Coral Reefs
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REPORT

Snapping shrimp sound production patterns on Caribbean coral reefs: relationships with celestial cycles and environmental variables

Ashlee Lillis[1] · **T. Aran Mooney**[1]

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Abstract The rich acoustic environment of coral reefs, including the sounds of a variety of fish and invertebrates, is a reflection of the structural complexity and biological diversity of these habitats. Emerging interest in applying passive acoustic monitoring and soundscape analysis to measure coral reef habitat characteristics and track ecological patterns is hindered by a poor understanding of the most common and abundant sound producers on reefs—the snapping shrimp. Here, we sought to address several basic biophysical drivers of reef sound by investigating acoustic activity patterns of snapping shrimp populations on two adjacent coral reefs using a detailed snap detection analysis routine to a high-resolution 2.5-month acoustic dataset from the US Virgin Islands. The reefs exhibited strong diel and lunar periodicity in snap rates and clear spatial differences in snapping levels. Snap rates peaked at dawn and dusk and were higher overall during daytime versus nighttime, a seldom-reported pattern in earlier descriptions of diel snapping shrimp acoustic activity. Small differences between the sites in snap rate rhythms were detected and illustrate how analyses of specific soundscape elements might reveal subtle between-reef variation. Snap rates were highly correlated with environmental variables, including water temperature and light, and were found to be sensitive to changes in oceanographic forcing. This study further establishes snapping shrimp as key players in the coral reef chorus and provides evidence that their acoustic output reflects a combination of environmental conditions, celestial influences, and spatial habitat variation. Effective application of passive acoustic monitoring in coral reef habitats using snap rates or snapping-influenced acoustic metrics will require a mechanistic understanding of the underlying spatial and temporal variation in snapping shrimp sound production across multiple scales.

Keywords Soundscape · Acoustic ecology · Alpheidae · Noise · Passive acoustic monitoring · US Virgin Islands

Introduction

Coral reef habitats can harbor high densities of sound-producing marine organisms, producing a rich and varied acoustic environment. The soundscapes of coral reefs are distinct from surrounding areas, a reflection of both the biodiverse assemblages present (with high numbers of soniferous fish and invertebrates) and the geophysical interactions between reef structure and wave action (Radford et al. 2014; Staaterman et al. 2014; Kaplan et al. 2015). These soundscapes are a fundamental component of the sensory environment and are known to influence myriad ecological processes, including fish and invertebrate orientation and settlement to reefs (Simpson et al. 2005; Radford et al. 2011; Stanley et al. 2012; Lillis et al. 2016). Because coral reefs are complex three-dimensional habitats, conventional sampling techniques can substantially underestimate biodiversity, particularly that of crustaceans and other infaunal invertebrates (Plaisance et al. 2011). Passive acoustic recording methods have long been

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✉ Ashlee Lillis
alillis@whoi.edu

[1] Woods Hole Oceanographic Institution, Woods Hole, MA, USA

employed in marine environments and are increasingly applied to coral reefs, to detect and observe species that are visually enigmatic, often at higher resolution than traditional sampling (Mann and Lobel 1995; Lobel 2002; Cotter 2008; Lobel et al. 2010). Moreover, there is a rapidly growing field of applied research seeking to use soundscape characteristics and passive acoustic monitoring to efficiently measure coral reef habitat attributes including coral cover and biodiversity (Kennedy et al. 2010; Kaplan et al. 2015; Harris et al. 2016).

Reef-dwelling snapping shrimp, members of the *Alpheus* and *Synalpheus* genera, are commonly the most ubiquitous and audible sound source on coral reefs (Simpson et al. 2008; Staaterman et al. 2014; Piercy et al. 2014). These shrimp "snap" via the collapse of a cavitation bubble during rapid claw closure, generating broadband signals (up to 200 kHz), typically peaking between 2 and 20 kHz (Au and Banks 1998; Ferguson and Cleary 2001). Individual snapping shrimp measure only millimeters to centimeters in average length (depending on species), but produce snap amplitudes up to 190 dB (re 1 μPa at 1 m), among the highest amplitude sounds in the sea (Au and Banks 1998; Versluis et al. 2000). Snapping shrimp are most often visually cryptic, with populations inhabiting crevices in rubble, sponges, coral heads, and other invertebrates (e.g., anemones, tunicates). The two genera comprise several hundred species with a variety of social structures, symbiotic relationships, and life history traits (Anker et al. 2006). Their snaps are reported to occur during aggressive conspecific and interspecific territorial interactions (Nolan and Salmon 1970; Schein 1975, 1977; Hughes et al. 2014; Lillis et al. 2017), as well as in response to environmental disturbances, during burrowing, and, possibly for prey capture (Anker et al. 2006). Still, the eco-acoustics of most species of coral reef snapping shrimp, including their responses to local physical variables of the reef and surrounding waters, has not been examined, and to our knowledge, snapping shrimp populations have not been enumerated. Due to their cryptic nature, the ecology and behaviors of these abundant and speciose animals are difficult to study. However, given that they can be measured acoustically, sound recordings and snap analyses offer a method to illuminate the activity patterns of these abundant reef dwellers.

