Ground-truthing daily and lunar patterns of coral reef fish call rates on a US Virgin Island reef

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ABSTRACT: Coral reefs comprise some of the most biodiverse habitats on the planet. These ecosystems face a range of stressors, making quantifying community assemblages and potential changes vital to effective management. To understand short- and long-term changes in biodiversity and detect early warning signals of decline, new methods for quantifying biodiversity at scale are necessary. Acoustic monitoring techniques have proven useful in observing species activities and biodiversity on coral reefs through aggregate approaches (i.e. energy as a proxy). However, few studies have ground-truthed these acoustic analyses with human-based observations. In this study, we sought to expand these passive acoustic methods by investigating biological sounds and fish call rates on a healthy reef, providing a unique set of human-confirmed, labeled acoustic observations. We analyzed acoustic data from Tektite Reef, St. John, US Virgin Islands, over a 2 mo period. A subset of acoustic files was manually inspected to identify recurring biotic sounds and quantify reef activity throughout the day. We found a high variety of acoustic signals in this soundscape. General patterns of call rates across time conformed to expectations, with dusk and dawn showing important and significantly elevated peaks in soniferous fish activity. The data reflected high variability in call rates across days and lunar phases. Call rates did not correspond to sound pressure levels, suggesting that certain call types may drive crepuscular trends in sound levels while lower-level critical calls, likely key for estimating biodiversity and behavior, may be missed by gross sound level analyses.

KEY WORDS: Marine protected area · Soundscape · Noise · Biodiversity · Acoustic behavior · Monitoring · Tropics

1. INTRODUCTION

As global biodiversity continues to decline (Butchart et al. 2010), cost-effective and scalable ecosystem monitoring techniques are of increasing importance (Cardinale et al. 2012). Passive acoustic monitoring (PAM) is a non-invasive and highly scalable monitoring method which has been used to examine the health and biodiversity of marine and terrestrial ecosystems by extracting significant biological patterns from acoustic recordings over days to several months (Buxton et al. 2018, Gibb et al. 2019, Mooney et al. 2020). Animals produce and use sound for a wide variety of behaviors, including intentional acoustic signals for mate attraction, echolocation, group cohesion, and territorial defense as well as unintentional sounds from movement and feeding (Bradbury & Vehrencamp 1998). By detecting and

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monitoring changes in biological sounds of interest, it is possible to gain insight into the presence and activity of species and perhaps detect ecologically important behaviors such as foraging or spawning events (Myrberg 1986, Mann & Lobel 1995, Nordeide & Kjellsby 1999, Lobel 2002, Jones et al. 2004).

Coral reefs comprise some of the most biodiverse habitats on the planet (Odum & Odum 1955, Connell 1978, Birkeland 1997). PAM on coral reefs has been implemented in multiple studies (e.g. Kennedy et al. 2010, Kaplan et al. 2015, Staaterman et al. 2017, Dimoff et al. 2021) but is just beginning to gain traction as a reef-habitat monitoring and management tool. Yet PAM on reefs is rapidly expanding due to its potential in tracking environmental changes happening in these critical habitats. Many reefs are threatened by a range of local and global stressors, from overfishing (Jackson et al. 2001, Pandolfi et al. 2003) and pollution (McCulloch et al. 2003) to climate change (Gardner et al. 2003, Hughes et al. 2003). Reef ecosystems not only foster abundant biodiversity in our oceans but also provide countless ecosystem services, including fisheries (Smith 1978), coastal protection (van Zanten et al. 2014), recreational activities (Brander et al. 2007), and cultural importance (Johannes 2002). It is evident that changes in reef complexity and biodiversity have significant impacts on these ecosystem services (Pratchett et al. 2014).

New methods for quantifying biodiversity at scale are therefore necessary to detect short- and long-term changes in reef complexity and health as global and local threats increase (Beijbom et al. 2012, Mooney et al. 2020, Kennedy et al. 2021). The most common method of reef population and community surveys is diver-based underwater visual censuses (Brock 1954). These observations can be extremely time-consuming, cost-prohibitive in remote locations, can introduce observer bias, and may alter fish behavior, likely confounding biodiversity metrics (Brock 1982, Sale & Sharp 1983, Thompson & Mapstone 1997, Edgar et al. 2004, Harvey et al. 2004). To reduce these biases, there has been increasing interest in non-invasive methods that monitor species abundance and biodiversity. Reefs lend themselves particularly well to PAM because of the abundance of intentional and unintentional biotic sounds from soniferous fish and invertebrates (Rice et al. 2022), and so by listening for reef sounds associated with soniferous fish and invertebrates, researchers can monitor reefs passively. Sound is an important component of many reef fish behaviors such as mating, feeding, and communication (Myrberg 1981, 1986, Mann & Lobel 1997, Tricas & Boyle 2021). Reef soundscapes also contain many ancillary sound cues which cause changes in fish and invertebrate activity (Radford et al. 2008, Lillis & Mooney 2018).

An increasing number of studies leverage these sounds and use a higher-level aggregate approach and proxies (i.e. energy, diel patterns, various indices) to estimate community assemblages, complexity, and reef fish diversity due to difficulty in assigning call type to species (Kennedy et al. 2010, Kaplan et al. 2015, Bertucci et al. 2016, Lin et al. 2017, Staaterman et al. 2017). However, these methods can be biased by certain factors, such as the choruses of acoustically dominant species of fish and invertebrates (Mooney et al. 2020), and often fail to verify the actual diversity of call types and their respective call rates. Consequently, bulk analyses can potentially induce inconsistencies when they are used as proxies for biodiversity and biotic activities on a reef.

Here, we sought to expand acoustic methods and data sets by investigating patterns and changes in fish call rates throughout the day using a manual survey method (e.g. Kaplan et al. 2014, Tricas & Boyle 2014, Silva et al. 2016) to identify call presence and discrimination. We examined and analyzed recurring biotic sounds to determine fish vocalization trends and variability at Tektite Reef in St. John, US Virgin Islands (USVI). We selected Tektite Reef based on its relatively high health condition compared to nearby reefs (Kaplan et al. 2015) and its long history of ecological and bioacoustic assessments (Edmunds 2013, Kaplan & Mooney 2015, Kaplan et al. 2015, Lillis & Mooney 2018, Lillis et al. 2018), which provide an important regional baseline and sufficient data to observe overall daily patterns in fish call rates. We then compared trends with existing bulk analytical methods applied to our data.

