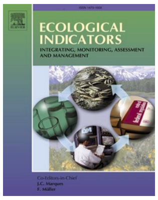
Ecological Indicators 124 (2021) 107435

Contents lists available at ScienceDirect

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind



The utility of different acoustic indicators to describe biological sounds of a coral reef soundscape

Sean A. Dimoff[a], William D. Halliday[a,b,*], Matthew K. Pine[a], Kristina L. Tietjen[a], Francis Juanes[a], Julia K. Baum[a,c,*]

[a] Department of Biology, University of Victoria, PO Box 1700 Station CSC, Victoria, British Columbia V8W 2Y2, Canada
[b] Wildlife Conservation Society Canada, 169 Titanium Way, Whitehorse, Yukon Y1A 0E9, Canada
[c] Hawai'i Institute of Marine Biology, University of Hawai'i, 46-007 Lilipuna Road, Kāne'ohe, Hawai'i 96744, USA

ARTICLE INFO

Keywords:
Soundscapes
Coral reefs
Underwater acoustics
Acoustic indices
Passive acoustic monitoring

ABSTRACT

Monitoring coral reefs is vital to the conservation of these at-risk ecosystems. While most current monitoring methods are costly and time-intensive, passive acoustic monitoring (PAM) could provide a cost-effective, large scale reef monitoring tool. However, for PAM to be reliable, the results must be field tested to ensure that the acoustic methods used accurately represent the certain ecological components of the reef being studied. For example, recent acoustic studies have attempted to describe the diversity of coral reef fish using the Acoustic Complexity Index (ACI) but despite inconsistent results on coral reefs, ACI is still being applied to these ecosystems. Here, we investigated the potential for ACI and sound pressure level (SPL – another common metric used), to accurately respond to biological sounds on coral reefs when calculated using three different frequency resolutions (31.2 Hz, 15.6 Hz, and 4 Hz). Acoustic recordings were made over two to three-week periods in 2017 and 2018 at sites around Kiritimati (Christmas Island), in the central equatorial Pacific. We hypothesized that SPL would be positively correlated with the number of nearby fish sounds in the low frequency band and with snapping shrimp snaps in the high frequency band, but that ACI would rely on its settings, specifically its frequency resolution, to describe sounds in both frequency bands. We found that nearby fish sounds were partially responsible for changes in low frequency SPL in the morning, during crepuscular chorusing activity, but not at other times of day. Snapping shrimp snaps, however, were responsible for large changes in high frequency SPL. ACI results were reliant on the frequency band chosen, with the 31.2 Hz frequency resolution models being chosen as the best models. In the low frequency band, the effect of fish knocks was positive and significant only in the 31.2 Hz and 15.6 Hz models while in the high frequency band snapping shrimp snaps were negatively associated with ACI in all frequency resolutions. These results contribute to a growing body of evidence against the continued use of ACI without standardization on highly energetic underwater ecosystems like coral reefs and highlight the importance of extensive field testing of new acoustic metrics prior to their adoption and proliferation.

1. Introduction

Coral reefs are among the most diverse ecosystems on the planet, providing important ecosystem services to populations worldwide (Bell et al., 2009; Moberg and Folke, 1999). However, these essential ecosystems are threatened (Hughes et al., 2018) and of increasing conservation concern globally (Bellwood et al., 2019). At the global scale, anthropogenic carbon emissions are causing the world's oceans to warm and become more acidic, negatively impacting coral growth and survival (Hughes et al., 2017; Prada et al., 2017). Locally, stressors including pollution, coastal development, sedimentation and noise pollution exacerbate the stress on these systems (Cox et al., 2018; Magel et al., 2019; Slabbekoorn et al., 2010). Monitoring these ecosystems and their functions is vital to determine the management techniques that will be advantageous to their conservation. Historically, visual monitoring of coral reefs has provided most of the information used in determining coral reef health (Hill and Wilkinson, 2004), however, this monitoring is often expensive and time consuming, limiting its utility on

---

* Corresponding authors.
E-mail addresses: whalliday@wcs.org (W.D. Halliday), baum@uvic.ca (J.K. Baum).

https://doi.org/10.1016/j.ecolind.2021.107435
Received 30 June 2020; Received in revised form 31 December 2020; Accepted 16 January 2021

a large scale. However, recent growth in the study of underwater acoustics has created new passive tools for the study and monitoring of these ecosystems (Staaterman et al., 2017).

For >80 years passive acoustics have been used both to describe fish vocal behaviour and as a tool in marine fisheries (Rountree et al., 2006). In one of the initial reviews of fish acoustics, Fish et al. (1952) detailed 26 species of North Atlantic sound-producing fish. Since then, over 800 species of soniferous (sound producing) fishes have been identified worldwide and behavioural studies have revealed the communicative role of sound production in fishes (Lobel, 2013; Rountree et al., 2006; Tricas and Boyle, 2014). Recently, the underwater acoustics field has shifted toward the study of spatial and temporal differences in sound production at the ecosystem level (Farina and James, 2016; Piercy et al., 2014; Wall et al., 2013), enabling comparisons between ecosystems and correlations linking ecosystem health to sound production.

On coral reefs, this shift to the ecosystem level has revealed links between coral reef acoustic communities and their associated soundscapes. In one of the first ecosystem-wide acoustic studies of coral reefs, Piercy et al. (2014) found that reefs with high coral cover and fish abundance produced louder sounds when compared with unprotected and overfished sites. Nedelec et al. (2015) found diel patterns in sound production and positive correlations between adult fish density, live coral cover, coral type and the acoustic output of the reef, suggesting that the acoustic output was determined by a variety of organisms on the reef. Along with these studies connecting reef inhabitants to the reef biophony (biological contributors to underwater soundscapes), new sound metrics suggest that acoustic approaches could be used to quantify specific components of reef health, rather than simply describing the overall sound output of an ecosystem (the soundscape).

Two of the most commonly applied sound metrics in contemporary fish acoustic studies are sound pressure level (SPL) and the Acoustic Complexity Index (ACI) (Elise et al., 2019; Lindseth and Lobel, 2018). SPL is quantified by calculating the root mean square of the pressure level recorded (Lindseth and Lobel, 2018; Slabbekoorn et al., 2010) and represents the overall volume of a soundscape in decibels (dB). This makes it useful in comparing differences within and across ecosystems, and in identifying temporal patterns in the biophony (Archer et al., 2018; McWilliam and Hawkins, 2013; Staaterman et al., 2014). Recently, several other acoustic metrics have been applied to coral reefs, with the intention of describing the diversity of sounds on a reef and using them as a proxy for biological diversity (McPherson et al., 2016; Sueur et al., 2014). The most popular of these is ACI, which describes acoustic complexity by comparing sound intensity at subsequent time steps by calculating and summing their differences. ACI was originally developed to study terrestrial avian communities (Pieretti et al., 2011) before being applied to underwater systems and proliferating in marine soundscape studies (e.g. Bertucci et al., 2016; Elise et al., 2019; Gordon et al., 2019; Kaplan et al., 2015; McWilliam and Hawkins, 2013; Staaterman et al., 2017, 2014).

Despite its frequent use in ecosystem experiments on coral reefs, only two studies have attempted to validate the ability of ACI to describe fish sounds. Bolgan et al. (2018) found that ACI was not able to distinguish between changes in sound abundance and call diversity and that ACI was dependent upon the settings used for its calculation, including temporal and frequency resolution. Bohnenstiehl et al. (2018) found that the diversity of fish calls in the marine environment was not necessarily responsible for assumed corresponding changes in ACI. Prior to these two validation studies, the use of ACI produced inconsistent results. Kaplan et al. (2015), found that ACI did not correlate with fish species composition at any of their sites on coral reefs, while Bertucci et al. (2016) found that low frequency ACI values were strongly correlated with fish diversity. Recent studies such as Lyon et al. (2019), however, found no correlation between ACI and fish diversity, evenness, or density. Discrepancies in results among these studies might be due to different frequency resolutions used, as there are no standards for ACI calculation (Bohnenstiehl et al., 2018). Despite these inconsistent results and repeated evidence highlighting ACI's inability to describe highly energetic soundscapes (Bertucci et al., 2016; Bohnenstiehl et al., 2018; Bolgan et al., 2018; Kaplan et al., 2015), new studies continue to use it (e.g. Elise et al., 2019; Lyon et al., 2019).

We had three objectives in this study. First, we tested if SPL and ACI reliably respond to changes in the number of biological sounds on coral reefs. To do this, we counted fish vocalizations and snapping shrimp snaps in acoustic recordings made at five sites over two years on the world's largest coral atoll (Kiritimati (Christmas Island); central equatorial Pacific Ocean) and examined their relationship with SPL and ACI in low (160 Hz–1 kHz) and high frequency bands (1 kHz–22 kHz). We hypothesized that the number of fish calls would correlate with low frequency SPL and the number of snaps would correlate with high frequency SPL, because of the ability of reef inhabitants to influence SPL combined with SPL's capacity to encompass all sounds produced. In contrast, we hypothesized that neither fish calls nor snaps would be related to ACI because the high energy environment of a coral reef would overwhelm the ability of ACI to detect differences between sound production events. Second, we examined if the frequency resolution used to calculate ACI influenced its relationship to coral reef sounds in our study system, and determined the best frequency resolution. Finally, we described the temporal patterns of the snapping shrimp and fish communities around Kiritimati over our entire deployments.

2. Methods

2.1. Study site and design

We deployed individual SoundTrap acoustic recorders (model: ST300 STD; Ocean Instruments, Auckland, New Zealand) at five sites on the forereef (10–12 m depth) of Kiritimati (Republic of Kiribati) in July 2017 and June 2018 (Fig. 1). Acoustic recorders were secured roughly 1 m above the reef by fastening them to stainless steel stakes that had been installed previously to denote site locations for our long-term monitoring program on this coral atoll Underwater visual censuses (UVCs) of reef fishes conducted at our deployment sites reveal a highly diverse fish community (Magel et al., 2020) that contains several of the sound producing species identified by Tricas and Boyle (2014), including the acoustically active damselfish identified by Lobel et al. (2010). Acoustic recorders were set at a 96 kHz sample rate with the 'high gain' setting selected, and 5-minute duty cycles were recorded every 10 min in 2017 and every 15 min in 2018. The difference in duty cycle between years was not related to the goals of this study. Access to each site resulted in different deployment and recovery schedules, but we analyzed only the overlapping days within each year (July 11–25, 2017; June 18–27, 2018) to maximize comparability between sites.

