

Acoustic and biological trends on coral reefs off Maui, Hawaii

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Received: 6 May 2017 / Accepted: 31 October 2017
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Abstract Coral reefs are characterized by high biodiversity, and evidence suggests that reef soundscapes reflect local species assemblages. To investigate how sounds produced on a given reef relate to abiotic and biotic parameters and how that relationship may change over time, an observational study was conducted between September 2014 and January 2016 at seven Hawaiian reefs that varied in coral cover, rugosity, and fish assemblages. The reefs were equipped with temperature loggers and acoustic recording devices that recorded on a 10% duty cycle. Benthic and fish visual survey data were collected four times over the course of the study. On average, reefs ranged from 0 to 80% live coral cover, although changes between surveys were noted, in particular during the major El Niño-related bleaching event of October 2015. Acoustic analyses focused on two frequency bands (50–1200 and 1.8–20.5 kHz) that corresponded to the dominant spectral features of the major sound-producing taxa on these reefs, fish, and snapping shrimp, respectively. In the low-frequency band, the presence of humpback whales (December–May) was a major contributor to sound level, whereas

in the high-frequency band sound level closely tracked water temperature. On shorter timescales, the magnitude of the diel trend in sound production was greater than that of the lunar trend, but both varied in strength among reefs, which may reflect differences in the species assemblages present. Results indicated that the magnitude of the diel trend was related to fish densities at low frequencies and coral cover at high frequencies; however, the strength of these relationships varied by season. Thus, long-term acoustic recordings capture the substantial acoustic variability present in coral-reef ecosystems and provide insight into the presence and relative abundance of sound-producing organisms.

Keywords Coral reefs · Soundscapes · Biodiversity · Soniferous

Introduction

Coral reefs vary in their species assemblages in space and time (Parravicini et al. 2013; Williams et al. 2015), and identifying the drivers of this variability has long been a focus of the ecological literature. Much effort has gone into characterizing links between biophysical attributes of coral reefs and fish species assemblages. Parameters such as depth, substrate complexity (rugosity), live coral cover, and coral species richness appear to be important correlates with fish species richness and abundance (McCormick 1994; Friedlander et al. 2003; Messmer et al. 2011; Komyakova et al. 2013).

Just as the biological composition of coral reefs changes over time, so too do the associated ambient soundscapes (Staaterman et al. 2014; Kaplan et al. 2015; Nedelec et al. 2015). For example, in an approximately year-long study

Communicated by Biology Editor Mark R. Patterson

Electronic supplementary material The online version of this article (<https://doi.org/10.1007/s00338-017-1638-x>) contains supplementary material, which is available to authorized users.

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of two Caribbean reefs, sound levels were found to vary on diel and lunar scales (Staaterman et al. 2014). However, the relationship to species present was not well characterized, which limited understanding of the influence of species assemblages on local soundscapes. Contemporaneous work sought to link visual survey data to soundscape measurements and found a relationship between the strength of diel trends in sound production to fish density and coral cover on Caribbean reefs (Kaplan et al. 2015). However, that study was relatively short (four months) and was conducted using only three reefs (Kaplan et al. 2015). While others have compared acoustic parameters to biophysical variables such as coral cover, fish density, and sea state across several reefs (Nedelec et al. 2014; Bertucci et al. 2016), this has often come with the trade-off of using relatively brief recordings that likely overlook the appreciable variation in sound cues over longer timescales (Radford et al. 2008; Staaterman et al. 2014; Kaplan et al. 2015).

Collectively, these studies present initial characterizations of some of the putative drivers of this acoustic variability, such as water temperature and the biota present, suggesting a link between reef species assemblages and the local soundscape. Individually, however, these studies often do not adequately characterize the temporal or spatial variability that is likely present. For example, the relevant factors influencing biological sound production may vary in importance over multiple timescales and among communities of sound-producing organisms (Radford et al. 2008, 2014). Thus, data collected from several sites over relatively long timescales are most likely to yield insight into the relationships between biodiversity and ambient soundscapes.

Despite the limitations of the aforementioned studies, this growing body of work suggests that monitoring the sounds produced by the diverse array of soniferous coral reef organisms may be a cost-effective and efficient means of assessing reef community assemblages and their changes over time (Lammers et al. 2008; Radford et al. 2014). Acoustic observations could supplement or reduce the need for frequent, traditional, diver-based visual surveys. However, to develop the capability to infer species assemblages and ecological dynamics from acoustic data (i.e., inverse prediction), it is first necessary to examine the relationship between biological sounds on reefs and fundamental ecological parameters, such as fish species richness and abundance and benthic cover.

In recent years, there has been interest in applying acoustic biodiversity metrics developed for terrestrial ecosystems to marine soundscapes (e.g., Parks et al. 2014; Bertucci et al. 2016; Staaterman et al. 2017); however, there has been little compelling evidence to suggest that such metrics provide valuable information not available from more traditional measurements like sound pressure

level (Staaterman et al. 2017). For example, a recent effort attempted to apply the acoustic complexity index (ACI) to recordings of coral reefs (Bertucci et al. 2016), but its utility was not obvious. Higher ACI values were found in recordings of marine protected areas (MPAs) compared to non-MPAs. However, there were no significant differences between protected and unprotected areas in any visual survey parameter, suggesting that differences in ACI values between protected and non-protected reefs were not reflective of the species assemblages observed in the study (Bertucci et al. 2016). Furthermore, previous work has shown that these indices may be predominately influenced by snapping shrimp activity, which is a major component of coral-reef and temperate soundscapes (Kaplan et al. 2015). At present, more traditional bioacoustic metrics such as sound pressure level (SPL) and the variability in sound level in specific frequency bands over time are likely to be more robust and easier to comprehend than indices such as the ACI.

In addition to biological sounds, anthropogenic noise can modify reef soundscapes in significant ways (e.g., Kaplan and Mooney 2015). The extent of human activity can and does vary among reefs because of differing degrees of remoteness, protection (e.g., areas closed to vessels), and heterogeneous utilization rates. Recent work suggests that noise from small vessels may increase the predation risk for some reef fish (Simpson et al. 2016). Accordingly, these human-mediated elements could also influence biological sound production and species assemblages on coral reefs.

To parameterize the factors that might influence sound production on reefs across space, time, and ecological gradients such as live coral cover and fish density, long-term assessment of a range of geographically and ecologically disparate reefs is needed. This study measured soundscapes and examined visually observable species assemblages at seven Hawaiian reefs that varied in benthic cover and fish species assemblages over an approximately 16-month period. Here, we present results from visual and acoustic surveys of these reefs and describe a new method to quantitatively assess the magnitude of sound production on coral reefs.

