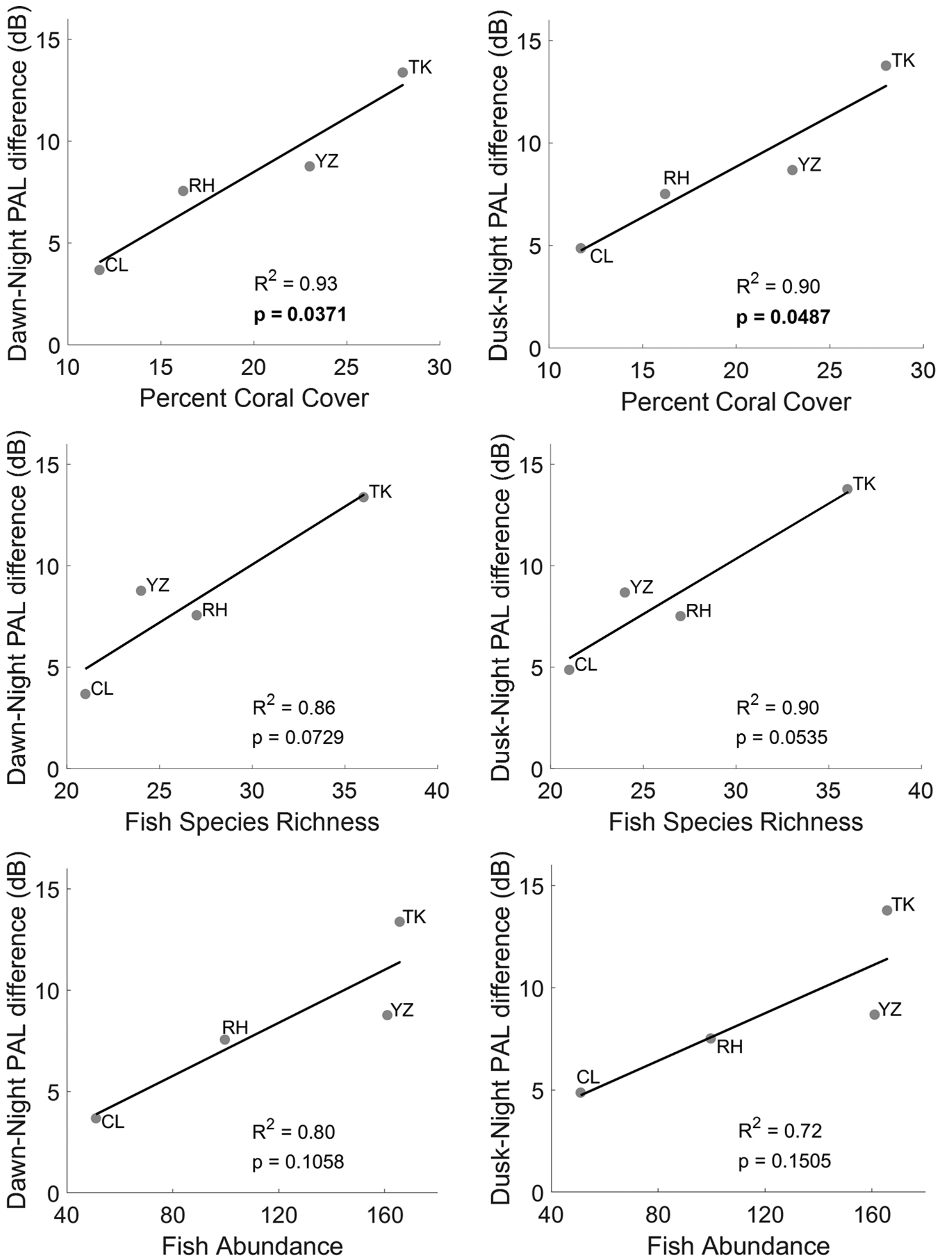

FIG. 9. Diel strength of 3D root-mean square particle acceleration (PAL_{rms}) at each site, of dawn peaks relative to night (left column), and dusk peaks relative to night (right column) versus visual survey metrics including percent coral cover, fish species richness, and fish abundance. R^2 and p values were obtained from Pearson's correlation. Significant p values ($p < 0.05$) are in bold.

expected for relatively low frequencies and shallow environments, and for sounds recorded close to boundaries or close to the sound source (Horch and Salmon, 1973; Jesus *et al.*, 2020; Nedelec *et al.*, 2016).