2. MATERIALS AND METHODS

Data were collected using a single-channel Soundtrap 300ST recorder (Ocean Instruments). The recorder was placed at Tektite Reef (18° 18′ 26.8″ N, 64° 43′ 14.7″ W; Fig. 1), 0.5 m above the benthos, attached to a rebar stake. From prior acoustic monitoring studies, we knew Tektite was acoustically rich relative to surrounding reefs and that this richness corresponded with observed high fish diversity (Kaplan et al. 2015). The SoundTrap was deployed from 19 March to 12 July 2017 and set to record on a duty cycle with 3 s of self-calibration and 60 s of recording every 10 min. For data analysis, 8 d were sampled by 2 independent, trained analysts in April
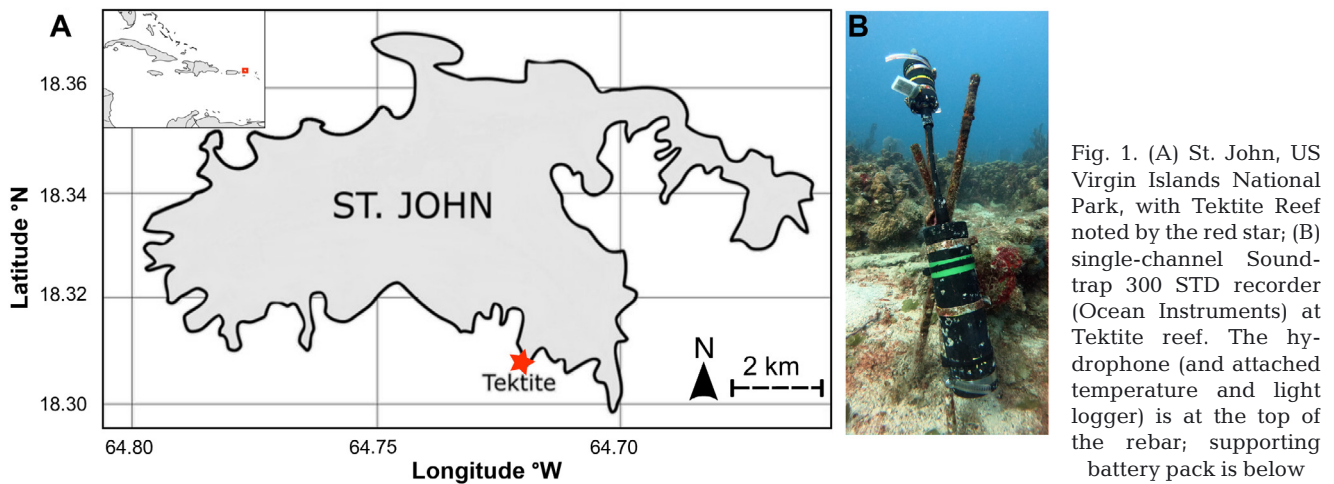
Fig. 1. (A) St. John, US Virgin Islands National Park, with Tektite Reef noted by the red star; (B) single-channel Sound-trap 300 STD recorder (Ocean Instruments) at Tektite reef. The hydrophone (and attached temperature and light logger) is at the top of the rebar; supporting battery pack is below

and May 2017 during the full (11 April, 12 May), third-quarter (19 April, 18 May), new (26 April, 25 May), and first-quarter (2 May, 1 June) moons. Because such manual analysis was extremely time-intensive, the goal here was not to characterize all fish sounds found on Tektite Reef but to investigate prominent call types and quantify call rates during early summer, an acoustically active season (Kaplan et al. 2015), as a first look into call patterns and fine-scale acoustic diversity. This analysis would then provide a key comparison to batch analyses, for example using bandpass-filtered sound pressure levels (SPLs) as a proxy for fish activity (Staaterman et al. 2014, Bertucci et al. 2015, Kaplan et al. 2015). Furthermore, our analyses include fine-scale labels which will help validate subsequent automated acoustic event detection and classification efforts.

To label individual acoustic events, we used an interactive graphical user interface created in MAT-LAB R2020a (MathWorks) to visualize and analyze 1 min sound files every 30 s for each recording day. Recordings were first down-sampled from their original 48 kHz sampling rate to 4000 Hz, allowing for analysis of sounds in the frequency band from 0–2000 Hz containing nearly all fish vocalizations (Tricas & Boyle 2014, Kaplan et al. 2015). Spectrograms (128 point, 32 ms Hamming window, 75% overlap, 1024 point Fast Fourier Transform size) were visualized in 10 s time frames to better observe calls. Individual calls were manually labeled with time–frequency bounding boxes within those 10 s spectrograms (see Fig. 2A). Time and frequency limits and corresponding labels were saved to a text file associated with each audio file. Because these reefs experience intermittent small boat traffic (Dinh et al. 2018), we labeled and removed periods with audible boat

noise that could mask detection of fish calls, similar to Kaplan et al. (2015). A final check of each file was made after initial auditing to parse out dense vocalization sequences.

Call rate for each file was calculated as the number of calls per minute (of all call types) of audio after excluding periods with vessel noise (e.g. Kaplan et al. 2015). Average call rate per minute was determined throughout the 8 d of data for each 1 h interval. To observe patterns in dawn and dusk chorusing peaks, call rates were aggregated and averaged among night, dawn, day, and dusk (defined as 20:01–04:34, 04:35–05:53, 05:54–18:42, and 18:43–20:00 h, respectively) following data on www.timeanddate.com (Table 1).

As a comparison to call rate estimates, we quantified the received SPL within the fish band, a 50–1200 Hz low-frequency band that includes most fish acoustic activity, as a proxy for large-scale biotic activity, following previous studies (Kaplan et al. 2018, Au & Banks 1998, Tricas & Boyle 2014). Files containing vessel noise were removed from the analysis. We filtered each file with a 50–1200 Hz 4-pole Butterworth bandpass filter, then calculated the root-mean-square (RMS) SPL for each 1 s period, transformed it to decibels, and corrected for the acoustic

Table 1. Corresponding times of analysis periods

Time period	Start time (h)	End time (h)
Night	20:01	4:34
Dawn	4:35	5:53
Day	5:54	18:42
Dusk	18:43	20:00

sensitivity of the instrument using calibration levels from the manufacturer. Finally, we calculated the arithmetic mean RMS SPL for each file as a direct comparison to the manual call count estimates.

A linear mixed-effects model was used to observe how time of day and lunar phase affected call rates, using the 'lme4' toolbox (Bates et al. 2015) in R v.4.1.2 (www.r-project.org/). We modeled time of day and lunar phase as fixed effects to examine their importance to call rate and mean sound level. To account for variation between individual days, we added day as a random effect on the intercept. We generated 4 nested models: a null model with only day as a random effect, 2 extending models that were the same as previous but sequentially added time of day and lunar phase, and finally a full model that included the interaction between time of day and lunar phase. A stepwise likelihood ratio test was performed from most to least complicated model using the 'anova' function from the 'car' package in R (Fox & Weisberg 2019) to evaluate the importance of each fixed effect and determine which model was best fitted to the data. A pairwise comparison using the 'lsmean' toolbox (Lenth 2016) in R was then used to determine whether average call rates at night, dawn, day, and dusk were significantly different from each other.