Methods

Site selection

Reefs were selected for study on the west side of Maui, Hawaii, in September 2014. The sites were chosen to be similar in depth but different in terms of benthic cover, fish species richness and abundance, structural complexity, geographic location, and degree of protection. These parameters were assessed in an ad hoc manner during the

site selection period and confirmed ex post using visual surveys described below. Because of an instrument malfunction, one reef was ultimately excluded from the study, leaving six reefs and one sandy control site (MM17) for data analysis (Fig. 1a; Table 1). Of these, one (Ahihi) was completely closed to vessel traffic, two were Marine Life Conservation Districts closed to some forms of fishing (Honolua and Molokini), and one was a Fishery Management Area closed to the fishing of herbivores (Kahekili).

Visual surveys

Visual surveys were carried out at each study reef in September 2014, February/March 2015, October 2015, and January 2016. Data were collected by the same two divers for the duration of the study to ensure consistency among surveys, with each specializing in either fish or benthic surveys. Fish sizing estimates were calibrated underwater using artificial fish models and inter-observer comparisons prior to data collection. Survey methods were modified from Kaplan et al. (2015). Four benthic transects per reef were conducted using a 10-m sinking lead line that followed the contours of the reef. Each transect started adjacent to the acoustic recorder moored at that reef and fanned out in a radial pattern. At each 10-cm increment, benthic cover was recorded as one of the following categories: live coral (identified to genus), macroalgae, turf algae, sand, bare rock, dead coral, bleached coral, and other invertebrates. All benthic transects were compiled for each survey using the following categories: live coral, bleached coral,

macroalgae, crustose coralline algae, turf algae, and “other” (e.g., bare rock, sand, dead coral, other invertebrates).

To quantify structural complexity, the straight line distance of the lead line was measured with a fiberglass tape, and rugosity was then calculated as the ratio of the length of the lead line to the length of the straight line distance.

Belt transect surveys for fish were carried out concurrently. These consisted of four transects (30 m long by 2.5 m on either side of the transect). Start points adjacent to the acoustic recorder were selected randomly. Each fish transect took approximately 10 min to complete. The surveyor first swam rapidly along the transect line, recording larger mobile fishes transiting the line, mid-water species, and any conspicuous, rare, or uncommon species. They then turned around and returned along the transect line, slowly and carefully recording all other fishes with a focus on cryptic species. Each observed fish was identified to species and categorized by size (total length) in the following bins: A (0–10 cm), B (11–15 cm), C (16–20 cm), D (21–30 cm), E (31–40 cm), and F (> 40 cm). Fish survey data were combined across transects and summarized by species and size classes. Species that have previously been identified as soniferous (Tricas and Boyle 2014) were noted as such in the data set.

Acoustic data

Acoustic data were collected at each reef using ecological acoustic recorders (EARs; Lammers et al. 2008) equipped

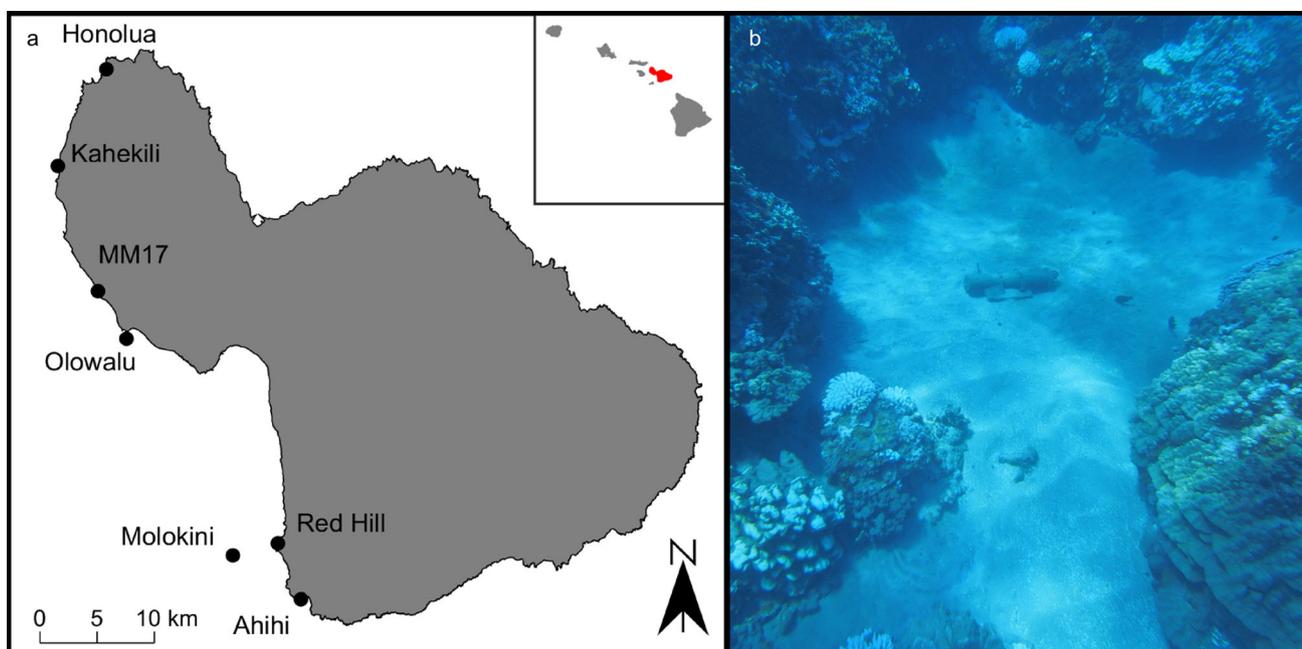


Fig. 1 a Map depicting the location of the seven study sites in Maui, Hawaii. b An ecological acoustic recorder deployed at Olowalu

Table 1 Summary of study reef location, degree of protection, and physical attributes

Reef	Latitude	Longitude	Conservation/protection status	Depth (m)	Rugosity
Ahihi	20.59529	– 156.42462	NAR	9.1	1.36
Honolua	21.01577	– 156.64055	MLCD	6.2	1.43
Kahekili	20.93892	– 156.6947	FMA	11.2	1.25
MM17	20.83076	– 156.64317	N/A	11.2	1.04
Molokini	20.63222	– 156.49603	MLCD	14.6	1.18
Olowalu	20.80203	– 156.61855	N/A	10.1	1.24
Red Hill	20.63982	– 156.45059	N/A	7.1	1.24

NAR natural area reserve, *MLCD* Marine Life Conservation District, *FMA* fishery management area

Table 2 Number of 30-s recordings collected at each reef over the study period and the number and percentage retained after exclusion based on clipping or presence of anthropogenic noise