Because snapping shrimp are closely tied to the reef environment, their sound production has been suggested as a possible metric for comparing benthic habitats and assessing reef quality (Radford et al. 2008a, 2010; Watanabe et al. 2002). Such an application requires an improved understanding of the drivers of spatial and temporal variation in snapping shrimp sound production. At present, relationships between snapping shrimp sound parameters (levels, snap rates) and even basic physical variables (e.g., temperature, light) are not well understood, while reports of the relationships between snapping and ecological variables (e.g., diversity, reef health) are conflicting. A short-term study by Kennedy et al. (2010) found a significant relationship between sound levels in shrimp-dominated frequencies (> 2 kHz) and coral diversity, and Butler et al. (2017) recorded higher snap rates in healthy areas compared to degraded ones in sponge-rich hard-bottom habitats of Florida. However, other studies of coral reef soundscapes have not observed consistent links between biodiversity and snapping shrimp frequency band sound level measurements (Kaplan et al. 2015; Freeman and Freeman 2016; Staaterman et al. 2017). This discrepancy exists, in part, because our knowledge of the existing spatial and temporal variation and ecological significance of snapping shrimp acoustic activity on coral reefs remains limited.

Snapping shrimp sounds in previously studied locations typically exhibit diel periodicity, in concert with dawn and dusk (Johnson et al. 1947; Au and Banks 1998). However, the temporal and spatial variation in this crepuscular periodicity, as well as the trend for dominant daytime or nighttime snapping, appears to vary over multiple scales. Early reports of snapping shrimp frequency band levels indicated that they are most acoustically active at dawn and dusk with overall higher nocturnal sound production (Johnson et al. 1947; Everest 1948), and this pattern has been widely referenced in the subsequent soundscape literature. However, more recent longer-term acoustic observations in disparate geographical locations reveal more complex spatial and temporal variation, including contrasting diel cycles in space and time (Lammers et al. 2008; Bohnenstiehl et al. 2016; Lillis and Mooney 2016). Additionally, the development and application of new snap detection algorithms has uncovered unexpected fine-scale patterns in shrimp-driven soundscapes (Bohnenstiehl et al. 2016), providing information supplementary to previous coarser analyses that used solely a broad frequency band to represent snapping shrimp acoustic output.

Here, we investigated variation in the snapping shrimp acoustic activity for coral reef soundscapes in the US Virgin Islands National Park. The overarching goal was more closely examine how snapping shrimp sound production varies on coral reefs and the drivers of that variability. Using existing high-temporal resolution acoustic datasets, we compared the shrimp snap rates and levels at diel and monthly scales within and between adjacent coral reefs, to ask the questions: (1) How do snap rates vary over daily and lunar scales? (2) Do environmental variables (i.e., light, temperature) relate to snap rate variation? and (3) How do snap rates and their temporal patterns vary between adjacent reefs?

Materials and methods

Field recordings and data

Beginning in April 2013, a long-term program was initiated to record underwater soundscapes and conduct biological surveys at coral reef sites in St. John, within the US Virgin Islands National Park (Fig. 1). The Spring/Summer 2013 effort included deployments of DSG (Loggerhead Instruments, FL, USA) recorders to make acoustic measurements at two closely spaced coral reef sites, Tektite and Yawzi (further described in Kaplan et al. 2015). Temperature/light loggers (HOBO Pendant, Onset Computer Corporation, Bourne, MA, USA) were deployed with the acoustic moorings, sampling once every 10 min. From this dataset, snap analyses were performed to evaluate temporal trends and variation between the two reef sites, using 84 d of acoustic samples from April 19 to July 6, 2013 (1 min sample every 20 min, 5% duty cycle, yielding 5650 samples at each site).