Located in the central equatorial Pacific Ocean (01°52′N 157°24′W), Kiritimati is the world's largest atoll by land mass. The atoll supports a population of approximately 6500 people (Beretitenti, 2012), the vast majority of which are highly dependent on reef resources for subsistence and income (Burke et al., 2011; Watson et al., 2016). Kiritimati's reefs experienced prolonged heat stress during the 2015–2016 El Niño event, resulting in the loss of approximately 90% of the atoll's live coral cover (J.K. Baum, unpublished data). Although at the time of this study, sites had <5% coral cover (J.K. Baum, unpublished data), reef fish abundances were similar to what they had been prior to the event (Magel et al., 2020). Using fishing pressure data from Watson et al. (2016) we replicated the methods described in Magel et al. (2020) combining the intensity of fishing pressure with the number of people living within a 2 km radius at each of our sites to serve as quantitative measure of local disturbance for our five sites.

2.2. Sound analyses

Acoustic recordings were processed in MATLAB (version 2017a, Mathworks, Natick, Massachusetts, USA) to calculate root mean squared

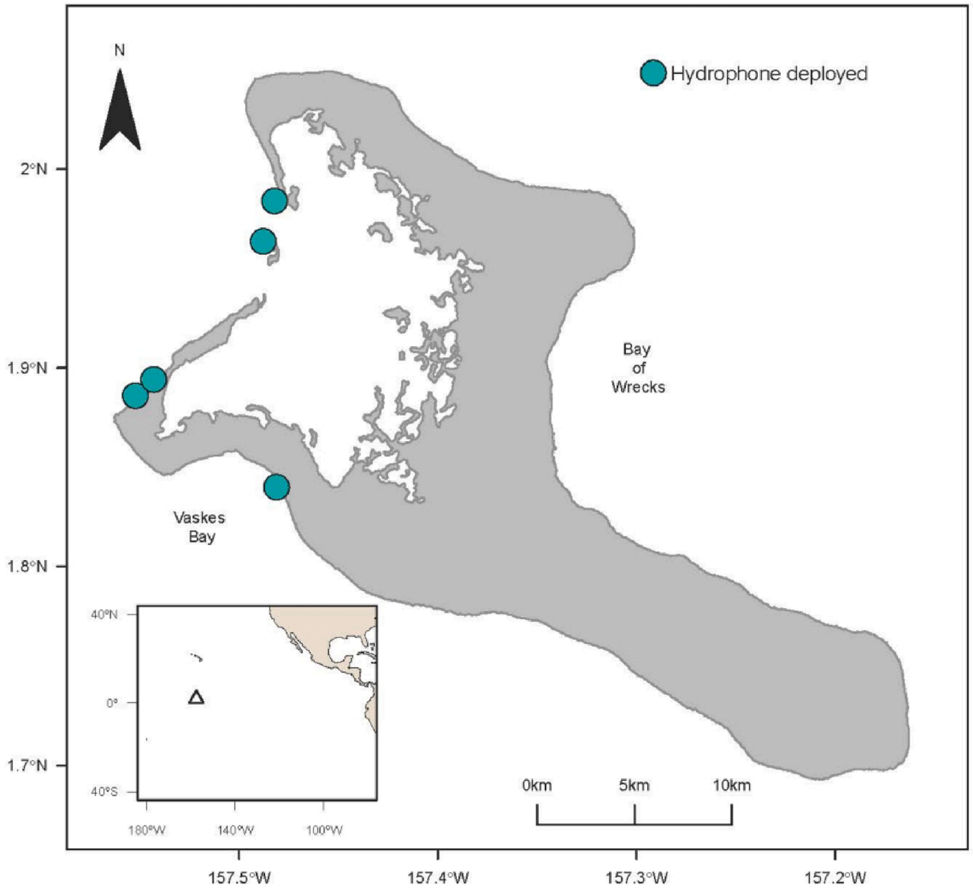


Fig. 1. Map of Kiritimati atoll (Republic of Kiribati) with hydrophone sites marked by blue circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

SPL. Both SPL and ACI were calculated in two frequency bands to determine the effects of distinct sound producers: 1) the high frequency band incorporated frequencies between 1 kHz and 22 kHz to separate the band with snapping shrimp snaps (Lillis et al., 2017); 2) the low frequency band included frequencies between 160 Hz and 1 kHz to represent the bandwidth of fish sounds. Most of the energy in herbivorous sounds, marked by a unique crunching sound in our samples, was below the 1 kHz cut-off, however, some herbivorous sounds can extend beyond 1 kHz although they typically overlap the same range as fish sounds (Tricas and Boyle, 2014). The maximum frequency of 22 kHz was chosen to encompass the broad frequency range of snapping shrimp snaps and to resemble frequency ranges chosen by similar studies (Lillis et al., 2017), while the minimum frequency of 160 Hz was chosen to match the bandwidths used in Slabbekoorn et al. (2018) for sounds made by fish. Within each frequency band, SPL and ACI were calculated for each five-minute file, resulting in a single value for each file, and providing a time-series for the entire deployment from each year of data.

2.3. ACI calculations

Each individual recording (across all sites and seasons) was processed in MATLAB using specifically written code for this study, whereby the variation in acoustic energy within each recording was calculated. We first produced spectrograms for the selected bandwidths (generated using Hanning windows of various sizes equating to 4 Hz (FFT = 24,000, Δt = 0.25 s), 15.6 Hz (FFT = 6,156, Δt = 0.06 s), and 31.2 Hz (FFT = 3,078, Δt = 0.03 s), with no overlap and no time averaging) before applying the *ACI* algorithm from Pieretti et al. (2011) with a 0.5 s temporal step. We then follow the steps outlined by Pieretti et al. (2011), the first of which calculates the absolute differences (d_k) between two adjacent sound pressures (intensities) in a single frequency bin within a matrix of intensities created from the *PSD* spectrogram:

$$d_k = |I_k - I_{(k+1)}|$$

where I_k and $I_{(k+1)}$ are the two adjacent intensities. The algorithm then sums all the d_k values within that particular temporal step of the recording (*j*, and defined by the temporal resolution of the *PSD* spectrogram):

$$D = \sum_{k=1}^{n} d_k$$

where *D* is the sum of all d_k contained in *j*. The result is then divided by the total sum of the intensity values contained in *j*:

$$ACI = \frac{D}{\sum_{k=1}^{n} I_k}$$

where ACI is for a single temporal step (*j*) and frequency bin (Δf_l). ACI was calculated for every temporal step within a single recording and for every individual frequency bin. The total ACI for each single frequency bin ($ACI_{(\Delta f_l)}$) was then calculated by

$$ACI_{(\Delta f_l)} = ACI_{(\Delta f_l)} = \sum_{j=1}^{m} ACI$$

where m = the number of temporal steps (*j*) in the entire recording. Finally, the broadband *ACI* (across all frequencies up to 24 kHz) was calculated by

$$ACI_{tot} = \sum_{l=1}^{q} ACI_{(\Delta f_l)}$$

where ACI_{tot} is the ACI value for the entire recording (Pieretti et al., 2011). Finally, the ACI_{tot} for each bandwidth (high frequency (1–22 kHz) and low frequency (160 Hz–1 kHz)) was calculated.

2.4. Fish sound analysis

To test the relationships between each of our acoustic indicators (SPL and ACI) and fish sounds, we quantified three distinct types of fish sounds on a subset of our overall dataset. The amount of effort required for this manual bioacoustics analysis was quite large, therefore we subsampled the data. Machine learning or deep learning techniques were not developed for this study due to the lack of a reliable training dataset. We subset each deployment to include five days from each of the five sites in both 2017 and 2018, with the proviso that days could only be included if no divers were in the water at any of the recording sites. This was to eliminate sounds made by divers and any influence that they caused on the reef fish community. We then subset each of the days (10 days × 5 sites) into four quarters (03:00, 09:00, 15:00, 21:00) and visually analyzed the first 5-minute file in each quarter. These times were chosen based on our initial exploratory analysis of daily patterns in SPL, which showed a peak at 09:00 at all sites and variations in sound levels at the other 3 sampled times.

Each of the 200 files included in this analysis were visually inspected by a single analyst using Raven Pro software (Version 1.5, Cornell Lab of Ornithology, Ithaca, New York, USA), with the window size set to 7000 samples, the frequency range set to 0–3000 Hz, and the time range of the view window set at 10 s. To ensure that only fish calls or herbivory sounds were counted and all sounds were quantified consistently, each file was listened to by only one analyst and, in any cases of uncertainty, a second underwater acoustic expert was consulted. Within each visually inspected file, we recorded and summed the number of fish knocks (Fig. 2C), fish long calls (Fig. 2A), and herbivorous feeding sounds (Fig. 2B). Fish knocks were determined to be of a short duration (<200 ms) and within the 160–1200 Hz frequency range (Fig. 2C). Long calls, which were within the same frequency range as fish knocks, were identified by a longer duration (>200 ms; Fig. 2C) and encompassed a variety of different call types including ‘grunts’, ‘buzzes’, ‘chirps’, ‘purrs’, and ‘trumpeting’ (Lobel et al., 2010). Herbivorous feeding sounds were identified through a combination of listening and visually inspecting each file to ensure that consistent sounds were counted. The energy in herbivorous sounds was typically between a 160–1000 Hz