To understand the impact of individual calls on total energy content of the soundscape, we filtered all manually labeled fish sounds with a 50–1200 Hz 4-pole bandpass filter. We then defined the call duration as the period containing 95 % of the total acoustic energy (following Madsen et al. 2006) and calculated the received level (RL) as the RMS SPL over the 95 % energy duration. Finally, we estimated the sound exposure level (SEL) for each call by multiplying the average intensity by the total duration (in decibels, by adding $10 \times \log_{10}[d]$ to the RMS SPL in dB).

3. RESULTS

We addressed fish call rates on a coral reef across 8 d of recordings spread over 2 mo. Like many coral reefs, Tektite Reef provides habitat to a community of fish and invertebrates across trophic levels (Kaplan et al. 2015, Mooney et al. 2017); consequently, a diversity of call types were noted across these days and months. Given the previous efforts to address sound energy on reefs, this particular effort sought to address the temporal patterns of these reef fish calls with respect to overall sound levels. Call classification was not addressed here specifically but is

a focus of ongoing work. To provide some context, Fig. 2 shows a series of example spectrograms with 4 call types that were seen most often. The low-frequency soundscape was primarily dominated by a variety of pulsed calls (Fig. 2B–D), though occasional tonal calls were also present, and at least one tonal call type (Fig. 2E) was seen intermittently throughout the 8 d.

Hourly rates of individual biological calls showed general peaks around dawn (05:30 h) and dusk (19:30 h) (Fig. 3). However, there appears to be a wide variety in call rate throughout each day. The highest call rate was seen at 19:30 h on 19 April (Fig. 3C), with 149.5 calls min^{-1}. The lowest call rate was 8.5 calls min^{-1} at 15:30 h on 2 May (Fig. 3E).

The linear mixed-effects model showed that time of day had a significant effect on call rate and that the effect of time of day depended on lunar phase (Table 2, Fig. 4A). However, phase alone did not have an impact on call rate. Akaike's information criterion (AIC) suggests the full model is best (AIC = 3145.2), while Bayesian information criterion (BIC) suggests Model 1 is the best (BIC = 3170.4). This discrepancy indicates that the effect of the interaction between time of day and lunar phase is tentative.

Mean nighttime call rates (65.3 ± 5.17 calls min^{-1}) and daytime call rates (59.8 ± 5.08 calls min^{-1}) were lower than the mean call rate at dawn (81.3 ± 7.84 calls min^{-1}) and dusk (79.3 ± 7.11 calls min^{-1}). Using pairwise comparisons, the dawn and dusk periods showed significantly higher call rates compared to day (t_{331} = 3.269, p = 0.0065 and t_{331} = −3.418, p = 0.0039, respectively). Dusk and dawn were only borderline significant from dawn (t_{331} = 2.410, p = 0.0771) and dusk (t_{331} = 2.423, p = 0.0748). No other pairwise comparisons were significant.

Received SPL values (dB$_{rms}$ re 1 µPa) between 50 and 1200 Hz showed similar trends, with general peaks at dawn and dusk (Fig. 5). There was variation in energy during each of the 8 d; however, the highest variability was seen during the day (~05:54–18:42 h), with large peaks such as that at 09:30 h on 10 May (Fig. 5B) and 12:30 h on 26 April (Fig. 5D). The average received SPL depended only on time of day and not on lunar phase (Table 3).

Nighttime RLs (93.14 ± 0.25 dB re 1 µPa) were lower than dawn (98.49 ± 0.65 dB re 1 µPa), day (97.58 ± 0.21 dB re 1 µPa), and dusk (98.03 ± 0.55 dB re 1 µPa) (Fig. 4B). Using pairwise comparisons, night showed significantly lower RLs from dawn (t_{380} = 7.782, p = 0.001), day (t_{379} =15.044, p = 0.001), and dusk (t_{379} = 8.278, p = 0.001). All other comparisons were not significant.

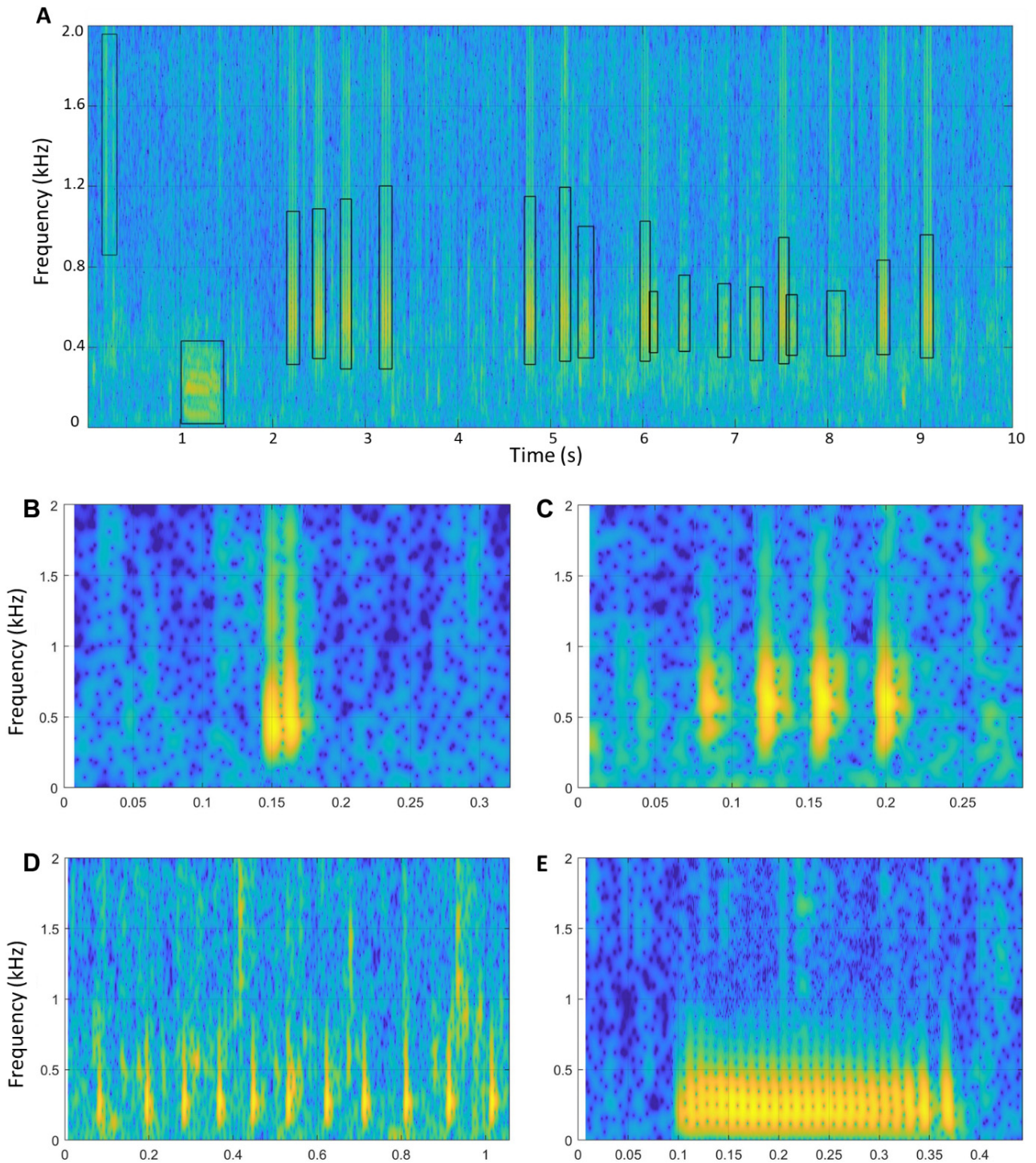Fig. 2. (A) Example spectrogram with bounding boxes around fish sounds and 4 commonly seen call types: (B) double pulse between ~0.2–1 kHz, (C) multipulsed between ~0.2–1 kHz, (D) rapid pulse between ~0.1–0.5 kHz, and (E) low-frequency burst pulse call between ~0–0.5 kHz