Conversely, longer-term daily trends (Fig. 2) and diel trends (Fig. 4), were similar when quantified in either particle acceleration or sound pressure. Therefore, fishes and invertebrates experience the same long-term trends and diel cycles in particle acceleration levels as those observed in sound pressure. Accordingly, sound pressure is likely sufficient in describing these temporal trends of coral reef soundscapes. Potentially, future soundscape studies could estimate a time window "threshold", where sound pressure and particle motion are equally represented in longer time windows, but may diverge in shorter time windows.

B. Particle motion of fish sounds: Temporal and spectral variability

Diel trends of sound pressure were consistent with those of prior studies that reported data from the same reefs (Kaplan *et al.*, 2015; Lillis *et al.*, 2018). Tektite had the strongest crepuscular peaks of particle acceleration and sound pressure, also consistent with sound pressure data at Tektite over the same months in 2013 (Kaplan *et al.*, 2015). At coral reefs in Maui, Hawaii, low-frequency (50–1200 Hz) sound pressure was significantly positively correlated with soniferous fish abundance (Kaplan *et al.*, 2018). Reasons for the higher peaks and higher variance in diel levels at Tektite are unknown, but these could be attributed to a higher abundance or diversity in soniferous species, greater number of different types of fish sounds, or variability in distance of sound-producing fish from the acoustic array. Additional work is needed to investigate these phenomena.

C. Directionality of particle motion

Generally, variability in single-axis particle motion levels across sites may have risen due to different orientations of the array with respect to surrounding physical reef structures and sound sources. For three of the reef sites, the vertical axis had slightly lower particle acceleration than horizontal axes, on average. The acoustic array at Yawzi was surrounded by more vertical reef structure than arrays at other sites, which may explain why the vertical particle motion axis at that site was about equal to or slightly higher than the horizontal axes. Directional differences in underwater particle motion have previously been tied to nearby benthic structure and the presence of rocky boundaries (Jesus *et al.*, 2020). On the other hand, directional differences in long-term (e.g., daily) averages of ambient particle acceleration were relatively small (within 3 dB, Fig. 2), suggesting that sounds were coming from many directions with respect to the array. Though particle motion fields likely carry ecologically significant directional cues for invertebrates and fishes (Wilson *et al.*, 2018; Zeddies *et al.*, 2012), the directionality of individual, specific cues (e.g., fish calls) may be more relevant than that of average ambient levels. Future study focusing on the directionality of individual calls or choruses would enhance understanding of the spatial distribution of these sounds and their producers. Recent localization algorithms have been successfully applied to data from two-dimensional hydrophone arrays deployed on coral reefs to determine the direction and spatial distribution of transient fish sounds (Thode *et al.*, 2021).

D. What aspects of the particle motion soundscape are detectable by fishes and invertebrates?

The present dataset suggests invertebrates and many fishes could rarely detect ambient natural soundscape cues or boat noise present on these reefs, especially above 100 Hz. Similarly, particle acceleration measurements directly above reefs in Maui, Hawaii, were below published particle acceleration thresholds of many species except Atlantic croaker (Kaplan and Mooney, 2016). Pressure-derived hearing thresholds of butterflyfish (native to the Indo-Pacific) also are above the ambient levels of their reef habitats from 100–1000 Hz, but the sound pressure of some signals produced by conspecifics slightly exceed hearing thresholds (Tricas and Webb, 2016). These butterflyfish predominantly sense particle motion over sound pressure, yet their particle acceleration thresholds from 100–1000 Hz are still above the maximum values recorded on St. John and Maui reefs (Tricas and Webb, 2016).

Though determination of communication and detection distances was not a goal of the present study, these results reinforce prior studies that estimate short communication and detection distances of fish calls, such as those of damselfish and oyster toadfish, at only 5–10 m away (Higgs and Radford, 2016). These results also reinforce the idea that particle motion cues from coral reefs are likely of limited use to fishes and invertebrates for navigation toward reefs, as discussed in Kaplan and Mooney (2016). Currently, the present study lacks data on the distance of fish calls and other sounds from the array, and there is a further lack of empirical data on the distances over which fishes and invertebrates can detect particle motion of ecologically relevant cues (e.g., a sound from a conspecific or competing animal, versus experimental pure tones). The present dataset provides baseline empirical measurements of ambient reef particle acceleration levels, which can be leveraged in future studies investigating detection distances of particle motion cues for reef inhabitants.