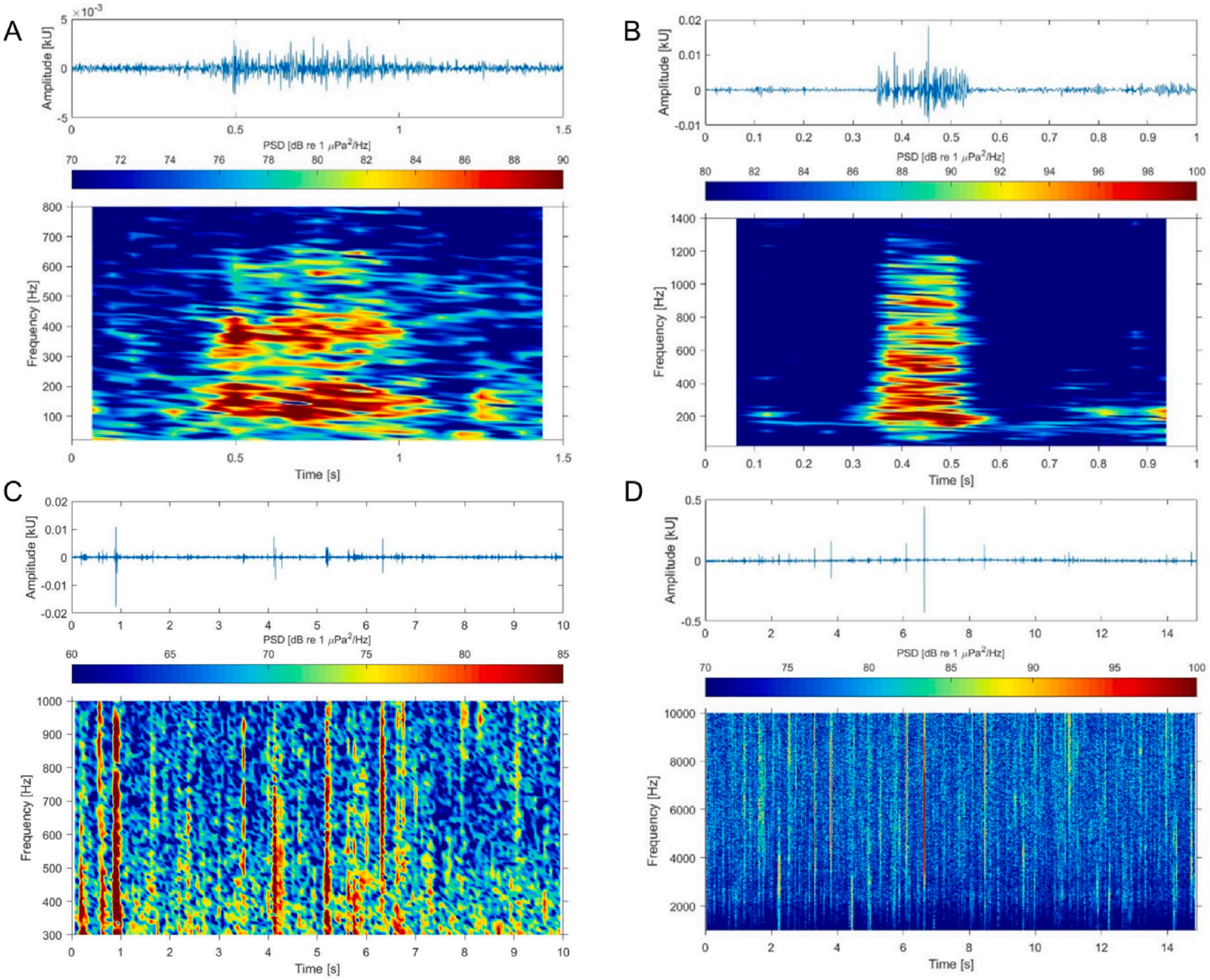


Fig. 2. Example waveforms and spectrograms of each sound type counted: A-C in the low frequency, D in the high frequency: A) long call, B) herbivory sounds, C) fish knocks, and D) snapping shrimp snaps in the high frequency band. Spectrograms were computed with sample rate = 96 kHz, window size = 12000 samples, and using a Hanning window with 50% overlap.

frequency range, although exceptions stretched beyond 1 kHz, and these long duration sounds ($\sim$250 ms) were also marked a distinctive crunching sound (Fig. 2B). If boat noise was observed in a file, then we removed the file from the overall sample, leading to the removal of 9 files ($n = 191$). Each file was also analyzed to ensure that weather, waves, and wind were not interfering with sound identification, however none of our samples revealed any obvious interference from these factors.

To investigate if there were changes in the sound intensity of individual sounds between our 4 sampled times, we also examined the characteristics of individual fish knocks from a small subset of files. Knocks were selected as they were a consistent call type present in all files. 20 acoustic files were selected, split between 2017 and 2018 and across all four of our sampling times (03:00, 09:00, 15:00, 21:00). Within each file we selected the first 10 individual knocks with a good signal-to-noise ratio using Raven Pro. We used the selection table tool in Raven Pro to collect different metrics on the individual knocks that were selected, including minimum and maximum frequency and time, peak frequency, and in-band power. We used in-band power as a metric of the uncalibrated received level of each call and converted these values to a calibrated received level by correcting for the end-to-end sensitivity of the individual recorder.

2.5. *Snapping shrimp snap analysis*

Next, to test the relationships between each of our acoustic metrics and snapping shrimp sounds, we estimated the number of snaps in each 5-minute file from our overall dataset using a band limited energy detector on spectrograms in Raven Pro (version 1.5) with window size set to 7000 samples. The settings for the band limited energy detector were set to minimum frequency = 1.5 kHz, maximum frequency = 4.5 kHz, minimum duration = 0.036 s, maximum duration = 0.109 s, minimum separation = 0.036 s, minimum occupancy = 70%, signal-to-noise ratio threshold = 2 dB, block size = 10 s, and hop size = 5 s. We visually inspected a small subset of the detector results and determined that the detector was actually detecting snapping shrimp snaps rather than other extraneous sounds. We used our entire dataset for this analysis, resulting in a large sample size ($n = 15{,}987$).

2.6. *Statistical analysis*

All statistical analyses were conducted using R version 3.6.1 (R Core Team, 2019). Data and the code for figures and data analyses are available through GitHub at https://github.com/baumlab/fish_sounds 2017.

To validate the responsiveness of SPL and ACI to the number of biogenic sounds recorded we fit linear mixed models (R package: *lme4*) for each of these two response variables, in both the low and high frequency bands. Our 'low frequency band' models included numbers of knocks, long calls, and herbivorous sounds as fixed effects (with each standardized to a mean of zero), and with lunar phase (continuous), fishing pressure (continuous), time of day (03:00, 09:00, 15:00, 21:00) and year (categorical) as fixed effects to assess changes in sound production responsible for the diurnal patterns observed in SPL (Fig. 2C) and between our two sampling years. Due to boat noise, nine observations were removed from the low frequency dataset ($n = 191$). Our 'high frequency band' models included number of snapping shrimp snaps (continuous), day/night (categorical), year (categorical), lunar phase (continuous), and fishing pressure (continuous) as fixed effects, as well as the interaction between the snaps and day/night, to allow for the relationship between snaps and SPL to vary between night and day. Day/night was based on approximate times of sunrise and sunset near the equator (6:00–18:00). Due to irregular snap counts (<200), three observations were removed from the high frequency dataset ($n = 15{,}987$). Prior to our analyses, all continuous parameters were standardized to a mean of zero and a standard deviation of 0.5 using the rescale function in the *arm* package (Gelman et al., 2020). For SPL models, we ran models with all combinations of covariates described above and compared using small-sample corrected Akaike Information Criterion (AICc) to select the final model. To determine the best-fit models for ACI we first created models with all combinations of covariates described above for three different frequency resolutions. We first selected for the best model within each frequency resolution using AIC$_c$. We then compared the best ACI models from each frequency resolution using AIC$_c$ to determine which frequency resolution best described variations in fish calls or snapping shrimp snaps.

Finally, we examined variation in the received levels of individual knocks through time based on the subset of knocks where we measured received levels (dB). We used a linear model in R (package: *Stats*; function: lm) with received level (dB) as the dependent variable and hour as a categorical independent variable. We tested all assumptions of this model (normality, homoscedasticity of variance), and it met all assumptions.

3. Results

3.1. *Sound pressure level*

Low frequency SPL was significantly influenced by knocks (Fig. 2C), herbivory, time of day, year, and the interaction between knocks and time of day. The effect of knocks differed between the four hours sampled (Fig. 3). Knocks had a significantly positive effect on low frequency at 09:00 (parameter estimate = 7.3, S.E. = 1.231, $t_{197} = 5.93$, $p < 0.0001$), but the interaction was not significant at the other sampled periods (03:00, 15:00, 21:00; Table 1). Herbivory also had a significant positive effect on low frequency SPL (parameter estimate = 1.28, S.E. = 0.395, $t_{197} = 3.23$, $p = 0.002$). Year was the only other significant factor and 2018 had significantly higher SPL than 2017 (parameter estimate = 3.53, S.E. = 0.348, $t_{197} = 10.15$, $p < 0.0001$). Lunar phase and fishing pressure were also included in the model although neither was significant (Table 1). This model explained 53.38% of variation in low frequency SPL. The only other model that fell within ΔAIC < 2 was identical to the selected model except that it also included long calls, although they were non-significant (Table 1). Comparisons between knocks at each of the four sampling periods revealed that individual knocks had significantly higher received levels at 09:00 compared to knocks during the other three times examined (Supp. Fig. 1; difference between 09:00 and 03:00 = 7.7 dB, S.E. = 0.9, $t_{197} = 8.1$, $p < 0.0001$; no significant difference between 03:00 and both 15:00 and 21:00, $p > 0.40$; model $R^2 = 0.33$; Supp. Table 7).

High frequency SPL was significantly influenced by snaps (Fig. 2D), day/night, and their interaction, as well as lunar phase, year, and fishing pressure (Supp. Table 1). Snaps had a small but positive effect during the day (parameter estimate = 0.872, S.E. = 0.034, $t_{15980} = 14.696$, $p < 0.001$), and roughly twice the effect size at night compared to during the day (parameter estimate = 0.974, S.E. = 0.092, $t_{15980} = 10.65$, $p < 0.001$). Each of our abiotic parameters were also significant. Lunar phase had a positive effect (parameter estimate = 0.212, S.E. = 0.045, $t_{15980} = 4.767$, $p < 0.001$), 2018 had significantly higher SPL than 2017 (parameter estimate = 3.396, S.E. = 0.045, $t_{15980} = 74.472$, $p < 0.001$), and fishing pressure had a significant positive effect on high frequency SPL (parameter estimate = 1.004, S.E. = 0.0450, $t_{15890} = 22.314$, $p < 0.001$). Overall, this model explained 37.14% of variation in high frequency SPL (Supp. Table 1).