While call rates and SPLs appeared to follow a generally similar diel trend, fish calls were generally short (median 95% energy duration: 0.13 s; Fig. 6A) and low amplitude (median RL: 98.5 dB re 1 µPa; Fig. 6B),

resulting in very little energy contributed to the overall soundscape (Fig. 6C). As a consequence, we did not find a significant correlation between received SPLs and call rate (Fig. 6D).
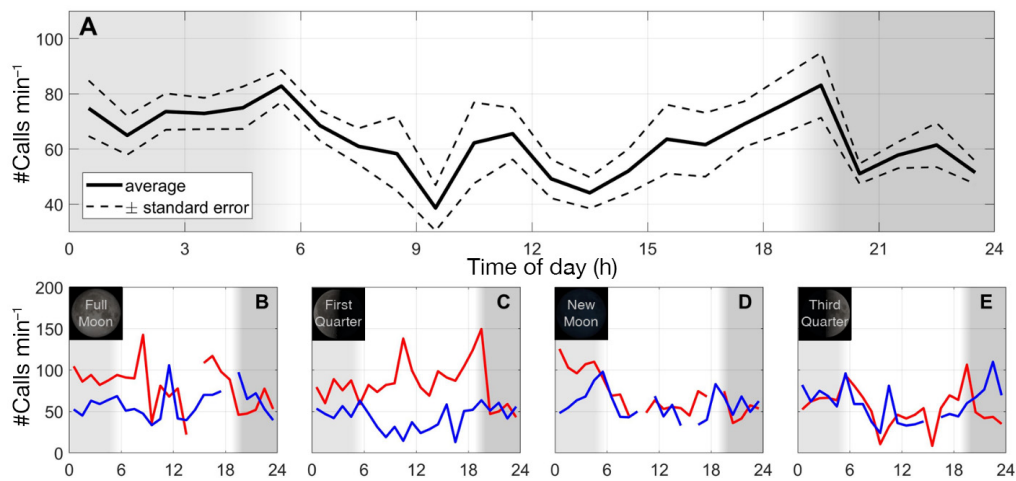
Fig. 3. Temporal variation in hourly acoustic call rates: (A) hourly call rate throughout the day shown across 8 full (24 h) days. Hourly call rate for individual days during (B) full moon on 11 April (red) and 10 May (blue); (C) third-quarter moon on 19 April (red) and 08 May (blue); (D) new moon on 26 April (red) and 25 May (blue); and (E) first-quarter moon on 2 May (red) and 1 June (blue). All call rates were calculated as number of calls in periods without vessel noise divided by the total duration without vessel noise. Gaps: periods where vessel noise masked biotic sounds in both recording files for that hour. Note that call rates are not measured continuously but at 30 min intervals
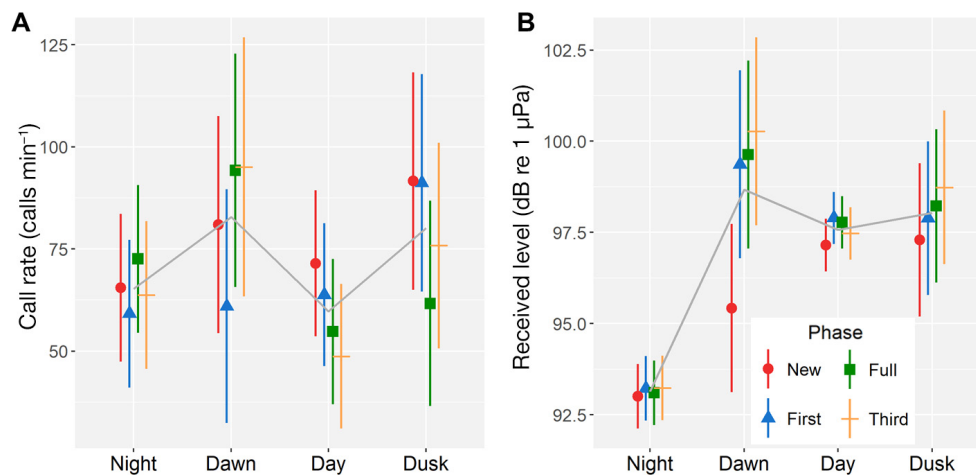

Fig. 4. Relationship between time of day (night, dawn, day, and dusk) and lunar phase (new, first, full, and third moons) on (A) call rate and (B) received levels. Grey line: mean of all lunar values at that time of day. Note that hierarchical model selection showed that, in contrast to call rate, received level was best modeled without accounting for lunar phase but is shown here for comparison

Table 2. Linear mixed-effects model and likelihood-ratio test for call rates. Four linear mixed-effects models were implemented to examine drivers of fish and invertebrate call rate on the reef. Time of day (categorical: night, dawn, day, dusk) and lunar phase (categorical: new, 1st, full, 3rd) were modeled as fixed effects along with their interaction (all in **bold**). Stochastic differences between days were modeled by including day as a random effect on the intercept (in *italics*). Models were tested hierarchically in order of decreasing model complexity, with χ^2 and p-values for each model representing a likelihood-ratio test against the model one level below with a single fixed effect removed (with * and bolded values when p < 0.05). Results show that time of day significantly improved the model, and Akaike's information criterion (AIC) score and likelihood-ratio test further suggest that the effect of time of day depends on lunar phase. BIC: Bayesian information criterion