Reef	Total number of recordings made	Number of recordings after exclusion of clipped recordings and recordings containing anthropogenic noise	Percentage of recordings analyzed
Ahihi	110,219	104,650	94.9
Honolua	116,651	113,033	96.9
Kahekili	108,264	105,089	97.1
MM17	119,845	91,152	76.1
Molokini	178,672	92,860	52.0
Olowalu	94,357	79,834	84.6
Red Hill	127,444	113,381	89.0

with an SQ26-01 hydrophone (Sensor Technology Ltd., Collingwood, ON, Canada) with a sensitivity of approximately -193.5 dBV re $1 \mu\text{Pa}$ and configured with 47.5 dB of gain. Recordings were collected at a sample rate of 50 kHz (25 kHz at Molokini) on a 10% duty cycle (30 s/300 s). For all deployments, EARs were affixed to concrete blocks using hose clamps and cable ties and placed in sand patches adjacent to or within a reef (Fig. 1b). Hydrophones were approximately 6 inches above the bottom. All EARs, except at Molokini, were deployed in September 2014, refurbished in February/March 2015 and July 2015, and recovered in January 2016. The Molokini EAR was involved in a separate study and was deployed and refurbished on different schedules (November 2013, June 2014, October 2014, February 2015, October 2015, October 2016).

Analyses were carried out in MATLAB 9.1 (MathWorks, Natick, MA). Sound files were corrected for hydrophone sensitivity and resampled to 44 kHz for improved computational efficiency and to retain frequencies of interest (except for recordings from Molokini, which were not resampled because of the lower sample rate). An initial review of the recordings indicated that in some cases clipping was present as a result of high-amplitude shrimp snaps. Accordingly, every 30-s sound file was split into 100 ms windows and every window that contained normalized voltage readings of ± 0.99 ,

indicative of the presence of clipping, was automatically excluded (Table 2). The entire file was discarded in cases where fewer than 150 windows (i.e., 15 s) were retained. All remaining windows of each retained sound file were individually analyzed as follows. Root-mean-square SPL (dB re $1 \mu\text{Pa}$) was calculated in two frequency bands—low (50–1200 Hz) and high (1800–20,500; 2000–12,000 Hz for Molokini)—using four-pole Butterworth bandpass filters. These frequency bands were chosen to correspond with the published frequency ranges of fish calls and snapping shrimp pulses, respectively (Au and Banks 1998; Tricas and Boyle 2014). The intermediate frequencies (1200–1800 Hz) were not assessed given the paucity of biological signals of interest in this range and to provide a spectral buffer between the frequency bands analyzed. To obtain an average SPL value for each sound file, the mean SPL of the first 150 windows was then computed (on a linear scale in Pa). While a narrower bandwidth at high frequencies was used for Molokini, this choice did not affect results because no explicit comparisons of sound levels were made among reefs.

To ensure that these analyses focused on sounds of biological origin, vessel and other extrinsic anthropogenic noises were identified and excised. This was done individually for each reef by visually identifying and aurally confirming such sounds in long-term spectral average plots

Table 3 Equations of the line, evaluations of fit (R^2), and significance level for relationships depicted in Fig. 9

Parameter	Low frequency			High frequency		
	October 2014	October 2015	October 2014	February/March 2015	October 2015	January 2016
Rugosity	ns	ns	ns	ns	ns	ns
Coral cover	ns	ns	$y = -7.3 + 99.96x$	$y = -80.6 + 147.74x$	$y = 77.6 + 1.45x$	ns
Soniferous fish density	ns	$y = 74.8 + 0.79x$	ns	ns	ns	ns

ns not significant

produced in Triton version 1.91 (Scripps Whale Acoustics Lab, San Diego, CA).

Humpback whales (*Megaptera novaengliae*), present during the winter months (approximately December–May), represented an undesired biological sound source, in particular when making among-reef comparisons of low-frequency sound, where humpback whale song overlaps with and can mask lower amplitude fish calls. Thus, low-frequency sound data were not considered between 1 December and 30 April except in visualizations of daily average levels.

Comparisons between diel and lunar periodicity were made by constructing periodograms of the SPL time series in both frequency bands. Linear interpolation to fill in missing data was necessary to ensure a constant sampling rate of one recording per 5 min or 288 samples d^{-1} . This was done for all reefs; results from Kahekili, generally representative of all reefs, are presented here.

Crepuscular periodicity was a distinct feature of these acoustic data. To quantify the magnitude of those diel changes in sound level, the median sound level at each sampling time (i.e., 288 times d^{-1}) was computed by month for the low- and high-frequency bands. This yielded monthly median curves of sound level by time of day in each frequency band. These curves were normalized to a zero minimum sound level to facilitate comparisons among reefs irrespective of background noise levels. Subsequently, the total area under the curve at dawn and dusk was computed in MATLAB using the *trapz* function to quantify the strength of the diel trend. Dawn was defined as 1 h before to 15 min after sunrise, and dusk was defined as 15 min before to 1 h after sunset. All other times were not considered. The timing of sunrise and sunset at each reef was identified for each day of the deployment in MATLAB using the reef coordinates and the *suncycle* tool.

Environmental parameters

Temperature data loggers (HOBO pendant models UA-001-64 and UA-002-64, Onset Computer Corporation, Bourne, MA), sampling every 10 min, were deployed alongside EARs at all reefs for the duration of the study, except for Molokini, where temperature data were only collected from July 2015 until January 2016. Wind speeds were gathered from a nearby NOAA National Ocean Service weather buoy (20.895°N, 156.469°W). Lunar illumination data were obtained from the US Naval Observatory website (<http://aa.usno.navy.mil/data/docs/MoonFraction.php>).