3.2. *Acoustic Complexity Index*

For low frequency ACI, the best model according to AIC$_c$ had a frequency resolution of 31.2 Hz and suggested that ACI was influenced by knocks, hour, herbivory, fishing pressure, and an interaction between knocks and hour. The effect of knocks was, however, different between the four times of day sampled (Table 2). The interaction was significant

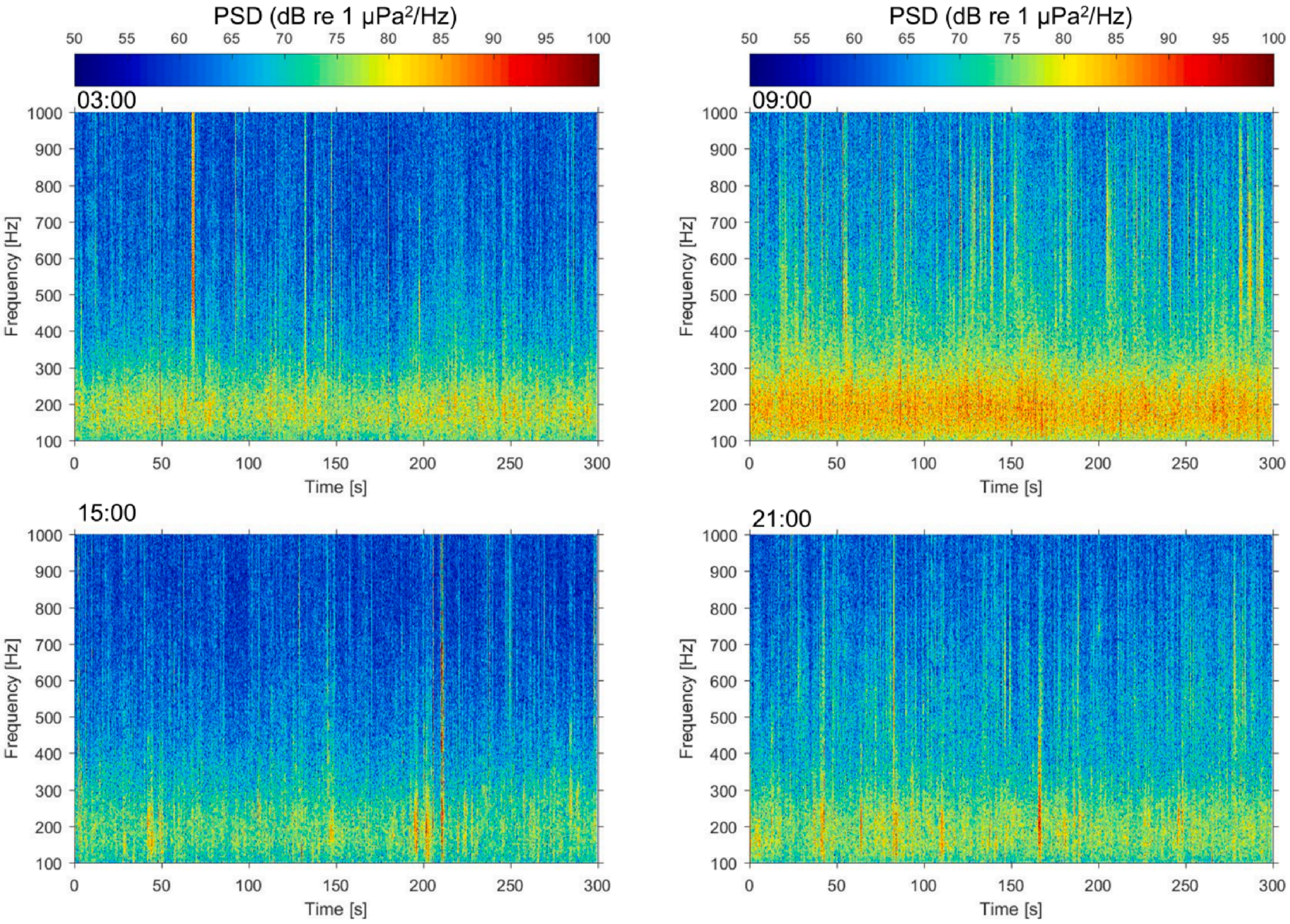


Fig. 3. Low frequency (100–1000 Hz) spectrograms from one representative site visualizing patterns in sound production levels (SPL) among our four sampled times of day: 3:00, 9:00, 15:00, and 21:00. Spectrograms were computed with sample rate = 96 kHz, window size = 24000 samples, and using a Hanning window with 50% overlap.

Table 1

Top models from AIC$_c$ stepwise comparisons (ΔAIC$_c$ < 6) and results (parameter estimates) for final model fixed effects from linear mixed-effects model examining changes in low frequency SPL associated with changes in fish calls at four times of day. The intercept and all continuous main effects represent our 15:00 sampling time.

Model	K	AICc	ΔAIC	Adjusted R^2	P value
Knocks* Hour + Herbivory + Year + Lunar Phase + Fishing Pressure	13	884.55	0.284	0.534	<0.0001
Knocks* Hour + Herbivory + Long Calls + Year + Lunar Phase + Fishing Pressure	14	885.71	1.433	0.534	<0.0001

Parameter estimates for final model

Parameter	Estimate	Std. Error	t value	P value
(Intercept)	102.67	0.497	206.72	<0.0001
Knocks	−1.94	1.070	−1.81	0.071
21:00	1.54	0.567	2.71	0.007
03:00	0.50	0.586	0.85	0.395
09:00	2.26	0.589	3.83	<0.001
Herbivory	1.28	0.395	3.23	0.002
Year	3.53	0.348	10.15	<0.0001
Lunar Phase	0.08	0.385	0.22	0.829
Fishing Pressure	−0.41	0.390	−1.05	0.293
Knocks * 21:00	2.14	1.243	1.73	0.086
Knocks * 03:00	2.31	1.216	1.90	0.059
Knocks * 09:00	7.30	1.231	5.93	<0.0001

and positive at 09:00 (parameter estimate = 1.196, S.E. = 0.354, t_{179} = 2.347, p = 0.020) and 21:00 (parameter estimate = 1.331, S.E. = 0.358, t_{179} = 2.701, p = 0.008) but there was no significant difference between 03:00 and 15:00 (Table 2). Additionally, both herbivorous sounds (parameter estimate = 0.330, S.E. = 0.114, t_{179} = 2.905, p = 0.004) and fishing pressure (parameter estimate = 0.593, S.E. = 0.112, t_{179} = 5.280, $p < 0.001$) had a positive effect on low frequency ACI. This model explained 50.7% of the variation in low frequency ACI. .

Both the 15.6 Hz and the 4 Hz frequency resolution models contained the same covariates as the selected 31.2 Hz model (Table 2) but had a diminished effect size of the interaction between knocks and time of day, and the main effect for knocks was no longer significant in either model. The 15.6 Hz model explained 41.8% of the variation in low frequency ACI. Within this model, the interaction between knocks and hour was significant at 09:00 (parameter estimate = 1.493, S.E. = 0.581, t_{179} = 2.570, p = 0.011), while herbivorous sounds and fishing pressure were both still significant (Supp. Table 2). The 4 Hz model explained only 40.6% in low frequency ACI and the interaction between knocks and hour was no longer significant at any time of day (Supp. Table 3).

In the high frequency band, the best model selected by AIC$_c$ also had a frequency resolution of 31.2 Hz and was significantly influenced by snaps, day/night, and their interaction, as well as year and fishing pressure. Snaps had a statistically significant negative effect on ACI during the day (parameter estimate = −6.829, S.E. = 0.243, t_{15584} = −28.187, $p < 0.001$) and a smaller but still negative effect on ACI at night (parameter estimate = −5.904, S.E. = 0.374, t_{15584} = 2.47, p = 0.132). Year had a positive effect on ACI (parameter estimate = 12.78, S.

Table 2

Top models from AIC_c stepwise comparisons and results (parameter estimates) for each frequency resolution from linear mixed-effects model examining changes in low frequency ACI associated with changes in fish vocalizations. The intercept and all main effects represent our 15:00 sampling time.

Frequency Resolution Model		K	AICc	ΔAIC	Adjusted R^2	P value
32.1 Hz	**LF ACI ~ Knocks * Hour + Herbivory + Year + Lunar Phase + Fishing Pressure**	**11**	**408.88**	**0**	**0.507**	**0.23**
15.6 Hz	LF ACI ~ Knocks * Hour + Herbivory + Year + Lunar Phase + Fishing Pressure	11	597.83	188.94	0.418	0.31
4 Hz	LF ACI ~ Knocks * Hour + Herbivory + Year + Lunar Phase + Fishing Pressure	11	745.99	337.12	0.405	0.48

Parameter estimates for final model

Parameter	Estimate	Std. Error	t value	P value
(Intercept)	20.199	0.143	141.281	<0.0001
Knocks	0.365	0.308	1.184	0.238
21:00	−0.0482	0.163	−0.295	0.768
03:00	1.292	0.169	7.663	<0.0001
09:00	0.397	0.170	2.344	0.020
Herbivory	0.330	0.114	2.905	0.004
Lunar Phase	−0.096	0.111	−0.862	0.495
Year (2018)	0.069	0.100	0.684	0.390
Fishing Pressure	0.593	0.112	5.280	<0.0001
Knocks * 21:00	0.967	0.358	2.701	0.008
Knocks * 03:00	0.345	0.350	0.986	0.326
Knocks * 09:00	0.832	0.354	2.347	0.020

E. = 0.187, $t_{15584} = 68.495$, $p < 0.001$), while fishing pressure had a negative effect (parameter estimate = −8.70, S.E. = 0.185, $t_{15584} = -47.073$, $p < 0.001$). Lunar phase was near-significant and had a small positive effect on ACI as well (Supp. Table 4). The selected model explained 37.03% of the variation in high frequency ACI. Of the high frequency ACI models, the selected models in all three frequency resolutions contained the same covariates (Supp. Table 4). The 15.6 Hz model explained 33.49% and the 4 Hz model explained 28.46%. While the effect sizes changed within each model, there were no differences in the significance or positivity/negativity of the covariates (Supp. Table 5 and 6).