It may be advantageous for coral reef fishes and invertebrates to be unable to detect lower amplitude, ambient reef sounds. They may primarily need to detect sounds from conspecifics or other species at close range and higher amplitudes, e.g., for communication or detecting predators or prey. The "background" biological cacophony of ambient noise on reefs may be less ecologically relevant. Essentially, animals might "filter" cues out from the noise by only detecting higher sound levels, i.e., by having relatively high hearing thresholds; this phenomenon has been demonstrated in several fish species (Ladich, 2019; Wysocki and Ladich, 2005). Thus, detection of nearby sounds above hearing thresholds could be less prone to masking from ambient noise.

Although the present results are consistent with prior studies reporting ambient particle acceleration levels below fish and invertebrate thresholds, there are many challenges and unknowns in making these comparisons, which preclude concluding *with certainty* that invertebrates and fish could rarely detect particle motion cues of these reef soundscapes. These include: (1) limitations and differences in methods used to collect audiograms, and (2) unknowns regarding how invertebrates and fishes perceive particle motion.

Generally, fishes and invertebrates are most sensitive to particle motion at frequencies below 100 Hz (Packard *et al.*, 1990; Sand and Karlsen, 2000), where soundscape data from St. John reefs had the highest peak PSD values. Fishes are thought to rely on particle motion more at lower frequencies to detect signals, and pressure more at higher frequencies (Ladich and Fay, 2013; Wysocki *et al.*, 2009). However, audiogram data for most of these species has only been obtained as low as 80–100 Hz due to methodological limitations, such as the limited frequency output range of commonly used underwater speakers (Tricas and Webb, 2016). Thus, there is a need for more studies addressing lower frequencies of hearing thresholds. Also, other species inhabiting St. John and Caribbean reefs may have different particle motion sensitivities than the species presented here.

There are technical limitations and methodological differences among many audiogram studies that may lead to higher measured thresholds (lower sensitivity) than the "true" thresholds of animals. First, audiograms measured *via* neurophysiological methods tend to be higher than those measured *via* behavioral responses, sometimes by 20 dB, as demonstrated in some fishes (Kojima *et al.*, 2005). Nearly all of the audiograms shown in Fig. 7 are based on neurophysiological data (auditory evoked potentials). Also, many hearing studies use monopole speaker setups, whereas natural sounds such as fish calls may be more dipole or multipole, and thus more highly directional (Kalmijn, 1988; Teddies *et al.*, 2012). For example, white-spotted bamboo sharks had lower hearing thresholds for dipole stimuli (shown in Fig. 7) compared to monopole stimuli (Casper and Mann, 2007).

There are many uncertainties in the neural mechanisms of how invertebrates and fishes utilize particle motion cues to perceive, locate, and respond to ecologically relevant signals. How exactly these animals integrate particle motion cues along multiple vectors to determine the propagation direction or origin of sounds remains unclear (Budelmann, 1992; Budelmann and Williamson, 1994; Hawkins and Popper, 2018). There is also poor understanding of how fishes and especially invertebrates integrate acoustic particle motion cues across time and frequencies, both at sensory peripheries and higher neural processing centers (Popper *et al.*, 2019). Further, hearing thresholds of fishes can shift ontogenetically, with body size, and with stimulus duration (Popper, 1972; Salas *et al.*, 2018; Stanley *et al.*, 2020; Wright *et al.*, 2011). For more complete and accurate comparisons of invertebrate and fish hearing abilities with particle motion soundscape data, more detailed understanding of hearing mechanisms including directional, frequency, and temporal filtering, more measurements of behavioral responses to ecologically realistic stimuli, and more studies testing hearing of multiple life stages of given species are needed.

E. Particle motion of boat noise at coral reefs

Similar to the fish sounds examined, particle acceleration levels of the highest amplitude boat sounds were above hearing thresholds for invertebrates and for many fish. The highest particle acceleration levels of boat noise in the present study were similar to those recorded from a boat in an Australian marine reserve, which reached 40–50 dB re 1 (μm s^{-2})^2 (Mensinger *et al.*, 2018). This suggests many species of these taxa would have limited detection of boat noise, though they are not necessarily free from potential masking effects. The closer ambient or boat noise spectral levels are to those of ecologically relevant signals, i.e., the lower the signal-to-noise ratio (SNR), the greater the potential for masking effects (Clark *et al.*, 2009). When exposed to boat noise at similar particle motion levels to those recorded on St. John reefs, behavioral changes in fishes have been found, including decreased feeding activity, boldness, and nest care time (Magnhagen *et al.*, 2017; McCormick *et al.*, 2018; Mensinger *et al.*, 2018; Picciulin *et al.*, 2010). Among invertebrates exposed to boat noise at similar sound levels (pressure or acceleration) observed in the present study, past studies have found increased mortality of sea hare larvae (Nedelec *et al.*, 2014), and impaired foraging and antipredator behavior of crabs (Wale *et al.*, 2013). Due to the multitude of adverse effects observed in fishes and invertebrates when exposed to boat noise at similar amplitudes to those recorded in the present study, noise pollution from boats is still of concern for these taxa. Ideally, future studies investigating noise effects should measure particle motion and report dose-response curves to determine minimum particle motion magnitudes needed to elicit behavioral or physiological responses (Wale *et al.*, 2021).