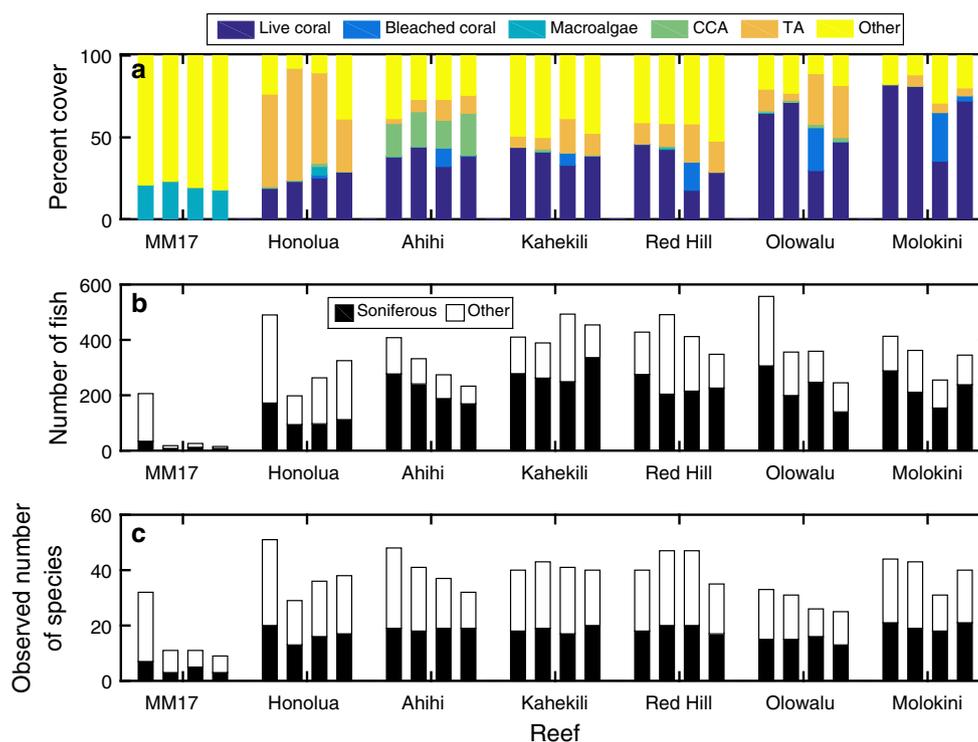


Fig. 2 Visual survey results by reef (ordered by low to high coral cover as recorded in the first survey) and survey period (September 2014, February/March 2015, October 2015, January 2016). **a** Benthic

cover, **b** abundance of soniferous and other fish, **c** fish species richness. Data on sound-producing species were obtained from Tricas and Boyle (2014). CCA crustose coralline algae, TA turf algae

Statistical analysis

To investigate whether there were differences in fish assemblage characteristics within and among reefs, Bray–Curtis dissimilarity values were computed and visualized using non-metric multidimensional scaling (MDS) routines implemented in MATLAB. Correlations between wind speed and SPL were assessed using hourly averages for each variable. Correlations between temperature and SPL were assessed using daily averages for each variable.

Only acoustic data collected within 30 d of the visual survey dates were used in comparisons with visual surveys to limit potential impact of temporal changes in the biological community of the reef over longer timescales. Accordingly, high-frequency correlations were made for each of the four visual survey periods, whereas low-frequency correlations were only made for visual surveys conducted in September 2014 and October 2015, to avoid including any acoustic data that contained humpback whale song (Au et al. 2000). All correlations were tested for significance using linear regression models.

Results

Benthic cover varied among and within the study reefs (Fig. 2a). Live coral cover was generally highest at Molokini and Olowalu and lowest (i.e., zero) at MM17, a sandy non-reef control site. Honolua had the highest proportion of turf algae, and Ahihi had the highest crustose coralline algal cover. Within-reef cover was relatively consistent over time except during the October 2015 survey, when an appreciable proportion of live coral was bleached at every reef, except sand-dominated MM17. Reefs with highest live coral cover, such as Molokini and Olowalu, also had the greatest proportion of bleaching. By January 2016, most of the bleaching had diminished and recovery was observable at every bleached reef, although some, such as Red Hill, suffered mortality.

Corals of the genus *Porites* dominated live coral cover at Ahihi, Kahekili, Olowalu, and Red Hill, whereas corals of the genus *Montipora* were dominant at Molokini. At Honolua, live cover was more evenly split between *Porites* and *Montipora* corals. Other observed genera included *Pocillopora*, *Pavona*, and *Fungia*.

Fish survey results were less consistent, with both abundance and observed number of species following different trends at each reef (Fig. 2b–c). For example, both

Fig. 3 **a** Relationship between number of soniferous fish individuals (small: open circles; large: filled circles) and live, unbleached coral cover. **b** Relationship between number of soniferous fish species and live, unbleached coral cover. Non-metric multidimensional scaling (MDS) plots of Bray–Curtis dissimilarity values for **c** soniferous and **d** all fishes. Results from all four visual survey periods are included and, for the MDS plots, are stratified by sampling period (circles: September 2014; diamonds: February 2015; squares: October 2015; pentagons: January 2016)

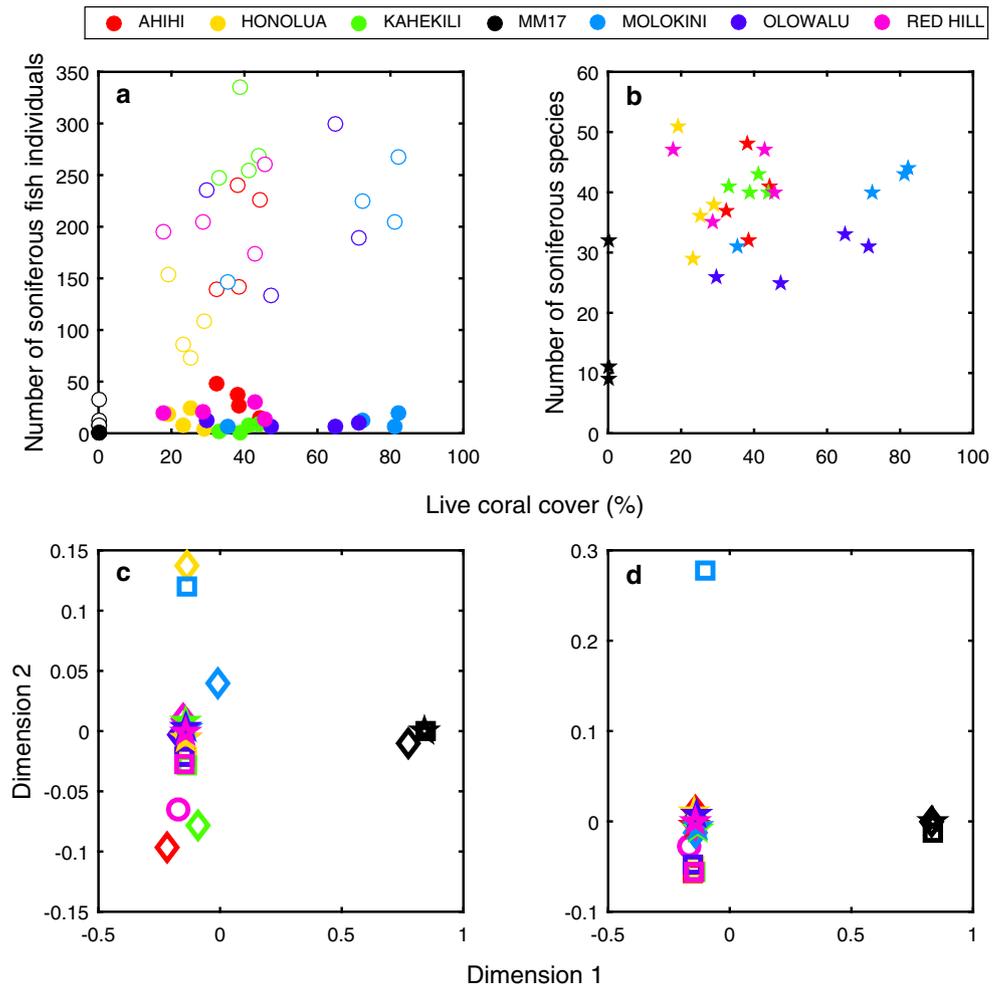


Fig. 4 Daily average sound pressure level (SPL) in **a** low-frequency and **b** high-frequency bands for the duration of the study at each reef