3.3. *Diel patterns*

Diel patterns were present in both the low and high frequency SPL bands (Fig. 4A, C). Low frequency SPL exhibited clear peaks in sound production at 09:00 and 22:00, and slightly higher levels of SPL produced at night compared to the day (Fig. 4C). High frequency SPL maintained a higher SPL at night compared to the day (Fig. 4A. The peaks in low frequency SPL also occurred around the times that high frequency SPL either increased (22:00) or decreased (09:00) (Fig. 4A, C). Diel patterns in ACI, however, were only observed in the high frequency band (Fig. 4B), where it appeared that ACI values were higher from 09:00 to 22:00, and slightly higher during the day compared to at night.

4. Discussion

Passive acoustic monitoring is potentially a useful tool for monitoring the health of coral reef ecosystems, however, its application must be based on field-tested evidence. The application and proliferation of new acoustic metrics to a variety of new ecosystems is common (Lindseth and Lobel, 2018), however, unless these new metrics are tested under a variety of conditions and in a variety of ecosystems, their results may reflect localized patterns rather than broadly applicable trends (Bolgan et al., 2018). Here, we tested two popular sound metrics to assess their applicability to coral reefs. Our SPL analyses partially supported our hypotheses that this metric would be representative of biogenic sounds on the coral reef: low frequency SPL responded to fish sounds, albeit only at certain times of day, and high frequency SPL was clearly driven by snapping shrimp snaps. As expected, ACI proved to be a less reliable metric. In the low frequency, the ability of each model to describe ACI was dependent upon the frequency resolution chosen for ACI calculation, while in the high frequency band it was negatively associated with the number of snaps. We speculate that the discrepancies between our SPL hypotheses and findings might be explained by the complex acoustic communities of coral reefs, whereas the differences between our ACI hypotheses and findings may be due to the reliance of ACI on its calculation settings and its inability to separate independent calling events on high-energy systems like coral reefs.

4.1. *Sound pressure level*

In the low frequencies (160–1000 Hz), fish knocks were partially responsible for the peak in SPL at 09:00 (Fig. 2C), with a positive relationship between the number of knocks and SPL at this time, but not at other times of day (Table 1). This peak in SPL appears to be evidence of chorusing behaviour of fishes (i.e. aggregations of fish vocalizing together) in Kiritimati. Although the number of knocks that we were able to count did not differ greatly between 09:00 and other times, the knocks that were recorded at 09:00 had a higher received level than knocks at other times (Supp. Fig. 1), suggesting that fish were closer to the acoustic recorder when knocking, or that fish increased the source level of their knocks at 09:00. If more fish were making this knocking vocalization at 09:00, overlap and amplitude loss due to distance from the hydrophone might mask distant knocks so that they are lost in elevated background noise, compared to other times of day, when we were able to count more distant knocks with lower received levels because there were fewer knocks (i.e. less overlapping signals) and less background noise in the same frequency band (Fig. 3). The phenomenon of fish increasing their sound intensity has been noted in both freshwater and marine species and can be a masking release strategy to overcome higher levels of background noise (Holt and Johnston, 2014; Luczkovich et al., 2016).

Fish choruses can be associated with reproduction and spawning events, and their timing and frequency range might be associated with avoiding overlap in the biophony (Lobel, 2013; McCauley and Cato, 2000). On coral reefs, several experiments have identified chorusing behaviour as a primary driver of low frequency SPL (Radford et al., 2014; Steinberg et al., 1965). McCauley and Cato (2000) on the Great Barrier Reef found that fish choruses raised ambient sound levels by 35 dB, representative of the impressive sound output fish can make together. The consistent increase in average SPL from 08:30 to 10:00 and 21:30 to 22:30 also suggest that chorusing activity is powerful enough to drive changes in SPL while non-chorusing behaviour is not. Here we define "non-chorusing behaviour" as periods when fish calls were present, but not in high enough intensity or quantity to create changes in SPL, which we observed at three of our four sampled times of day (03:00, 15:00, 21:00). However, to truly assess the influence of knocks and other fish calls on SPL at different times of day would require a more detailed analysis of received levels for each individual call, an extremely labour-intensive task considering the manual methodology

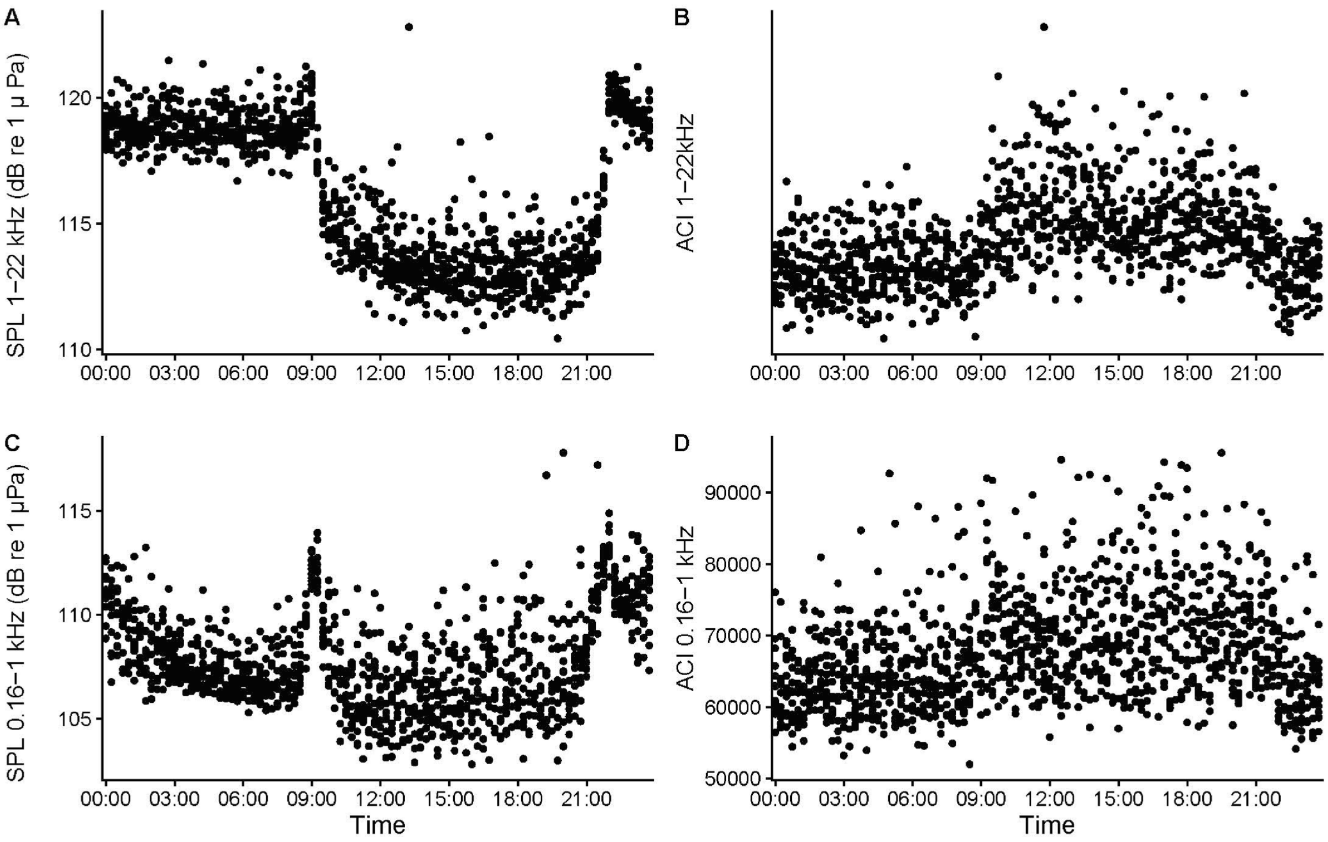


Fig. 4. All plots collect data from the entire deployment at one site in 2018. Each plot represents a 24-hour day. A) High frequency SPL values. B) High frequency ACI values. C) Low frequency SPL values. D) Low frequency ACI values. All ACI values displayed were calculated using a 31.2 Hz frequency resolution and 0.5 s temporal resolution.

we used, therefore we recommend an automated process for examining this relationship in the future.

In addition to knocks, herbivorous sounds also significantly affected low frequency SPL (Table 1). Although herbivorous sounds were infrequent in our dataset, they did contribute substantial acoustic energy to the soundscape when present (Fig. 2B). Tricas and Boyle (2014) found that parrotfish feeding sounds in Hawai'i overlap with social fish vocalizations but occupy a much larger frequency range, which varies by species. In temperate reefs, the sounds of feeding sea urchins fill a similar frequency band and can contribute to choruses at dawn and dusk (Radford et al., 2008a, 2008b). Herbivorous sounds in our recordings typically fit within our low frequency band (160 Hz–1000 Hz). Long calls, which consisted of grunts, buzzes, chirps, purrs, and trumpet calls were not significant in any of our top models (Table 1). It is interesting that long calls were not a significant component of low frequency SPL as they have been previously associated with chorusing activity on coral reefs (McCauley and Cato, 2000). However, their minimal input might be due to a low number of nearby long calls or high levels of different nearby sounds masking them.

Year was the only significant abiotic factor that we included in our low frequency model. SPL was roughly 3.5 dB higher in 2018 than 2017. Since weather conditions were similar between the two sampling years, this difference might be due to recordings taking place at different times of year; while both recordings were conducted in the summer, we sampled in June of 2017 and in July of 2018. These different months might be associated with differences in sound production related to reproductive events in fishes (Lobel et al., 2010). We also included lunar phase and fishing pressure, neither of which were significant, however these results might be due to our low sample size ($n = 197$). Conflicting results from Staaterman et al. (2014) found that lunar phase was significantly associated with changes in low frequency sound production at reefs in both Florida and Hawai'i, although using a sample size of over a year. Additionally, Piercy et al. (2014) found that reefs with higher coral cover and fish abundance were significantly louder than degraded reefs. Our use of fishing pressure does not provide a direct comparison of the biological health of a reef and is a proxy determined by distance from population centers and population density around Kiritimati (Magel et al., 2020). Therefore, fishing pressure might not adequately describe the contrast in the biological health of different reefs across the small scale used in this study.