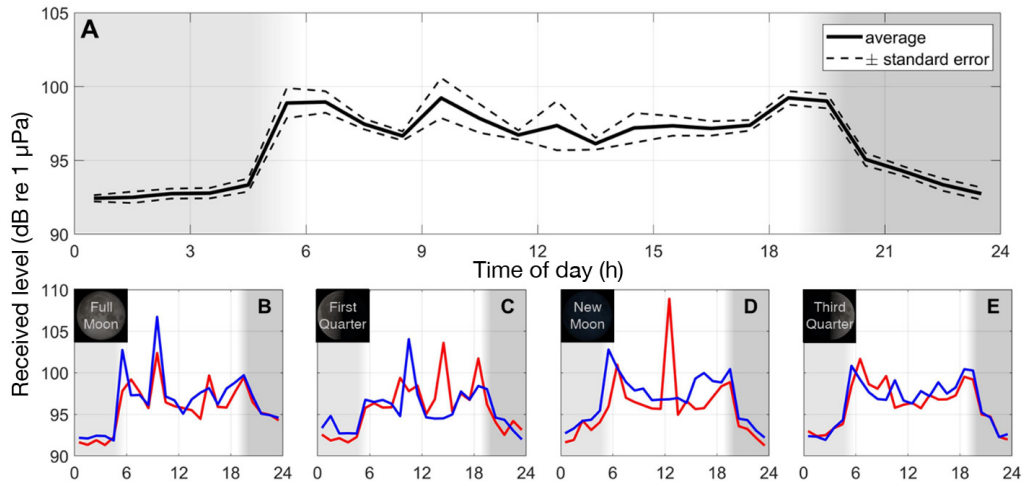| Model		df	AIC	BIC	χ^2	p
Full model:	CallRate ~ **TimeOfDay × Phase + TimeOfDay + Phase** + (*1/Day*)	318	**3145.2**	3213.9	25.349	**0.0026***
Model 2:	CallRate ~ **TimeOfDay + Phase** + (*1/Day*)	327	3152.5	3186.9	0.9373	0.8164
Model 1:	CallRate ~ **TimeOfDay** + (*1/Day*)	330	3147.5	**3170.4**	20.238	**0.0002***
Null model:	CallRate ~ (*1/Day*)	333	3161.7	3173.1		

Fig. 5. Temporal variation in hourly sound pressure level (SPL): (A) hourly received SPL in the 50–1200 Hz frequency band throughout the day shown across 8 d. Hourly received levels for individual days during (B) full moon on 11 April (red) and 10 May (blue), (C) third-quarter moon on 19 April (red) and 18 May (blue), (D) new moon on 26 April (red) and 25 May (blue), and (E) first-quarter moon on 2 May (red) and 1 June (blue). Note that per-file sound pressure level was measured at 30 min intervals for the same files analyzed in Fig. 3

Table 3. Linear mixed-effects models implemented to examine drivers of received sound levels (RL) on the reef. See Table 2 for further details. Results show that time of day significantly improved the model (* and bolded p-values for p < 0.05)

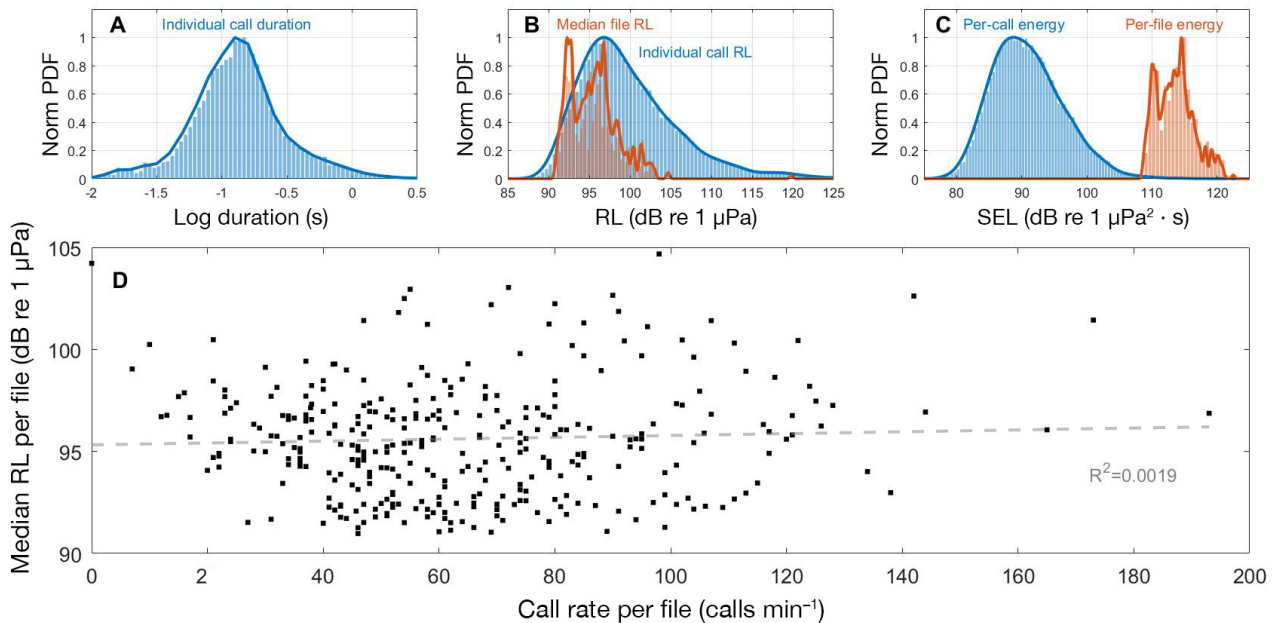| Model		df	ΔAIC	ΔBIC	χ^2	p
Full:	RL ~ **TimeOfDay × Phase + TimeOfDay + Phase** + (*1/Day*)	366	1866.1	1937.1	8.9948	0.4378
Model 2:	RL ~ **TimeOfDay + Phase** + (*1/Day*)	375	1857.1	1892.6	4.0427	0.2569
Model 1:	RL ~ **TimeOfDay** + (*1/Day*)	378	**1855.1**	**1878.8**	196.97	**<0.0001***
Null:	RL ~ (*1/Day*)	381	2046.1	2057.9		

Fig. 6. (A) Duration of individually labeled fish calls (95% energy criteria) shown as a normalized probability density function (Norm PDF); (B) root-mean-square received level (RL) in 50–1200 Hz fish bands for individual fish calls (blue) and median 1 s RL for individual files. (C) Sound exposure level (SEL) for individual fish calls (blue) and 60 s source files (red) showing the relatively low energy content of fish calls compared to the energy content of source files. (D) Relationship between call rate for each file (calls min^{-1}) and median RL for that file. Gray dashed line: linear best fit model (note that correlation is not significant)

4. DISCUSSION

New cost-effective ways to determine coral reef health and biodiversity are needed to understand changes in reef health due to many current stressors. Marine soundscapes have been of increasing interest because they facilitate scalable longer-term observations, are cost-effective, and can support near real-time detection of reef animal activity. However, to our knowledge, most acoustic methods for observing reef soundscapes take a higher-level aggregate approach with limited, albeit time-intensive, assessments of the *in situ* acoustic activity of reef fish and invertebrates. The goal of this study was to determine how call rates within a coral reef soundscape vary throughout the day using a detailed manual method that is often applied to the signals and calls of other vocalizing taxa but rarely applied to fish call rates and characterizations. This work highlights the temporal patterns of these call rates while comparing them to the overall acoustic sound levels on the reefs (Fig. 6).