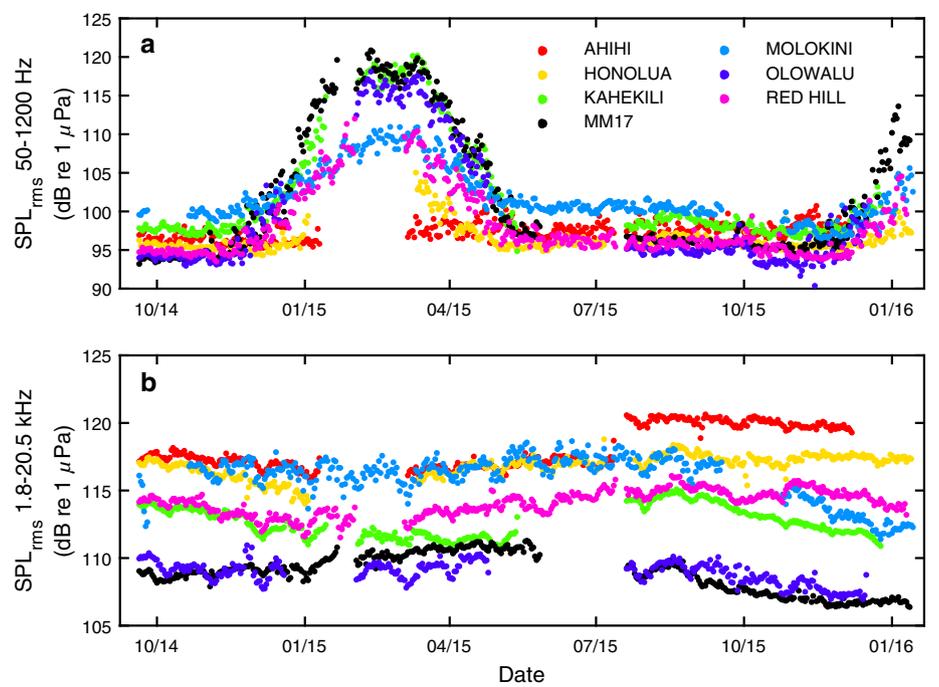
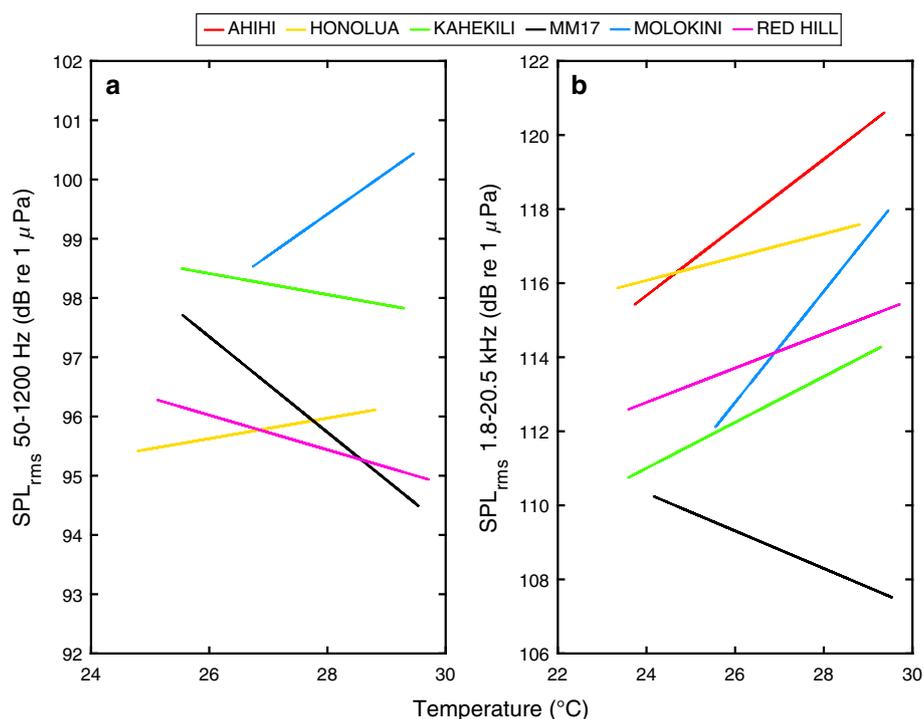


Fig. 5 Linear regression lines of daily average water temperature and sound pressure level (SPL) at **a** low and **b** high frequencies across the study reefs (only significant correlations are shown). Equations of the lines, evaluations of fit, and significance levels are in electronic supplementary material Figs. S3, S4



individual abundance and species richness appeared to decrease over time at Ahihi while staying relatively constant at Kahekili and increasing and then decreasing at Red Hill. Nevertheless, there were some consistent patterns. MM17 always had the lowest species richness and individual abundance and Kahekili and Red Hill consistently demonstrated the highest abundance, whereas the observed number of species appeared to be fairly stable at Kahekili, Molokini, and Red Hill.

The proportion of soniferous fish individuals and species varied among surveys and reefs but in general was approximately half of the total. For fish up to 15 cm total length (i.e., small fish), the most commonly observed soniferous species was the goldring bristletooth (*Ctenochaetus strigosus*, Acanthuridae). At MM17, the most common small soniferous species was the Hawaiian dascyllus (*Dascyllus albisella*, Pomacentridae), and at Molokini it was the blacklip butterflyfish (*Chaetodon kleinii*, Chaetodontidae). There was more variation among reefs,

Fig. 6 Boxplots representing **a** low-frequency and **b** high-frequency sound pressure level (SPL) at Kahekili during the new moon (black), first/last quarter (purple), and full moon (green) at four times of day