In the high frequency band (1–22 kHz), snapping shrimp snaps generated large changes in SPL (Supp. Table 1). Their snaps are created for a variety of intra- and inter-specific behaviours (Herberholz and Schmitz, 1998; Lillis et al., 2017; Versluis, 2000) and the number of snaps created within a habitat is considered representative of the density and abundance of local snapping shrimp (Butler et al., 2017). On coral reefs, due to their three-dimensional structure, snapping shrimp populations can thrive, creating sounds that dominate the high frequencies (Enochs et al., 2011). Therefore, these results contribute to the growing body of evidence across a range of habitats that snapping shrimp snaps are responsible for changes in high frequency SPL (Bohnenstiehl et al., 2016; Johnson et al., 1947; Lillis et al., 2014; Lillis and Mooney, 2018; McWilliam and Hawkins, 2013; Nedelec et al., 2015; Radford et al., 2010). High frequency SPL was also significantly explained by year, lunar phase, and fishing pressure. The pattern in year matched the pattern seen in the low frequency SPL: SPL in the high frequency band was also roughly 3.4 dB higher in 2018 than 2017. This discrepancy between years might be explained by community structure changes or population growth by species associated with sound production. Lunar phases have been associated with changes in snapping shrimp snap production on both temperate reefs and tropical Caribbean coral reefs (Radford et al., 2008a, 2008b; Lillis and Mooney, 2018). Degradation of three-dimensional structure, often seen on degraded reefs, has also been associated with lower snapping shrimp populations (Butler et al., 2016), but this did not match the pattern that we saw in fishing pressure. However, this again might be because our calculated index of fishing pressure was not a direct a direct measure of the biological health of our different reefs.

4.2. Acoustic Complexity Index

As we hypothesized, the ability of ACI to reflect changes in biogenic sounds was determined, in part, by the frequency resolution used. In both low and high frequency bands, the 31.2 Hz frequency resolution was selected as the best model, followed by the 15.6 Hz resolution model and then the 4 Hz resolution model (Table 2, Supp. Table 4). These results contrast with the results of Bolgan et al. (2018), who found that the 15.6 Hz model with a temporal resolution of 0.5 s provided the best representation of sound abundance and diversity in both controlled and field experiments. This discrepancy might be due to differences in the habitats that were analyzed, as Bolgan et al. (2018) conducted their field experiments on a sandy bottom habitat in Calvi, France and experienced minimal sound input from only five different fish calls and boats. Our recordings include a large variety of sounds created by a diverse group of soniferous fish and invertebrate species, as recordings were conducted on high energy coral reef systems.

The best low frequency ACI model explained 50.7% of the variation in ACI (Table 2), and included both knocks and herbivorous sounds as biogenic parameters, with the effect size of knocks changing between our four sampled time periods. These results resemble those found for low frequency SPL (Table 1), although the interaction between knocks and hour is significant at both 09:00 and 21:00 in the ACI model while it is only significant at 09:00 in the SPL model. This difference indicates that ACI might be more sensitive to subtle changes in knock volume or the number of knocks at 21:00 that were not discernable with SPL. Herbivorous sounds were loud and clear, obvious to identify in spectrograms (Fig. 2), and had a positive effect on ACI. Interestingly, none of the selected models at any frequency resolution included long calls (Table 2, Supp. Table 2 and 3), an important contributor to the biogenic soundscape in several environments (Bohnenstiehl et al., 2018; Bolgan et al., 2018; Locascio and Mann, 2008). This lack of significance in this experiment might be due to the low abundance of these calls and/or a lack of proximity to the hydrophones by the fish that made them. In a highly energetic environment like a coral reef, unless long calls are nearby and loud, they are difficult to identify and assess independently of constant background noise.

Year and fishing pressure were both significant abiotic factors that contributed to changes in ACI. The difference in ACI between 2017 and 2018 might, again, be due to differences in when the recordings took place in the year. As recordings were conducted in June 2017 and July 2018, fish reproductive events, which might be associated with different months could have created differences in the acoustic soundscape (Lobel et al., 2010). Fishing pressure had a significant positive effect on low frequency ACI, despite having no effect on low frequency SPL. Even though there was no significant change in SPL due to fishing pressure, degraded environments have less consistent and abundant biogenic sounds (Piercy et al., 2014), reducing the potential for “masking” changes in acoustic complexity (Bolgan et al., 2018; Staaterman et al., 2017). While it was included, we found no significant effect of lunar phase on low frequency ACI, unlike Staaterman et al. (2014), who observed lunar patterns in ACI on coral reefs in both Hawaii and Florida. This trend might have been obscured in this experiment by limited deployment durations and sampling due to the manual methods required for biogenic sounds in the low frequency band.

The 15.6 Hz and 4 Hz low frequency ACI models explained 41.84% and 40.57% of the variation, respectively. In the 15.6 Hz model, the interaction between knocks and hour was only significant at 09:00 while in the 4 Hz model, knocks no longer had a significant effect at any hour (Supp. Table 2 and 3). These results resemble those reported by Bolgan et al. (2018), who found that ACI was significantly different when calculated using different frequency resolutions. Importantly, here we present evidence that changing the frequency resolution also affects the ability of ACI to respond to and reflect changes in the abundance of different biogenic sounds. In the 4 Hz model, the only biogenic sound that had a significant effect on ACI was herbivorous sounds, which is likely due to their relatively high intensity in comparison to the other biogenic sounds recorded (Fig. 2B). The variable response by ACI to key biogenic sounds like knocks shows how important it is to test a variety of frequency resolutions on an ecosystem to determine a “best” resolution setting.

In the high frequency band, the selected model explained 37.03% of the variation in high frequency ACI. Despite this, increased snapping shrimp snaps resulted in a negative effect on high frequency ACI, indicating a potential drawback to its use in snap-dominated ecosystems (Supp. Table 4). Bohnenstiehl et al. (2018) similarly found that ACI reached a saturation threshold on a coral reef in the Bahamas while studies by Butler et al. (2016) in nearshore habitats in Florida and Staaterman et al. (2014) in reefs in both Florida and Hawai’i found that ACI followed diel patterns of snap frequency. These discrepancies in results might be due to differences in the number of snaps across different ecosystems and again raise questions about how comparable different ecosystems might be, even when using the same metric of complexity. The interaction between day/night and snapping shrimp snaps revealed that at night snaps had a significantly smaller negative effect on ACI, which could be associated with decreased snapping activity at night, reducing the “masking” effect that overwhelming and consistent sounds can have on ACI (Bolgan et al., 2018; Pieretti et al., 2011). Similar diurnal patterns in both low and high frequency ACI were observed by Staaterman et al. (2014) at reefs in Hawaii and Florida. Fishing pressure had a negative effect on ACI, similar to the results of a study by Bertucci et al. (2016), who found that MPA sites had significantly different ACIs compared to their adjacent non-MPA sites. 2018 had a significantly higher ACI than 2017 in the high frequency band as well, potentially due to differences in when the recordings took place in each year. Lunar phase was nearly significant in the high frequency band, similar to patterns observed in Staaterman et al. (2014) over a year-long study. Therefore, deployment limitations might have played a role in limiting its significance in our models.

In the high frequency models, changes in the frequency resolution did not create any differences in the significance or positive/negative slope of the covariates. Importantly, there was no change in the significant negative effect of snapping shrimp snaps among the three different frequency resolutions (Supp. Table 4–6). This is likely because regardless of frequency resolution, snapping shrimp snaps occurred in such high abundance that ACI was unable to detect changes in sound intensity between independent events. Pieretti et al. (2011) found similar results in terrestrial environments when assessing ACI’s ability to encompass consistent sounds like insect buzzing or airplanes. With significant changes to temporal frequency prior to calculation, ACI might be able to detect changes in intensity between individual snaps, but it is more likely that such a consistent sound will be attributed a near constant intensity which produces low levels of ACI.

When calculating ACI, changing key settings like frequency resolution can create significant changes to results and limits comparisons between studies. In our experiment, adjusting the frequency resolution resulted in models with the same covariates explaining different amounts of variation in both low and high frequency bands (Table 2, Supp. Table 4). Across the literature, there doesn’t appear to be any standardization in ACI settings prior to calculation. Bohnenstiehl et al. (2018) summarizes several key studies that use ACI and found that there was no consistent resolution used, even when studying the same ecosystem. Our results reveal that this discrepancy in frequency resolution could have a significant impact on the findings of each of these studies. A conclusion which is shared by Bolgan et al. (2018), who found that ACI was influenced by all settings, including temporal and frequency resolution, as well as the use of an amplitude filter. Our result might also be due to the inverse relationship between frequency and temporal resolution, in which our largest frequency resolution, 31.2 Hz, had the smallest temporal resolution and thus might have been better suited to detect short signals like fish knocks. Therefore, we recommend that more work is needed to standardize ACI calculations in the marine environment to provide a reliable and comparable metric of sound complexity.

4.3. Diel patterns

Chorusing patterns are typically associated with changes in light, with dawn and dusk choruses being most prevalent (Butler et al., 2016; Radford et al., 2014; Staaterman et al., 2014). However, our results found a shifted chorusing pattern with peaks in sound production at roughly 09:00 and 22:00 (Fig. 2; Fig. 3A, C). Sunrise and sunset in Kiritimati are typically near 06:30 and 18:30 in the summer months, roughly three hours from when our changes in sound production occurred. Not all choruses are associated with dawn and dusk, however, as nightly choruses have been recorded between dusk and midnight on the Great Barrier Reef (McCauley and Cato, 2000), and temperate fish such as the plainfin midshipman (*Porichthys notatus*) chorus in the middle of the night during the mating season (Halliday et al., 2018). While both fish and snapping shrimp chorusing activities have been linked to dawn/dusk choruses (Radford et al., 2008a, 2008b; Lillis and Mooney, 2018; Locascio and Mann, 2008), it is interesting that both snapping shrimp and fishes in this study showed changes in sound production around the same times despite not being associated with dawn or dusk.

Patterns in high frequency ACI were the inverse of patterns in high frequency SPL. These trends were also the opposite of those found by Staaterman et al. (2014), who found that acoustic complexity increased at night at both high and low frequencies. The opposing trends observed in high frequency SPL and ACI are likely due to the “masking effect”, in which a biogenic sound is produced frequently enough that it reduces ACI (Bohnenstiehl et al., 2018; Bolgan et al., 2018; Staaterman et al., 2017). The presence of this “masking effect” is exacerbated in underwater environments, like coral reefs, by the high sound propagation present in water, which allows for sounds to travel much further without losing intensity (Radford et al., 2011). Therefore, as SPL decreases during the day because of decreased snapping shrimp snap input, ACI is be better able to detect changes in complexity. In the low frequency band, no clear diurnal trends were present, unlike patterns seen in Hawaii and Florida (Staaterman et al., 2014). This could either indicate that there were no clear diurnal trends in sound diversity, or that ACI could not discern any trends with the settings used for its calculation (Bolgan et al., 2018).