Using PAM data from St. John (USVI) and manual analysis methods, we observed daily call rates at Tektite, a well-studied reef (Edmunds 2002, 2010). Call rates varied widely, ranging from 10 to 150 calls min^{-1}. We found an increase in call rates around dusk and dawn, similar to those seen in previous studies on this reef (Kaplan et al. 2015) and elsewhere (Staaterman et al. 2014, Kaplan et al. 2018). These methods tend to quantify overall SPLs and thus could be dominated by repeated, high-intensity calls from certain fish or invertebrate choruses (Radford et al. 2008, Parsons et al. 2016, Kahl et al. 2021, Bolgan et al. 2022) and miss more subtle lower-amplitude calls. Interestingly, we did not see a clear association between call SPL and call rate, despite generally similar diel trends (Fig. 6). Most calls were short, low-amplitude (and low signal-to-noise ratio) calls and thus did not contribute much acoustic energy to the larger soundscape (Fig. 6C). Given a median SEL of 90.3 dB re 1 µPa^2·s and a median SEL of 113.4 dB re 1 µPa^2·s per 60 s file, it would take an average of 204 calls to increase the total acoustic energy by 3 dB. There could be many reasons that many reef fish calls are relatively low amplitude, but in part, this may be an ecologically important strategy; to communicate sufficiently with your neighbor conspecifics but not necessarily acoustically advertise one's position on a predator-rich reef.

We also noted an approximate halving of call rates during the day (compared to the crepuscular time periods), suggesting a lower level of activity within the fish community during those periods. Further, these lower daytime call rates underscore the need for caution when applying brief 'snapshot' recordings, especially if they are made during the daytime (Kennedy et al. 2010), as they may not fully capture the acoustic diversity of the reef. Presumably, the fish community did not change substantially during the 8 d recording period, but these data show the call rates did change significantly.

Our current SPL data (Fig. 5) show an increase during the day similar to previous studies (Kaplan et al. 2015), which suggests an increase in biological activity. However, we suspect that these differences may be a result of bulk analyses picking up some component of the background soundscape. This may be simply wind-driven wave sounds from warmer daytime temperatures or an abundance of a few harder-to-discriminate call types (such as choruses and signals near background), which would elevate overall sound levels but be hard to discern and label in our manual analyses. Our analysis methods are not driven by the energy of calls, but each individual call is weighed equally. By taking a more individualized approach, we eliminate background noise sources, such as wind and vessels, that may dominate the soundscape and largely influence energy analyses. Of course, dominant, repetitive individual calls could influence this method, but at least anecdotally (Fig. 2), this was not the case. Further research on call-type characterization would help address this uncertainty.

We also observed variability in call rate throughout each individual day. There are evident peaks in the mornings of 11 and 19 April. Upon further investigation, these peaks appear to be dominated by a single call type, which appears as a triple pulse with a frequency range between 300 and 1200 Hz. During this chorusing, rapid pulsing occurs for about 10 min at a time with up to 40 individual calls within that period. While it is unclear what animal is causing these sounds and for what reason, it is possible that it may be one individual or species. Determining which species is making sounds has been a long-standing question and need in bioacoustics (Fish & Mowbray 1970). New methods such as rebreather or passive acoustic arrays and camera systems are now being applied to address such questions (Tricas & Boyle 2014, Mouy et al. 2018). In many cases, we are still discerning how fish call characteristics are influenced by environmental conditions. Compared to mammals, fish call repertoires are somewhat fixed, but it appears that key events such as changes in temperature, upwelling, or habitat loss may influence call rates and signal parameters (Connaughton

et al. 2002, Mann & Grothues 2009, Papes & Ladich 2011, Mooney et al. 2016, Lamont et al. 2022). More work is needed here to better apply our bioacoustic assessment analysis tools.

Finally, this study underscores that diel patterns are a major driver of call rates, more so than lunar trends observed in the USVI and Hawaiian coral reefs (Kaplan et al. 2015, 2018). Given that bulk analysis methods often compare reef health or biodiversity based on sound levels, a possible next step could be to apply these call rate observations to additional reefs and compare noted call rates and diversity across a range of reef conditions. However, one limitation is the time-intensive nature of such manual analyses (hence the application of diversity and sound-level metrics) (Mooney et al. 2020). Machine learning is also an approach recently applied to coral reef sounds which has been used to identify reef fish choruses and bioacoustic patterns (Lin et al. 2017, Lin & Tsao 2020). Manually labeled data sets provide an important ground-truth resource with which to validate automated machine-learning methods and ultimately allow for scaling up individual-level PAM. Quantifying the call rates of fish, the parameters of those calls, and how such sound patterns may be driven by environmental or human-induced (i.e. noise) changes is a rapidly emerging field (Munger et al. 2022). However, the optimal method of detecting potential changes has yet to be determined. The data here help lay the groundwork for applying emerging methods using traditional detectors or machine learning. SPLs on their own may not be the best metric, but actual call rates can certainly help support those methods as well as elucidate behaviors.

Open-source collections of fish sounds are still in their infancy but are rapidly developing (i.e. recently launched www.fishsounds.net; Looby et al. 2022). Manual identification and labeling of calls, such as this work, or manual labeling of calls and subsequent unsupervised identification of call types (Parra-Hernández et al. 2020, Sainburg et al. 2020) are critical for populating these data collections with a wealth of individual fish and invertebrate sounds.

While this was a quantitative analysis of call rates, a subsequent analysis is underway to examine call types, differentiation, and potential niche with over 100 call types defined (authors' unpubl. data). Discerning call types in coral reefs is challenging because of the high number of calls and the ability of individual species to make a variety of call types depending on behavior (Kasumyan 2008). Previous studies have attempted to determine call types in aquarium settings but have shown that it is impossible to recreate specific behaviors and sounds in captivity (e.g. Hawkins & Amorim 2000, Širović & Demer 2009). Therefore, peer-reviewed efforts to discern call categorization are needed. These can eventually be used for training automated algorithms to simultaneously detect and parse out the rich fauna found in coral reefs, similar to how current deep neural nets are now capable of classifying hundreds of bird sounds with high accuracy (Kahl et al. 2021). Such an individual-level approach to the analysis of coral reef soundscapes may be promising for tracking local abundance of keystone species, invasive species, or sentinel species that respond early to ecosystem changes (Tricas & Boyle 2021) and thus have the potential to transform coral reef ecosystem monitoring.