The DSG records using a standard omnidirectional HTI-96 hydrophone (sensitivity of $-$ 179.7 dBV μPa^{-1} and flat frequency response between $\sim$ 0.1 and 30 kHz; High-Tech Inc) and contains a 16-bit computer board, with a standard solid-state SD memory card. The DSGs were configured with a 20 dB gain and 80 kHz sample rate, with a duty cycle of 1 min recording every 20 min. Recorders were deployed on cinder blocks within the reef habitat, near the outer edges, on flat sandy patches between coral structures of a similar depth range at each reef site (instrument depths: Tektite—12 m; Yawzi—10 m).

Snap detection and analysis

Patterns in shrimp snapping throughout each deployment were quantified with an automatic snap detection algorithm. Snapping shrimp produce highly stereotyped broad-spectrum acoustic signals, with an extremely short-duration initial peak (< 100 µs) of relatively high acoustic energy followed by several lower amplitude oscillations (Au and Banks 1998; Versluis et al. 2000). Because no other organisms are currently known to generate such distinct high-amplitude short-duration signals at similar rates (i.e., thousands per minute), automatic detection approaches have been developed to quantify snaps (Radford et al. 2008a; Bohnenstiehl et al. 2016; Rossi et al. 2016). The snap detection routine used here is an envelope correlation method as described in Bohnenstiehl et al. (2016), whereby individual snaps are identified via their correspondence to a snap kernel (derived from sample snaps recorded within the reef sites), followed by the application of an amplitude threshold to limit the detection range and prevent false detections of lower amplitude signals. The snap kernel function is a smoothed envelope of a characteristic snap signal and includes a zero-padding segment on the trailing end of equal duration to the snap (2.0 ms) to avoid multiple detections of single snaps, for instance caused by surface reflections (Bohnenstiehl et al. 2016). This procedure was applied to 2–20 kHz band-passed waveforms, as this was determined to be the band primarily containing the snapping shrimp acoustic energy based on spectral analysis and is the frequency range used as a proxy for snapping shrimp sound production (Lammers et al. 2008; Staaterman et al. 2014; Kaplan et al. 2015). The 2-kHz high-pass filter also suppresses low-frequency noise interference, such as the sounds of boats and fish (see Supplementary Materials for examples of snap detector function in the presence of boat noise).

From this analysis, snap rates were estimated within each recording, as detections per minute. In addition to snap counts, the average sound pressure level in the band-passed data (2–20 kHz) was computed (root-mean-square SPL in dB re 1 µPa), as well as the peak-to-peak amplitude of the individual snaps (dB re 1 µPa) in each sample.

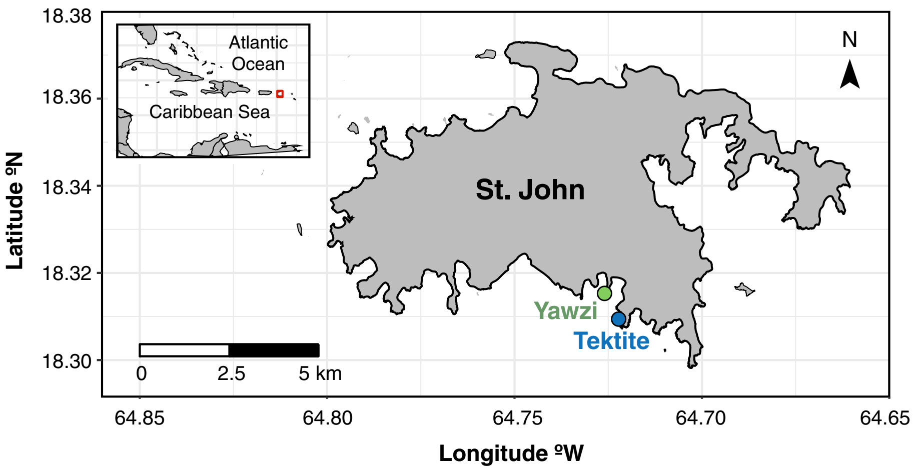

Fig. 1 Map of St. John, USVI, showing the locations of the acoustically sampled reef sites Yawzi and Tektite. Inset shows the position of the USVI within the Caribbean archipelago