4.4. Conclusions

Our results, which are in accordance with previous studies from across a range of ecosystems, indicate that ACI is not adequately developed to handle high energy systems like coral reefs (Bohnenstiehl et al., 2018; Kaplan et al., 2015; Staaterman et al., 2017). Despite its continued use in coral reef studies, ACI continues to produce inconsistent and non-significant results (Bertucci et al., 2016; Kaplan et al., 2015; Lyon et al., 2019). These inconsistencies might be a result of the lack of standardization in ACI settings and might require customizing ACI’s calculation at the ecosystem level (Bolgan et al., 2018). Meta-analyses investigating how distinct soundscapes create differing levels of complexity, and how to compare different ecosystems, might provide answers pertaining to the continued use of ACI and its potential to develop into a more useful acoustic metric.

Contemporary acoustic metrics are constantly evolving, and new technologies associated with event detection through machine learning techniques make passive acoustics more useful than ever before. While acoustic metrics can identify peaks in acoustic activity, they are not currently reliable enough to replace species-specific bioacoustic analyses. Current validation methodologies, such as the one used here, are labour-intensive and time-consuming and should eventually be replaced by automated detectors. Advances in machine learning is facilitating automation of passive acoustic monitoring with new studies investigating supervised and unsupervised methods of automatic biogenic sound detection (Lin et al., 2018, 2017), and these could be investigated for future studies of coral reef acoustics. Passive acoustic monitoring has the potential to help conserve coral reefs on a global scale; however, its application depends on a foundation of field-tested methods through studies such as this one.

CRediT authorship contribution statement

Sean Dimoff: Conceptualization, Investigation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **William D. Halliday:** Conceptualization, Methodology, Software, Data curation, Validation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing, Supervision. **Matthew K. Pine:** Conceptualization, Methodology, Software, Data curation, Validation, Formal analysis, Writing - review & editing. **Kristina L. Tietjen:** Investigation, Project administration, Writing - review & editing. **Francis Juanes:** Resources, Writing - review & editing, Funding acquisition, Supervision. **Julia K. Baum:** Conceptualization, Formal analysis, Resources, Writing - original draft, Writing - review & editing, Funding acquisition, Supervision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

We are grateful to the Government and people of Kiribati, especially Taratau Kirata, and Jacob and Lavinia Teem, for their support in conducting our fieldwork. SAD and KLT were supported by Mitacs Accelerate Fellowships. JKB received support from an NSERC Discovery Grant and the E.W.R. Steacie Memorial Fellowship, a Pew Fellowship in Marine Conservation, the Rufford Maurice Laing Foundation, the Canadian Foundation for Innovation, the British Columbia Knowledge Development Fund, the University of Victoria and University of Victoria’s Centre for Asia-Pacific Initiatives. FJ had support from the Canadian Foundation for Innovation, the British Columbia Knowledge Development Fund, the University of Victoria, and Liber Ero Foundation. MP was funded by a Mitacs Elevate Fellowship. WH was supported by the W. Garfield Weston Foundation.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecolind.2021.107435.

References

Archer, S., Halliday, W., Riera, A., Mouy, X., Pine, M., Chu, J., Dunham, A., Juanes, F., 2018. First description of a glass sponge reef soundscape reveals fish calls and elevated sound pressure levels. Mar. Ecol. Prog. Ser. 595, 245–252. https://doi.org/10.3354/meps12572.

Bell, J.D., Kronen, M., Vunisea, A., Nash, W.J., Keeble, G., Demmke, A., Pontifex, S., Andréfouët, S., 2009. Planning the use of fish for food security in the Pacific. Mar. Policy 33, 64–76. https://doi.org/10.1016/j.marpol.2008.04.002.

Bellwood, D.R., Pratchett, M.S., Morrison, T.H., Gurney, G.G., Hughes, T.P., Álvarez-Romero, J.G., Day, J.C., Grantham, R., Grech, A., Hoey, A.S., Jones, G.P., Pandolfi, J. M., Tebbett, S.B., Techera, E., Weeks, R., Cumming, G.S., 2019. Coral reef conservation in the Anthropocene: confronting spatial mismatches and prioritizing functions. Biol. Conserv. 236, 604–615. https://doi.org/10.1016/j.biocon.2019.05.056.

Beretitenti, T., 2012. Kiritimati (Census No. 20), Republic of Kiribati Island Report Series. Office of Te Beretitenti & T'Makei Services, Tarawa, Kiribati.

Bertucci, F., Parmentier, E., Lecellier, G., Hawkins, A.D., 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. https://doi.org/10.1038/srep33326.

Bohnenstiehl, D.R., Lillis, A., Eggleston, D.B., 2016. The curious acoustic behavior of estuarine snapping shrimp: temporal patterns of snapping shrimp sound in sub-tidal oyster reef habitat. PLoS ONE 11, e0143691. https://doi.org/10.1371/journal.pone.0143691.

Bohnenstiehl, D.R., Lyon, R.P., Caretti, O.N., Ricci, S.W., Eggleston, D.B., 2018. Investigating the utility of ecoacoustic metrics in marine soundscapes. J. Ecoacoust. 2 https://doi.org/10.22261/JEA.R1156L. R1156L.

Bolgan, M., Amorim, M.C.P., Fonseca, P.J., Di Iorio, L., Parmentier, E., 2018. Acoustic Complexity of vocal fish communities: a field and controlled validation. Sci. Rep. 8, 10559. https://doi.org/10.1038/s41598-018-28771-6.

Burke, L., Reytar, K., Spalding, M., Perry, A., 2011. Reefs at Risk Revisited. World Resources Institute, Washington, DC.

Butler, J., Butler, M.J., Gaff, H., 2017. Snap, crackle, and pop: acoustic-based model estimation of snapping shrimp populations in healthy and degraded hard-bottom habitats. Ecol. Ind. 77, 377–385. https://doi.org/10.1016/j.ecolind.2017.02.041.

Butler, J., Stanley, J.A., Butler, M.J., 2016. Underwater soundscapes in near-shore tropical habitats and the effects of environmental degradation and habitat restoration. J. Exp. Mar. Biol. Ecol. 479, 89–96. https://doi.org/10.1016/j.jembe.2016.03.006.

Cox, K., Brennan, L.P., Gerwing, T.G., Dudas, S.E., Juanes, F., 2018. Sound the alarm: a meta-analysis on the effect of aquatic noise on fish behavior and physiology. Glob. Change Biol. 24, 3105–3116. https://doi.org/10.1111/gcb.14106.

Elise, S., Bailly, A., Urbina-Barreto, I., Mou-Tham, G., Chiroleu, F., Vigliola, L., Robbins, W.D., Bruggemann, J.H., 2019. An optimised passive acoustic sampling scheme to discriminate among coral reefs' ecological states. Ecol. Ind. 107, 105627 https://doi.org/10.1016/j.ecolind.2019.105627.

Enochs, I., Toth, L., Brandtneris, V., Afflerbach, J., Manzello, D., 2011. Environmental determinants of motile cryptofauna on an eastern Pacific coral reef. Mar. Ecol. Prog. Ser. 438, 105–118. https://doi.org/10.3354/meps09259.

Farina, A., James, P., 2016. The acoustic communities: definition, description and ecological role. Biosystems 147, 11–20. https://doi.org/10.1016/j.biosystems.2016.05.011.

Fish, M.P., Kelsey Jr., A.S., Mowbray, W.H., 1952. Studies on the production of underwater sound by North Atlantic coastal fishes. J. Mar. Res. 11, 180–193.

Gelman, A., Su, Y.-S., Yajima, M., Hill, J., Pittau, M.G., Kerman, J., Zheng, T., Dorie, V., 2020. arm: Data Analysis Using Regression and Multilevel/Hierarchical Models.

Gordon, T.A.C., Radford, A.N., Davidson, I.K., Barnes, K., McCloskey, K., Nedelec, S.L., Meekan, M.G., McCormick, M.I., Simpson, S.D., 2019. Acoustic enrichment can enhance fish community development on degraded coral reef habitat. Nat. Commun. 10, 5414. https://doi.org/10.1038/s41467-019-13186-2.

Halliday, W., Pine, M., Bose, A., Balshine, S., Juanes, F., 2018. The plainfin midshipman's soundscape at two sites around Vancouver Island, British Columbia. Mar. Ecol. Prog. Ser. 603, 189–200. https://doi.org/10.3354/meps12730.

Herberholz, J., Schmitz, B., 1998. Role of Mechanosensory Stimuli in Intraspecific Agonistic Encounters of the Snapping Shrimp (Alpheus heterochaelis). Biol. Bull. 195, 156–167. https://doi.org/10.2307/1542823.

Hill, J., Wilkinson, C., 2004. Methods for Ecological Monitoring of Coral Reefs: Version 1. Australian Institute of Marine Science, Townsville.

Holt, D.E., Johnston, C.E., 2014. Evidence of the Lombard effect in fishes. Behav. Ecol. 25, 819–826. https://doi.org/10.1093/beheco/aru028.

Hughes, T.P., Anderson, K.D., Connolly, S.R., Heron, S.F., Kerry, J.T., Lough, J.M., Baird, A.H., Baum, J.K., Berumen, M.L., Bridge, T.C., Claar, D.C., Eakin, C.M., Gilmour, J.P., Graham, N.A.J., Harrison, H., Hobbs, J.-P.-A., Hoey, A.S., Hoogenboom, M., Lowe, R.J., McCulloch, M.T., Pandolfi, J.M., Pratchett, M., Schoepf, V., Torda, G., Wilson, S.K., 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359, 80–83. https://doi.org/10.1126/science.aan8048.

Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird, A.H., Babcock, R.C., Beger, M., Bellwood, D.R., Berkelmans, R., Bridge, T.C., Butler, I.R., Byrne, M., Cantin, N.E., Comeau, S., Connolly, S.R., Cumming, G.S., Dalton, S.J., Diaz-Pulido, G., Eakin, C.M., Figueira, W.F., Gilmour, J.P., Harrison, H.B., Heron, S.F., Hoey, A.S., Hobbs, J.-P.-A., Hoogenboom, M.O., Kennedy, E.V., Kuo, C., Lough, J.M., Lowe, R.J., Liu, G., McCulloch, M.T., Malcolm, H.A., McWilliam, M.J., Pandolfi, J.M., Pears, R.J., Pratchett, M.S., Schoepf, V., Simpson, T., Skirving, W.J., Sommer, B., Torda, G., Wachenfeld, D.R., Willis, B.L., Wilson, S.K., 2017. Global warming and recurrent mass bleaching of corals. Nature 543, 373–377. https://doi.org/10.1038/nature21707.

Johnson, M.W., Everest, F.A., Young, R.W., 1947. The Role of Snapping Shrimp (Crangon and Synalpheus) in the Production of Underwater Noise in the Sea. Biol. Bull. 93, 122–138. https://doi.org/10.2307/1538284.

Kaplan, M., Mooney, T., Partan, J., Solow, A., 2015. Coral reef species assemblages are associated with ambient soundscapes. Mar. Ecol. Prog. Ser. 533, 93–107. https://doi.org/10.3354/meps11382.

Lillis, A., Eggleston, D., Bohnenstiehl, D., 2014. Estuarine soundscapes: distinct acoustic characteristics of oyster reefs compared to soft-bottom habitats. Mar. Ecol. Prog. Ser. 505, 1–17. https://doi.org/10.3354/meps10805.

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

Lillis, A., Perelman, J.N., Panyi, A., Aran Mooney, T., 2017. Sound production patterns of big-clawed snapping shrimp (*Alpheus spp.*) are influenced by time-of-day and social context. J. Acoust. Soc. Am. 142, 3311–3320. https://doi.org/10.1121/1.5012751.

Lin, T.-H., Fang, S.-H., Tsao, Y., 2017. Improving biodiversity assessment via unsupervised separation of biological sounds from long-duration recordings. Sci. Rep. 7, 4547. https://doi.org/10.1038/s41598-017-04790-7.

Lin, T.-H., Tsao, Y., Akamatsu, T., 2018. Comparison of passive acoustic soniferous fish monitoring with supervised and unsupervised approaches. J. Acoust. Soc. Am. 143, EL278–EL284. https://doi.org/10.1121/1.5034169.

Lindseth, A., Lobel, P., 2018. Underwater soundscape monitoring and fish bioacoustics: a review. Fishes 3, 36. https://doi.org/10.3390/fishes3030036.

Lobel, P.S., 2013. THE "Choral Reef": the ecology of underwater Sounds. AAUS pp. 179–184.

Lobel, P.S., Kaatz, I.M., Rice, A.N., 2010. Acoustical behavior of coral reef fishes. In: Reproduction and Sexuality in Marine Fishes: Patterns and Processes. University of California Press, pp. 307–386.

Locascio, J.V., Mann, D.A., 2008. Diel periodicity of fish sound production in Charlotte Harbor. Florida. T. Am. Fish. Soc. 137, 606–615. https://doi.org/10.1577/T06-069.1.

Luczkovich, J.J., Krahforst, C.S., Kelly, K.E., Sprague, M.W., 2016. The Lombard effect in fishes: How boat noise impacts oyster toadfish vocalization amplitudes in natural experiments. Proc. Mtgs. Acoust. 27, 010035 https://doi.org/10.1121/2.0000340.

Lyon, R., Eggleston, D., Bohnenstiehl, D., Layman, C., Ricci, S., Allgeier, J., 2019. Fish community structure, habitat complexity, and soundscape characteristics of patch reefs in a tropical, back-reef system. Mar. Ecol. Prog. Ser. 609, 33–48. https://doi.org/10.3354/meps12829.

Magel, J.M.T., Burns, J.H.R., Gates, R.D., Baum, J.K., 2019. Effects of bleaching-associated mass coral mortality on reef structural complexity across a gradient of local disturbance. Sci. Rep. 9, 2512. https://doi.org/10.1038/s41598-018-37713-1.

Magel, J.M.T., Dimoff, S.A., Baum, J.K., 2020. Direct and indirect effects of climate change-amplified pulse heat stress events on coral reef fish communities. Ecol. Appl. 30, e02124 https://doi.org/10.1002/eap.2124.

McCauley, R.D., Cato, D.H., 2000. Patterns of fish calling in a nearshore environment in the Great Barrier Reef. Phil. Trans. R. Soc. Lond. B 355, 1289–1293. https://doi.org/10.1098/rstb.2000.0686.

McPherson, C., Martin, B., MacDonnell, J., Whitt, C., 2016. Examining the value of the Acoustic Variability Index in the characterisation of Australian marine soundscapes. Proc. Acoust. 1–13.

McWilliam, J.N., Hawkins, A.D., 2013. A comparison of inshore marine soundscapes. J. Exp. Mar. Biol. Ecol. 446, 166–176. https://doi.org/10.1016/j.jembe.2013.05.012.

Moberg, F., Folke, C., 1999. Ecological goods and services of coral reef ecosystems. Ecol. Econ. 29, 215–233. https://doi.org/10.1016/S0921-8009(99)00009-9.

Nedelec, S., Simpson, S., Holderied, M., Radford, A., Lecellier, G., Radford, C., Lecchini, D., 2015. Soundscapes and living communities in coral reefs: temporal and spatial variation. Mar. Ecol. Prog. Ser. 524, 125–135. https://doi.org/10.3354/meps11175.

Piercy, J., Codling, E., Hill, A., Smith, D., Simpson, S., 2014. Habitat quality affects sound production and likely distance of detection on coral reefs. Mar. Ecol. Prog. Ser. 516, 35–47. https://doi.org/10.3354/meps10986.

Pieretti, N., Farina, A., Morri, D., 2011. A new methodology to infer the singing activity of an avian community: The Acoustic Complexity Index (ACI). Ecol. Ind. 11, 868–873. https://doi.org/10.1016/j.ecolind.2010.11.005.

Prada, F., Caroselli, E., Mengoli, S., Brizi, L., Fantazzini, P., Capaccioni, B., Pasquini, L., Fabricius, K.E., Dubinsky, Z., Falini, G., Goffredo, S., 2017. Ocean warming and acidification synergistically increase coral mortality. Sci. Rep. 7, 40842. https://doi.org/10.1038/srep40842.

R Core Team, 2019. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Radford, C., Jeffs, A., Tindle, C., Montgomery, J., 2008a. Resonating sea urchin skeletons create coastal choruses. Mar. Ecol. Prog. Ser. 362, 37–43. https://doi.org/10.3354/meps07444.

Radford, C., Stanley, J., Jeffs, A., 2014. Adjacent coral reef habitats produce different underwater sound signatures. Mar. Ecol. Prog. Ser. 505, 19–28. https://doi.org/10.3354/meps10782.

Radford, C., Stanley, J., Tindle, C., Montgomery, J., Jeffs, A., 2010. Localised coastal habitats have distinct underwater sound signatures. Mar. Ecol. Prog. Ser. 401, 21–29. https://doi.org/10.3354/meps08451.

Radford, C., Tindle, C., Montgomery, J., Jeffs, A., 2011. Modelling a reef as an extended sound source increases the predicted range at which reef noise may be heard by fish larvae. Mar. Ecol. Prog. Ser. 438, 167–174. https://doi.org/10.3354/meps09312.

Radford, C.A., Tindle, C.T., Montgomery, J.C., 2008b. Temporal patterns in ambient noise of biological origin from a shallow water temperate reef. Oecologia 156, 921–929. https://doi.org/10.1007/s00442-008-1041-y.

Rountree, R.A., Gilmore, G.A., Goudey, C.A., Hawkins, A.D., Luczkovich, J.J., Mann, D.A., 2006. Listening to fish: applications of passive acoustics to fisheries science. Fisheries 31, 433–446.

Slabbekoorn, H., Bouton, N., van Opzeeland, I., Coers, A., ten Cate, C., Popper, A.N., 2010. A noisy spring: the impact of globally rising underwater sound levels on fish. Trends Ecol. Evol. 25, 419–427. https://doi.org/10.1016/j.tree.2010.04.005.

Slabbekoorn, H., Dooling, R.J., Popper, A.N., Fay, R.R. (Eds.), 2018. Effects of anthropogenic noise on animals. Springer Handbook of Auditory Research. Springer, New York, New York, NY. https://doi.org/10.1007/978-1-4939-8574-6.

Staaterman, E., Ogburn, M., Altieri, A., Brandl, S., Whippo, R., Seemann, J., Goodison, M., Duffy, J., 2017. Bioacoustic measurements complement visual biodiversity surveys: preliminary evidence from four shallow marine habitats. Mar. Ecol. Prog. Ser. 575, 207–215. https://doi.org/10.3354/meps12188.

Staaterman, E., Paris, C., DeFerrari, H., Mann, D., Rice, A., D'Alessandro, E., 2014. Celestial patterns in marine soundscapes. Mar. Ecol. Prog. Ser. 508, 17–32. https://doi.org/10.3354/meps10911.

Steinberg, J.C., Cummings, W.C., Brahy, B.D., MacBain, J.Y., 1965. Further bio-acoustic studies off the West Coast of North Bimini, Bahamas. Bull. Mar. Sci. 942–963.

Sueur, J., Farina, A., Gasc, A., Pieretti, N., Pavoine, S., 2014. Acoustic indices for biodiversity assessment and landscape investigation. Acta Acust. Acustica 100, 772–781. https://doi.org/10.3813/AAA.918757.

Tricas, T., Boyle, K., 2014. Acoustic behaviors in Hawaiian coral reef fish communities. Mar. Ecol. Prog. Ser. 511, 1–16. https://doi.org/10.3354/meps10930.

Versluis, M., 2000. How snapping shrimp snap: through cavitating bubbles. Science 289, 2114–2117. https://doi.org/10.1126/science.289.5487.2114.

Wall, C., Simard, P., Lembke, C., Mann, D., 2013. Large-scale passive acoustic monitoring of fish sound production on the West Florida Shelf. Mar. Ecol. Prog. Ser. 484, 173–188. https://doi.org/10.3354/meps10268.

Watson, M.S., Claar, D.C., Baum, J.K., 2016. Subsistence in isolation: fishing dependence and perceptions of change on Kiritimati, the world's largest atoll. Ocean Coast. Manag. 123, 1–8.