LITERATURE CITED

Au WWL, Banks K (1998) The acoustics of the snapping shrimp *Synalpheus parneomeris* in Kaneohe Bay. The Journal of the Acoustical Society of America 103:41–47

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Beijbom O, Edmunds PJ, Kline DI, Mitchell BG, Kriegman D (2012) Automated annotation of coral reef survey images. In: 2012 IEEE conference on computer vision and pattern recognition, 16–21 June, Providence, RI. IEEE, New York, NY, p 1170–1177

Bertucci F, Parmentier E, Berten L, Brooker RM, Lecchini D (2015) Temporal and spatial comparisons of underwater sound signatures of different reef habitats in Moorea Island, French Polynesia. PLOS ONE 10:e0135733

Bertucci F, Parmentier E, Lecellier G, Hawkins AD, Lecchini D (2016) Acoustic indices provide information on the status of coral reefs: an example from Moorea Island in the South Pacific. Sci Rep 6:33326

Birkeland C (ed) (1997) Life and death of coral reefs. Springer Science & Business Media, New York, NY

Bolgan M, Di Iorio L, Dailianis T, Catalan IA, Lejeune P, Picciulin M, Parmentier E (2022) Fish acoustic community structure in Neptune seagrass meadows across the Mediterranean basin. Aquat Conserv 32:329–347

Bradbury JW, Vehrencamp SL (1998) Principles of animal communication. Sinauer Associates, Sunderland, MA

Brander LM, Van Beukering P, Cesar HSJ (2007) The recreational value of coral reefs: a meta-analysis. Ecol Econ

63:209–218

Brock RE (1982) A critique of the visual census method for assessing coral reef fish populations. Bull Mar Sci 32: 269–276

Brock VE (1954) A preliminary report on a method of estimating reef fish populations. J Wildl Manag 18:297–308

Butchart SHM, Walpole M, Collen B, van Strien A and others (2010) Global biodiversity: indicators of recent declines. Science 328:1164–1168

Buxton RT, McKenna MF, Clapp M, Meyer E and others (2018) Efficacy of extracting indices from large-scale acoustic recordings to monitor biodiversity. Conserv Biol 32:1174–1184

Cardinale BJ, Duffy JE, Gonzalez A, Hooper DU and others (2012) Correction: corrigendum: biodiversity loss and its impact on humanity. Nature 489:326

Connaughton MA, Fine ML, Taylor MH (2002) Use of sound for localisation of spawning weakfish in Delaware Bay (USA) and effects of fish size, temperature and season on sound parameters. Bioacoustics 12:294–296

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–1310

Dimoff SA, Halliday WD, Pine MK, Tietjen KL, Juanes F, Baum JK (2021) The utility of different acoustic indicators to describe biological sounds of a coral reef soundscape. Ecol Indic 124:107435

Dinh JP, Suca JJ, Lillis A, Apprill A, Llopiz JK, Mooney TA (2018) Multiscale spatio-temporal patterns of boat noise on US Virgin Island coral reefs. Mar Pollut Bull 136: 282–290

Edgar GJ, Barrett NS, Morton AJ (2004) Biases associated with the use of underwater visual census techniques to quantify the density and size-structure of fish populations. J Exp Mar Biol Ecol 308:269–290

Edmunds PJ (2002) Long-term dynamics of coral reefs in St. John, US Virgin Islands. Coral Reefs 21:357–367

Edmunds PJ (2010) Population biology of *Porites astreoides* and *Diploria strigosa* on a shallow Caribbean reef. Mar Ecol Prog Ser 418:87–104

Edmunds PJ (2013) Decadal-scale changes in the community structure of coral reefs of St. John, US Virgin Islands. Mar Ecol Prog Ser 489:107–123

Fish MP, Mowbray WH (1970) Sounds of western North Atlantic fishes. A reference file of biological underwater sounds. Johns Hopkins University Press, Baltimore, MD

Fox J, Weisberg S (2019) An R companion to applied regression, 3rd edn. Sage Publications, Thousand Oaks, CA

Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. Science 301:958–960

Gibb R, Browning E, Glover-Kapfer P, Jones KE, Börger L (2019) Emerging opportunities and challenges for passive acoustics in ecological assessment and monitoring. Methods Ecol Evol 10:169–185

Harvey E, Fletcher D, Shortis MR, Kendrick GA (2004) A comparison of underwater visual distance estimates made by SCUBA divers and a stereo–video system: implications for underwater visual census of reef fish abundance. Mar Freshw Res 55:573–580

Hawkins AD, Amorim MCP (2000) Spawning sounds of the male haddock, *Melanogrammus aeglefinus*. Environ Biol Fishes 59:29–41

Hughes TP, Baird AH, Bellwood DR, Card M and others (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933

Jackson JB, Kirby MX, Berger WH, Bjorndal KA and others (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637

Johannes RE (2002) The renaissance of community-based marine resource management in Oceania. Annu Rev Ecol Syst 33:317–340

Jones GP, McCormick MI, Srinivasan M, Eagle JV (2004) Coral decline threatens fish biodiversity in marine reserves. Proc Natl Acad Sci USA 101:8251–8253

Kahl S, Wood CM, Eibl M, Klinck H (2021) BirdNET: a deep learning solution for avian diversity monitoring. Ecol Inform 61:101236

Kaplan MB, Mooney TA (2015) Ambient noise and temporal patterns of boat activity in the US Virgin Islands National Park. Mar Pollut Bull 98:221–228

Kaplan MB, Mooney TA, Sayigh LS, Baird RW (2014) Repeated call types in Hawaiian melon-headed whales (*Peponocephala electra*). J Acoust Soc Am 136:1394–1401

Kaplan MB, Mooney TA, Partan J, Solow AR (2015) Coral reef species assemblages are associated with ambient soundscapes. Mar Ecol Prog Ser 533:93–107

Kaplan MB, Lammers MO, Zang E, Mooney TA (2018) Acoustic and biological trends on coral reefs off Maui, Hawaii. Coral Reefs 37:121–133

Kasumyan AO (2008) Sounds and sound production in fishes. J Ichthyol 48:981–1030

Kennedy EV, Holderied MW, Mair JM, Guzman HM, Simpson SD (2010) Spatial patterns in reef-generated noise relate to habitats and communities: evidence from a Panamanian case study. J Exp Mar Biol Ecol 395:85–92

Kennedy EV, Roelfsema CM, Lyons MB, Kovacs EM and others (2021) Reef cover, a coral reef classification for global habitat mapping from remote sensing. Sci Data 8: 196

Lamont TA, Williams B, Chapuis L, Prasetya ME and others (2022) The sound of recovery: coral reef restoration success is detectable in the soundscape. J Appl Ecol 59:742–756