Following identification of snaps using the correlation step sensitive to the shape of the arriving signal, an amplitude threshold was applied to limit the detection catalog to snaps above 125 dB re 1 μPa (peak-to-peak), corresponding to the maximum background root-mean-square sound levels observed during the monitoring period at all sites, to restrict the detection range and prevent false positives (see Supplementary Materials for snap detection examples). This threshold was applied to calculate snap rates (per minute) for all the data used. At the 125 dB threshold level, the detection range was conservatively estimated to be no more than 300 m. This maximal range estimate is based on theoretical cylindrical spreading loss [TL = 10 log(r), used as an approximation here because the coral reef sites are shallow (< 10 m) with complex bathymetry that will act as boundaries to uniform propagation from a source]. To make this approximation, a reasonable estimate of maximal source level is required for this environment; we used a source level of 150 dB, the 99th percentile amplitude of snaps detected, under the assumption that these loudest amplitude snaps are closest to the sensor (i.e., @ ~ 1 m).

To quantify diel patterns in shrimp snapping, snap rates observed for day and night were compared for each day of recording by calculating the percent excess daytime snapping (Px):

$$Px = 100\frac{N_\mathrm{d} - N_\mathrm{e}}{N_\mathrm{e}},$$

where N_d is the number of snaps detected within daytime, based on local sunrise and sunset times and N_e is the number of expected snaps based on the fraction of daytime recordings and total number of snaps detected in the 24-h period (e.g., if daytime recordings make up 60% of the recordings in a day, N_e is calculated as 60% of total snaps counted in that 24-h). Daytime and nighttime were defined using local sunrise and sunset times for each day, with the exclusion of crepuscular periods (90 min before and after sunrise and sunset) since dawn and dusk show precipitous increases in snap rate (Lammers et al. 2008; Radford et al. 2008a; Bohnenstiehl et al. 2016). A nonzero Px value indicates significantly higher daytime or nighttime snap activity, and a positive Px signifies greater snap counts during the day compared to night. The number of snaps detected during dawn, midday, dusk, and midnight was also compared by calculating a snap rate for these periods (dawn = sunrise ± 1.5 h; midday = noon ± 1.5 h; dusk = sunset ± 1.5 h; midnight = midnight ± 1.5 h) for each sampling day at each site. Differences between snap rates during the four diurnal periods were then tested statistically using a nonparametric Friedman's test with repeated measures (Liu and Berger 2014), since snap rate data did not meet assumptions for parametric tests.

To further detect temporal periodicities in the snap rate datasets, particularly any repetitive daily, crepuscular, and lunar patterns, several time-series analysis techniques were employed such as a periodogram and autocorrelation function analyses (Shumway and Stoffer 2006). To complement these analyses, a wavelet scalogram approach, allowing the detection of the representative scales of a signal (Cazelles et al. 2008), was used to identify and examine the relative strength of periodicities in snap rates throughout the time series (MATLAB wavelet toolbox, Grinsted et al. 2004).

To examine the relationships between shrimp snapping patterns and abiotic variables observed during the 2.5-month time series, temperature (°C) and light intensity (relative irradiance) data were correlated with measured snap rates, both overall daily snap rates and snap rates separated into daytime, nighttime, and crepuscular periods (Pearson's correlations, statistically significant correlation coefficients reported as r-values). For water temperature correlations, mean daily water temperature was tested as a predictor of the mean daily snap rate. Snap rates for daytime samples (light > 0) were correlated with light level records. Lunar phase was also tested as a predictor variable for snap rates (daytime, nighttime, and crepuscular) and percent daytime excess, using data obtained from the US Naval Observatory's Astronomical Applications Department data services (http://aa.usno.navy.mil/data/docs). All statistical analyses were performed using MATLAB® Statistics package (v.9.1; Mathworks 2016).