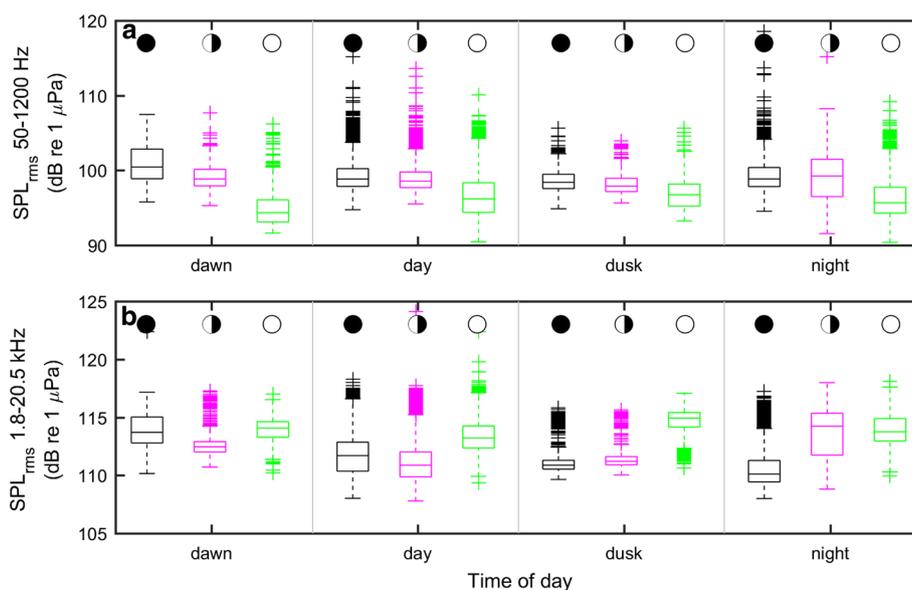
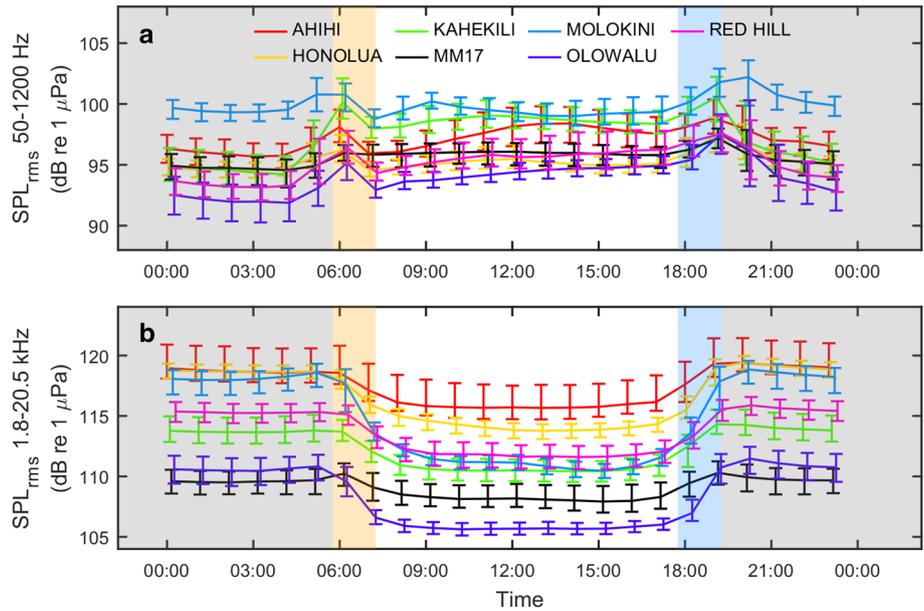


Fig. 7 Median sound pressure level (SPL) (25–75 percentiles) at **a** low frequency and **b** high frequency for each reef by hour of the day. Orange shading indicates dawn, and blue shading indicates dusk



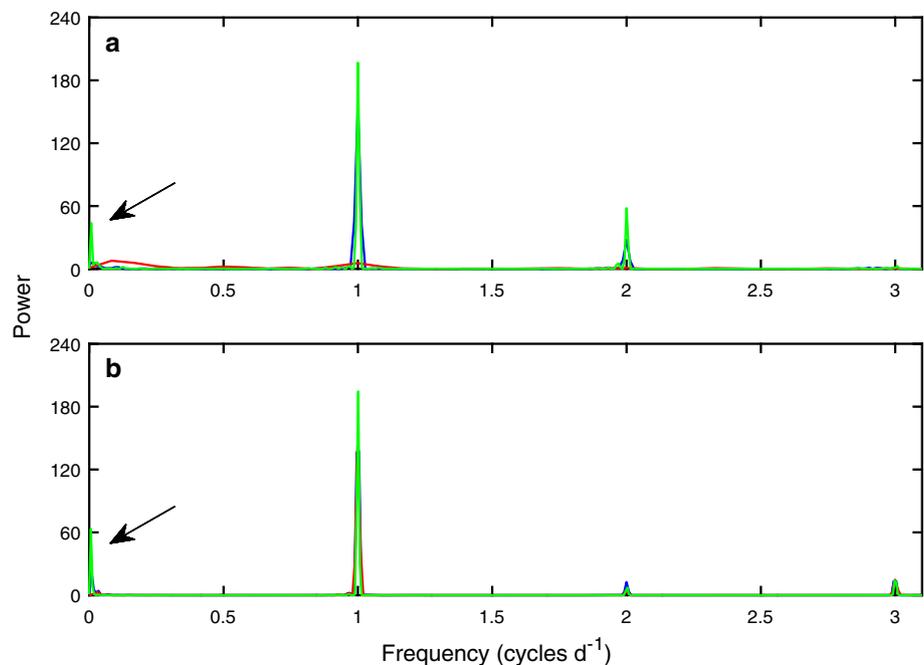
and within reefs among surveys, in terms of the most abundant large (> 15 cm) soniferous fishes. Representative families included Acanthuridae, Balistidae, Chaetodontidae, Holocentridae, Labridae, Monacanthidae, Mullidae, Pomacentridae, Serranidae, and Zanclidae.

Small soniferous fish abundance and soniferous fish species richness appeared to correlate positively but with high variability with live (unbleached) coral cover, but no such relationship was obvious for large soniferous fish

abundance (Fig. 3). There was some variability among reefs in the composition of soniferous fish assemblages (Fig. 3c); MM17 was a clear outlier, whereas other reefs were more similar to each other. When all fishes were considered, there was very little variation in fish assemblages among reefs or sampling periods (Fig. 3d).

Low-frequency SPL followed a strongly seasonal pattern at all sites except Ahihi, with daily average SPL elevated by over 20 dB in winter because of singing

Fig. 8 Fourier transforms depicting the magnitude of periodicity in sound pressure level (SPL) at **a** low and **b** high frequencies for Kahekili. Colors represent individual deployment periods. Arrows note the magnitude of the lunar trend