F. Utility and applications of particle motion data in coral reef soundscape studies

When quantifying coral reef soundscapes from the perspective of invertebrates and fishes, whether or not particle motion is important to measure depends on research goals. Particle motion measurement is important when absolute (rather than relative) amplitudes of discrete and transient signals are of interest. As discussed above, particle motion of individual signals on coral reefs, especially in shallower areas, in the near field, and at lower frequencies, may have higher particle motion levels than predicted for plane waves. Thus, for accurate level data (such as to understand or predict noise impacts), actual particle motion data are needed. Particle motion measurements are also critical when assessing detectability or noise impacts of soundscape components in relation to hearing abilities of fishes and invertebrates. Particle motion measurements can provide unique information and insight into acoustic listening and communication space that are particularly relevant to the umwelt of the animal.

As mentioned in Sec. I, particle motion will provide directional information about soundscape cues not present in pressure data from single hydrophones, i.e., the direction of a sound and how these cues vary in magnitude along different spatial axes at given points in an acoustic field (Thode *et al.*, 2021). This study did not focus on quantifying directionality of particle motion of individual soundscape components (fish sounds or boat sounds), but sound localization (*via* partial motion) is certainly biologically vital and should be investigated in future studies.

Strengths of diel particle acceleration and sound pressure cycles correlated strongly with percent coral cover and fish abundance, consistent with findings for sound pressure in 2013 at these reef sites (Kaplan *et al.*, 2015). At other tropical coral reefs, significant positive correlations have also been found between sound pressure levels at relatively low frequencies (< 2500 Hz) and visual metrics of reef health, biomass, and biodiversity, including percent coral cover, fish density, habitat complexity, and more (Elise *et al.*, 2019; Nedelec *et al.*, 2015; Staaterman *et al.*, 2017). When such trends in relative magnitudes are of interest rather than absolute magnitudes or directional information, and when applying these trends to monitor and predict changes in reef habitat health, reporting sound pressure may suffice (Mooney *et al.*, 2020).

V. CONCLUSIONS AND FUTURE DIRECTIONS

This study is the first to report spatial and temporal particle motion trends of coral reef soundscapes for a duration longer than a few days, and is the first to report particle motion data at Caribbean reefs. For these relatively shallow reefs, particle acceleration levels scaled similarly with sound pressure at higher frequencies and when averaged over time, but they diverged at lower frequencies and among individual, high amplitude signals. These empirical data provide new insights, and validations of concepts described in recent review papers (Nedelec *et al.*, 2016; Popper and Hawkins, 2018), on the contexts in which particle motion measurement is necessary for aquatic soundscape studies, and where it may not be necessary.

Particle motion measurements are essential when investigating invertebrates' and fishes' detection and utilization of soundscape cues. These data help place hearing abilities in context. Invertebrate and fish hearing thresholds were high relative to peak soundscape levels. This was surprising considering that many members of these taxa have shown phonotaxis and settlement responses to reef sounds, and produce sounds for communication. This brings into question how representative available particle motion audiogram data are of "true" hearing sensitivities. Indeed, many sources of uncertainty still exist in comparing animal hearing data to ambient soundscape data. Development of widely-accepted standards for hearing measurements in aquatic invertebrates and fishes and for particle motion measurement, as established for mammals and sound pressure, would aid in these efforts.

Baseline, long-term particle motion recordings, such as those from the present study, are useful for investigating the spatial and temporal scales over which reef animals utilize soundscape cues for diverse ecological functions. Reporting particle motion of anthropogenic soundscape components is key to monitoring and predicting anthropogenic impacts on invertebrates and fishes. Last, this study highlights the relevance of "rare", transient, and high amplitude sounds to invertebrates and fishes over lower amplitude ambient levels. Future studies should focus on describing and exploring automated detection of these transients, as well as identification of the species producing them.

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[1]See supplementary material at https://www.scitation.org/doi/suppl/10.1121/10.0012579 for additional supporting figures cited in the Methods and Results sections.

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