Results

Snapping shrimp sounds were present in all files recorded at Tektite and Yawzi reefs over the 84-d deployment period (April–July), and the acoustic signals were quantified in terms of both snap detection rate and sound pressure levels (Fig. 2). Snaps were detected approximately twice as frequently at the Yawzi site versus Tektite and corresponded to ~ 7 dB re 1 μPa higher sound pressure levels in the 2–20 kHz bandwidth at Yawzi compared to Tektite (Figs. 2, 3a). An anomalous decrease in snap rates was recorded 4–6 May, coincident with a switch in dominant wind and wave direction (from East to West) and the lowest recorded wave heights for the monitoring period (May 4–6: 0.44 ± 0.08 m, entire monitoring period: 1.22 ± 0.29 m), based on available ocean data from a nearby NOAA buoy (http://www.ndbc.noaa.gov: Station 41052). Snap rates were significantly correlated with sound pressure levels in the 2–20 kHz analysis band ($p < 0.01$), with a stronger relationship at Yawzi compared to Tektite (Fig. 3). Water temperature ranged from 26.7 to 28.5 °C throughout the monitoring period (Fig. 2), and the mean

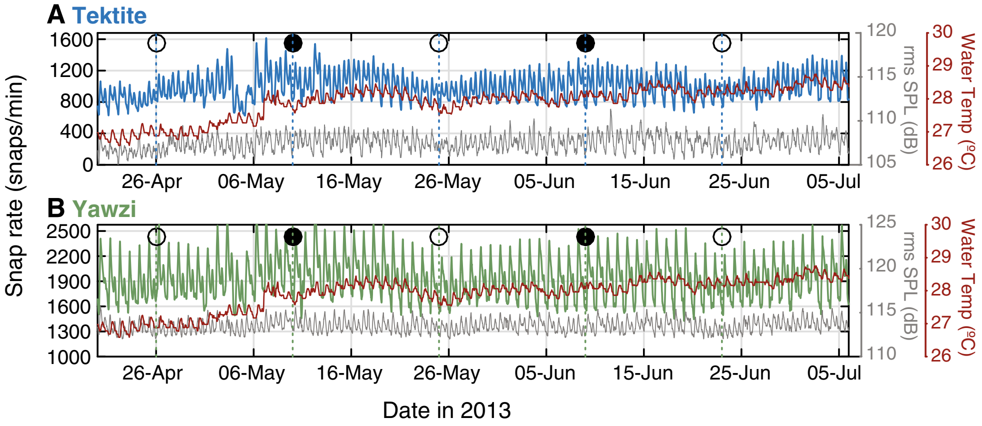

Fig. 2 Overall trends in snapping time series. Observed snap rates (min^{-1}), sound pressure levels in the snap analysis band (2–20 kHz rms dB re 1 µPa), and water temperature (°C) measured at reef sites **a** Tektite, and **b** Yawzi from April to July 2013. Open and closed circles denote full and new moons, respectively

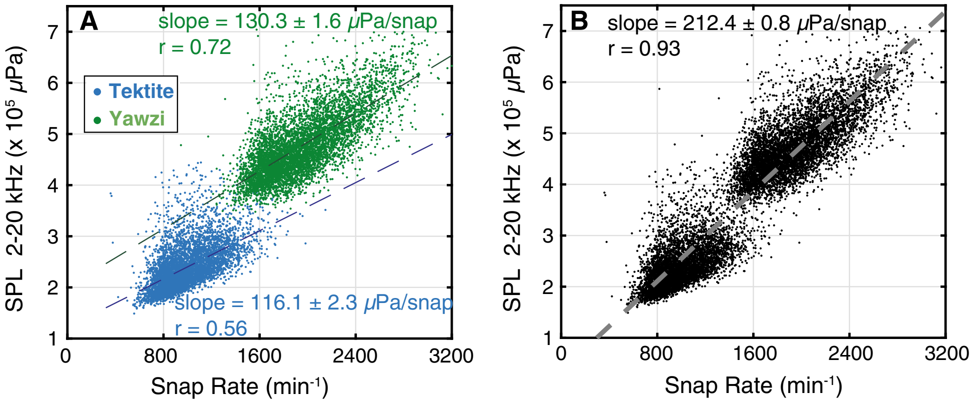

Fig. 3 Correlations between snap rate and sound pressure levels (SPL) in the snap analysis band (2–20 kHz dB re 1 µPa) measured for both reefs (**a**) and pooled data (**b**)

daily snap rate was significantly correlated with mean daily temperature (Fig. 4). Yawzi snap rate showed a weaker relationship between snap rate and water temperature compared to Tektite (Fig. 4).