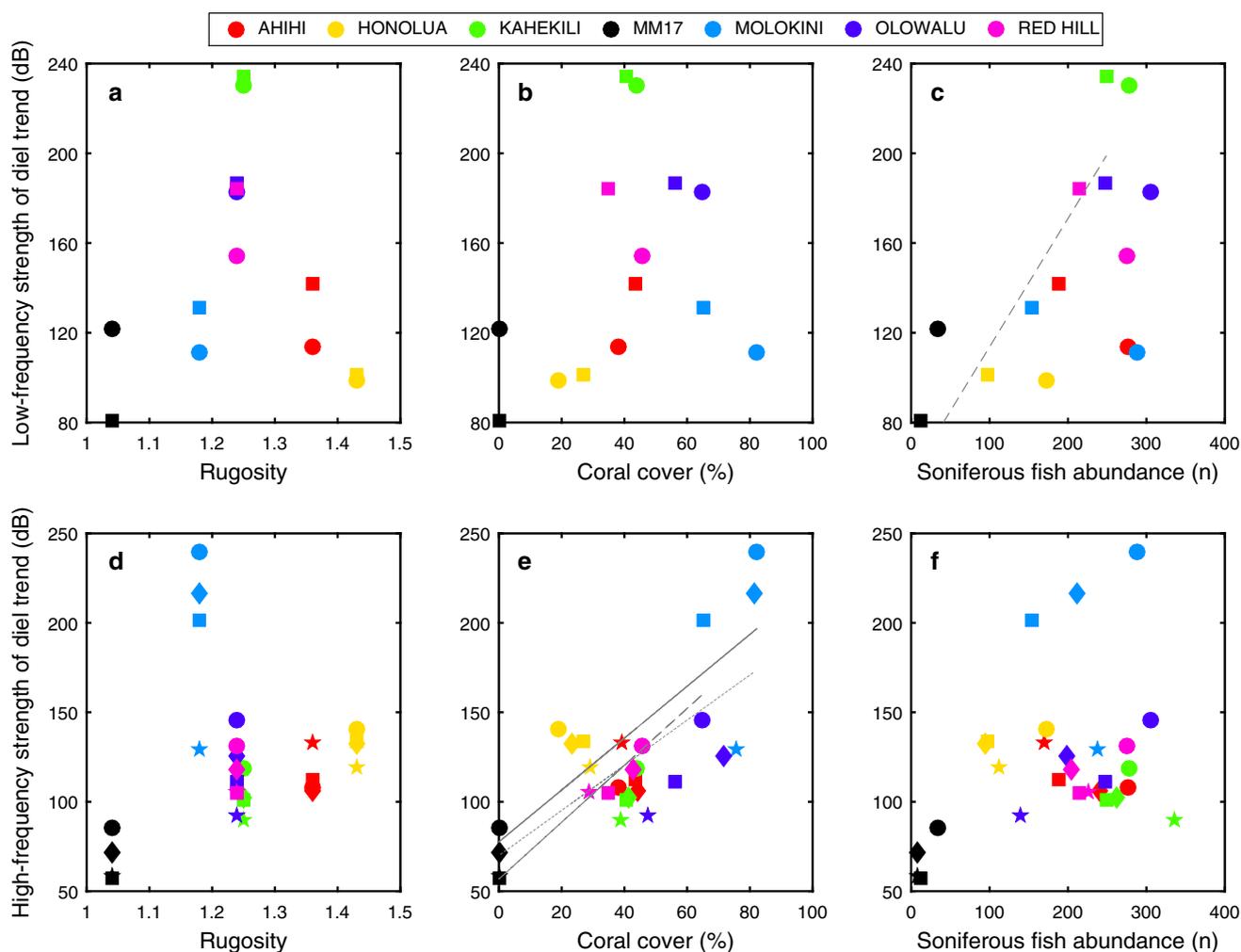


Fig. 9 Strength of diel trend at **a, b, c** low frequency and **d, e, f** high frequency by month and reef with associated rugosity (**a, d**), coral cover (bleached and unbleached) (**b, e**), and fish abundance (**c, f**). Lines of best fit were plotted only when significant relationships were

identified (gray lines; see Table 3 for equations of the lines and evaluation of fit). Circles: September 2014; diamonds: February 2015; squares: October 2015; pentagons: January 2016

humpback whales (Fig. 4). High-frequency SPL did not demonstrate such strong seasonality, and levels were more stable over the course of the year. High-frequency levels appeared elevated at Ahihi by 2–3 dB after instrument redeployment in July 2015 compared to other deployment periods. No such elevation was apparent in low-frequency levels, which suggests that this shift could be a result of a change in instrument orientation during the redeployment process.

There were weak positive relationships between wind speed and low-frequency SPL (electronic supplementary material, ESM, Fig. S1); however, there did not appear to be any relationship between wind speed and high-frequency SPL (ESM Fig. S2) or between temperature and low-frequency SPL (Fig. 5a; ESM Fig. S3) at any reef. Correlations between temperature and high-frequency SPL (Fig. 5b; ESM Fig. S4) were significant at every reef

except Olowalu and positive at every reef except MM17, the sandy control site, where the correlation was negative.

SPLs at Kahekili were generally representative of trends at other reefs and were consequently used to compare diel and lunar periodicity. Median low-frequency SPL was generally highest during new moon periods at all times of day, with levels decreasing from quarter to full moon. Overall, levels were highest at dawn during the new moon and lowest at dawn during the full moon, (Fig. 6a). Median levels did not vary substantially by time of day during the quarter moon, with day and nighttime sound levels relatively consistent.

Conversely, levels were typically highest during the full moon at high frequencies (Fig. 6b). However, there appeared to be more variability overall, with new moon levels nearly as high as full moon levels at dawn and with quarter moon levels highest at night.

Characteristic peaks in SPL at dawn and dusk were evident in both frequency bands (Fig. 7). After excluding times when humpback whales were present, the maximum SPL on a given day at low frequencies was often located around the crepuscular periods and levels were generally lower at night than during the day. At high frequencies, the greatest rate of change in sound level was almost always found before dawn or after dusk, reflecting the strong link between snapping shrimp activity and crepuscularity. Night levels were higher than daytime levels at every reef.

The magnitude of the diel trend appeared to be much greater than that of the lunar trend. Indeed, at Kahekili, the reef with the strongest lunar trend, diel periodicity was approximately four times stronger than lunar periodicity at both low and high frequencies (Fig. 8). The excess strength of the diel trend was even greater for other reefs.

The strength of the diel trend in sound production on a given reef—defined here as the area under the curve at dusk and dawn in each frequency band by month—was related to the biological attributes of that reef (Fig. 9). At low frequencies, soniferous fish abundance was positively correlated with the strength of the diel trend in October 2015 (Fig. 9c), but relationships to coral cover and rugosity were not significant (Fig. 9a, b). At high frequencies, positive correlations between coral cover and the strength of the diel trend were evident for all survey periods except January 2016 (Fig. 9e). However, there appeared to be no relationships between the strength of the diel trend at high frequencies and rugosity (Fig. 9d) or soniferous fish abundance (Fig. 9f).

Discussion

The goal of this study was to better understand the drivers of biological sound production on coral reefs and the extent to which acoustic records reflect fundamental ecological parameters such as coral cover and reef fish biodiversity. Results from integrating the magnitude of the crepuscular increase in biological sound production indicated that low-frequency sound levels, driven by fish calling activity, were related to fish abundance. High-frequency levels, indicative of snapping shrimp sounds, were related to coral cover. These data underscore the significance of diel periodicity and further support the need to consider time of day when making recordings of coral-reef soundscapes.