Lenth RV (2016) Least-squares means: the R package lsmeans. J Stat Softw 69:1–33

Lillis A, Mooney TA (2018) Snapping shrimp sound production patterns on Caribbean coral reefs: relationships with celestial cycles and environmental variables. Coral Reefs 37:597–607

Lillis A, Apprill A, Suca JJ, Becker C, Llopiz JK, Mooney TA (2018) Soundscapes influence the settlement of the common Caribbean coral *Porites astreoides* irrespective of light conditions. R Soc Open Sci 5:181358

Lin TH, Tsao Y (2020) Source separation in ecoacoustics: a roadmap towards versatile soundscape information retrieval. Remote Sens Ecol Conserv 6:236–247

Lin TH, Fang SH, Tsao Y (2017) Improving biodiversity assessment via unsupervised separation of biological sounds from long-duration recordings. Sci Rep 7:4547

Lobel PS (2002) Diversity of fish spawning sounds and the application of passive acoustic monitoring. Bioacoustics 12:286–289

Looby A, Riera A, Vela S, Cox K and others (2022) Fish-Sounds. www.fishsounds.net (version 1.1.; accessed July 11, 2022)

Madsen PT, Wahlberg M, Tougaard J, Lucke K, Tyack P (2006) Wind turbine underwater noise and marine mammals: implications of current knowledge and data needs. Mar Ecol Prog Ser 309:279–295

Mann DA, Grothues TM (2009) Short-term upwelling events

modulate fish sound production at a mid-Atlantic Ocean observatory. Mar Ecol Prog Ser 375:65–71

Mann DA, Lobel PS (1995) Passive acoustic detection of fish sound production associated with courtship and spawning. Bull Mar Sci 57:705–706

Mann DA, Lobel PS (1997) Propagation of damselfish (Pomacentridae) courtship sounds. J Acoust Soc Am 101: 3783–3791

McCulloch M, Fallon S, Wyndham T, Hendy E, Lough J, Barnes D (2003) Coral record of increased sediment flux to the inner Great Barrier Reef since European settlement. Nature 421:727–730

Mooney TA, Kaplan MB, Izzi A, Lamoni L, Sayigh L (2016) Temporal trends in cusk eel sound production at a proposed US wind farm site. Aquat Biol 24:201–210

Mooney TA, Lillis A, Kaplan MB, Suca J, Lammers M (2017) Variability in coral reef soundscapes, spatiotemporal differences, biophysical and behavioral drivers, and associations with local biota. J Acoust Soc Am 141:3939

Mooney TA, Di Iorio L, Lammers M, Lin TH and others (2020) Listening forward: approaching marine biodiversity assessments using acoustic methods. R Soc Open Sci 7: 201287

Mouy X, Rountree R, Juanes F, Dosso SE (2018) Cataloging fish sounds in the wild using combined acoustic and video recordings. J Acoust Soc Am 143:EL333–EL339

Munger JE, Herrera DP, Haver SM, Waterhouse L and others (2022) Machine learning analysis reveals relationship between pomacentrid calls and environmental cues. Mar Ecol Prog Ser 681:197–210

Myrberg AA (1981) Sound communication and interception in fishes. In: Fay RR, Popper AN, Tavolga WN (eds) Hearing and sound communication in fishes. Springer-Verlag, New York, NY, p 608

Myrberg AA (1986) Sound producing by males of a coral reef fish (Pomacentrus partitus): its significance to females. Anim Behav 34:913–923

Nordeide J, Kjellsby E (1999) Sound from spawning cod at their spawning grounds. ICES J Mar Sci 56:326–332

Odum HT, Odum EP (1955) Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol Monogr 25:291–320

Pandolfi JM, Bradbury RH, Sala E, Hughes TP and others (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955–958

Papes S, Ladich F (2011) Effects of temperature on sound production and auditory abilities in the striped Raphael catfish Platydoras armatulus (Family Doradidae). PLOS ONE 6:e26479

Parra-Hernández RM, Posada-Quintero JI, Acevedo-Charry O, Posada-Quintero HF (2020) Uniform manifold approx-

imation and projection for clustering taxa through vocalizations in a neotropical passerine (rough-legged tyrannulet, Phyllomyias burmeisteri). Animals (Basel) 10:1406

Parsons M, Erbe C, McCauley R, McWilliam J, Marley S, Gavrilov A, Parnum I (2016) Long-term monitoring of soundscapes and deciphering a usable index: examples of fish choruses from Australia. Proc Meet Acoust 27:010023

Pratchett MS, Hoey AS, Wilson SK (2014) Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. Curr Opin Environ Sustain 7: 37–43

Radford C, Jeffs A, Tindle C, Montgomery JC (2008) Resonating sea urchin skeletons create coastal choruses. Mar Ecol Prog Ser 362:37–43

Rice AN, Farina SC, Makowski AJ, Kaatz IM, Lobel PS, Bemis WE, Bass AH (2022) Evolutionary patterns in sound production across fishes. Ichthyol Herpetol 110:1–12

Sainburg T, Thielk M, Gentner TQ (2020) Finding, visualizing, and quantifying latent structure across diverse animal vocal repertoires. PLOS Comput Biol 16:e1008228

Sale PF, Sharp BJ (1983) Correction for bias in visual transect censuses of coral reef fishes. Coral Reefs 2:37–42

Silva TL, Mooney TA, Sayigh LS, Tyack PL, Baird RW, Oswald JN (2016) Whistle characteristics and daytime dive behavior in pantropical spotted dolphins (Stenella attenuata) in Hawai'i measured using digital acoustic recording tags (DTAGs). J Acoust Soc Am 140:421–429

Širović A, Demer DA (2009) Sounds of captive rockfishes. Copeia 2009:502–509

Smith SV (1978) Coral-reef area and the contributions of reefs to processes and resources of the world's oceans. Nature 273:225–226

Staaterman E, Paris CB, DeFerrari HA, Mann DA, Rice AN, D'Alessandro EK (2014) Celestial patterns in marine soundscapes. Mar Ecol Prog Ser 508:17–32

Staaterman E, Ogburn MB, Altieri AH, Brandl SJ and others (2017) Bioacoustic measurements complement visual biodiversity surveys: preliminary evidence from four shallow marine habitats. Mar Ecol Prog Ser 575:207–215

Thompson AA, Mapstone BD (1997) Observer effects and training in underwater visual surveys of reef fishes. Mar Ecol Prog Ser 154:53–63

Tricas TC, Boyle KS (2014) Acoustic behaviors in Hawaiian coral reef fish communities. Mar Ecol Prog Ser 511:1–16

Tricas TC, Boyle KS (2021) Parrotfish soundscapes: implications for coral reef management. Mar Ecol Prog Ser 666: 149–169

van Zanten BT, van Beukering PJH, Wagtendonk AJ (2014) Coastal protection by coral reefs: a framework for spatial assessment and economic valuation. Ocean Coast Manage 96:94–103