This study presents a new method of characterizing coral-reef soundscapes, using both the patterns of biological activity (diel trends) and acoustic parameters directly related to the frequencies of interest (sound pressure in the fish and snapping shrimp bands). In previous work, the magnitude of the diel trend was computed by taking the difference between the dawn or dusk peak in sound level

and a low point at midnight (Kaplan et al. 2015). While that crude measure also suggested links between biota and the soundscape, the approach was limited because of a relatively low sample rate. Furthermore, by sampling only a maximum and a minimum for each measurement, these results may have been more susceptible to influence by outliers. In the present study, observations were made for 16 months on a 10% duty cycle that provided recordings every 5 min. This long-term and fine-scale assessment of the magnitude of diel periodicity allowed for the area under the curve to be integrated, offering a more robust measure of crepuscular ecological trends.

Comparisons to physical parameters

Rugosity did not appear to relate to acoustic data in either frequency band. This is perhaps a surprising result, given that other work has identified links between rugosity and fish density (e.g., McCormick 1994), and it may have been anticipated that greater rugosity values would be suggestive of more habitat for snapping shrimp and even fishes. While there was no linear correlation, the strength of the low-frequency diel trend did peak at several reefs of mid-level rugosity. These reefs also tended to have higher fish abundance. While speculative, this may indicate that reefs whose rugosity is driven largely by coral cover and not rock formations (i.e., reefs with intermediate rugosity) may be associated with higher fish abundance and greater diel trend strengths.

Wind speed also did not appear to relate to acoustic data; however, such relationships have been identified in other studies (e.g., Staaterman et al. 2014). This divergence could be because wind speed data were obtained from a buoy in Kahului Harbor, near but not directly adjacent to any of the recording sites. Alternatively, these reefs, many of which were close to shore, may have been somewhat protected from the wind, which would suggest that soundscape parameters were influenced by other factors.

Temperature did correlate significantly and positively with the high-frequency sound levels of the snapping shrimp band, suggesting a relationship between snapping activity and local temperature. The magnitude of this relationship varied among reefs, indicating that reef-specific habitats may influence this relationship. This correlation between shrimp behavior and temperature is consistent with other coral and oyster reef studies (e.g., Kaplan et al. 2015; Bohnenstiehl et al. 2016); however, the causal link between temperature and snapping shrimp activity has yet to be fully elucidated. Further work should investigate the mechanistic or physiological drivers of this relationship. As seas warm, sound production rates may increase in this high-frequency band. The negative correlation noted at MM17 could be a result of early arrival of humpback whale

song in the fall months (i.e., before the December cutoff after which low-frequency recordings were not considered).

Comparisons of visual and acoustic data

Reefs were selected to cover the broadest possible gradient in benthic cover and fish density. While reefs did vary appreciably in benthic cover, fish species assemblages proved to be more similar among reefs than was originally desired (Fig. 3c–d). Furthermore, visually observed reef fish species assemblages varied within reefs among survey periods, despite relatively frequent observations (every 4–5 months). These changes may reflect community dynamics but might also be a limitation of this method. Visual surveys are only snapshots of the fish community at a particular point in time. These communities may vary by time of day, season, settlement, or in stochastic ways not captured by the surveys (e.g., Sale et al. 1984; Galzin 1987; Syms and Jones 2000). More frequent observations would provide a more comprehensive estimation of the community variability. Nevertheless, if timed correctly, visual surveys can reveal rare and potentially important events such as coral bleaching or pulses of abnormally high fish abundance, such as that at MM17 in September 2014, when abundance of pennant butterflyfish (*Heniochus diphreutes*) was uncharacteristically high. However, it is not yet clear whether acoustic records reveal such short-term changes. While acoustic data clearly identify temporal cycles on diel, lunar, and seasonal scales, additional replication would be needed to determine whether soundscape data have the resolution needed to identify transient ecological phenomena such as bleaching events.

The changes over time reflected in these visual and acoustic data underscore how short-term observations (in both visual and acoustic data sets) may not be generally representative of reef dynamics. Because there was no clear indication of how fast community changes took place, care was taken to relate visual survey data to acoustic data only in months where the two datasets overlapped.

Diel and lunar periodicity in SPL, which has been extensively described elsewhere (Staaterman et al. 2014; Kaplan et al. 2015), was also evident here in both frequency bands at all reefs. The exception was MM17, the sandy control site, where only limited and low-amplitude variability was evident. Diel periodicity was notable, appeared to be much greater in magnitude than lunar periodicity (Fig. 8), and may reflect the diversity of fish acoustic behaviors on these reefs.

Sound levels in the low-frequency band were highest during the new moon periods and lowest during the full moon. Larval fish settlement generally occurs during the new moon (D'Alessandro et al. 2007) and is often lowest

during the full moon, supporting the hypothesis that sound may play a role as a settlement cue (e.g., Simpson et al. 2005). Less is known about snapping shrimp behavior, which remains an area ripe for further investigation.

Notably, the strength of the diel trend provides a new means to assess coral-reef soundscapes and the activity of the local biological community. The low-frequency fish band diel trend values tended to increase with soniferous fish abundance (Fig. 9), although these correlations were variable and not always significant. This may be because an asymptote of soniferous fish abundance was reached on these reefs. However, this variability is reflective of reef environments which, as noted earlier, are not rigidly stable communities but areas in flux (Sale et al. 1984; Meyer and Schultz 1985; Shulman 1985; Galzin 1987; Syms and Jones 2000). High-frequency diel trend values increased with percentage coral cover, suggesting that snapping shrimp activity may correlate with benthic cover.

In conclusion, the results presented here broadly characterize the soundscapes of these study reefs. Overall, this study demonstrates that, despite the considerable variability in biological sound production within and among reefs, the magnitude of the diel trend in sound production was related at low frequencies to fish density and at high frequencies to coral cover. Thus, while inverse prediction of species assemblages using the analysis techniques employed here was not possible, acoustic recordings do provide a good indicator of community-level sound production and how it changes over time.

Acknowledgements Funding for this research was provided by the PADI Foundation, the WHOI Access To The Sea initiative and Ocean Life Institute, and the National Science Foundation Grant OCE-1536782. We thank Lee James and Meagan Jones for generously providing vessel support. This research benefited from helpful analysis advice from David Mann and Andy Solow and comments from three anonymous reviewers. Alessandro Bocconcelli, Steve Faluotico, Merrra Howe, Jim Partan, Laela Sayigh, Russell Sparks, and Darla White provided engineering and technical assistance in the field. This work was permitted by the Hawaii Department of Land and Natural Resources (SAP 2015-29 and Special Use Permit 95132).

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