At a 24-h timescale, both sites showed strong diel rhythms in snap rates, with sharp crepuscular increases in snapping activity (Figs. 2, 5, 6). These pronounced peaks in snapping shrimp acoustic activity, particularly at dawn, were the dominant consistent feature of the daily pattern throughout the sampling period (Figs. 2, 5, 6). Accordingly, overall daytime snap rates showed significant negative correlations with light levels across the sampling period (Tektite: $r = -0.40$, $p < .001$; Yawzi: $r = -0.27$, $p < .001$), i.e., the highest snap rates of the daylights hours were observed at times of low/changing light conditions. Comparisons of snap rates separated into dawn, midday, dusk, and midnight periods for each sampling day show significant differences between these times of day at both reef sites [Fig. 5; Tektite: $\chi^2(3307) = 200.6$, $p < .001$; Yawzi $\chi^2(3307) = 197.1$, $p < .001$], with significantly lower snap rates in the middle of the night and highest snap rates around sunrise. Dusk snap rates were higher than day and night at Tektite reef (Fig. 5a), but not at Yawzi reef where median dusk snap rate was not significantly higher than daytime (Fig. 5b).

All days in the sampling period showed daytime snap rates significantly higher than nighttime snap rates (Fig. 6i, light color bars indicate daytime snap rates), with mean percent excesses of 9.79 ± 0.39% and 9.34 ± 0.26% at Tektite and Yawzi, respectively. Due to the combination of the crepuscular peaks, as well as the daytime dominance, both sites demonstrated strong snap rate periodicity at once and twice a day frequencies (Fig. 6); however, the relative strength of these diel cycles differed slightly by site. At Tektite, the 0.5-d periodicity was more evident compared to Yawzi, where periodogram and autocorrelation function analysis showed the 1-d period to dominate (Fig. 6, panels ii and iii). A weaker periodicity was detected for both sites at a ~ 29-d cycle (Fig. 6ii). Wavelet scalograms further illustrate the persistence and relative strength of the periodicities over time (Fig. 7). Again, the 0.5- and 1-d periods are evident at the two reef sites, with the 0.5-d period more intense at Tektite and 1-d period more intense at Yawzi, though the strength of these periodicities varies over the sampling period. The most intense diel patterns were observed before, during, and after new moons, when the periodicities were the strongest (Fig. 7, black circles indicate new moon and white circles indicate full moons).

Figure 8 shows examples of diel rhythms in snap rates and SPL at each site throughout a lunar cycle. Crepuscular

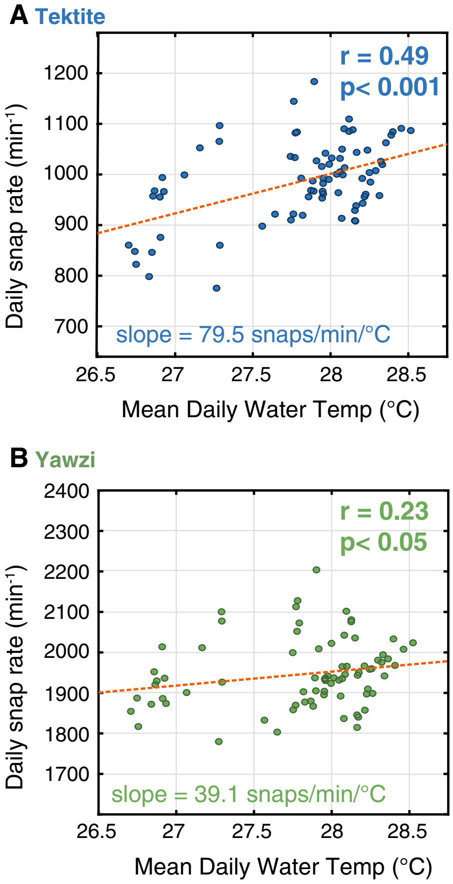

Fig. 4 Correlations between snap rate and water temperature. Mean daily snap rate (min^{-1}) versus mean daily water temperature (°C) measured at Tektite (**a**) and Yawzi (**b**) reefs

peaks show a 50–100% increase in snap rate over the 15–30 min around sunrise and sunset, compared to nighttime. Calculated daytime excesses also demonstrate the lunar pattern in diel periodicity strength, with highest levels of daytime dominant snapping during the new moon (Fig. 8). Particularly at Tektite, plots of diel snap rate show that the new moon is the lunar phase exhibiting the strongest crepuscular peaks in snap rate (Fig. 8a). Sound pressure levels in the snap analysis band generally matched these diel and lunar patterns, though with higher variability (see gray lines in Fig. 8), particularly at Tektite.

Correlations between snap rates and the proportion of moon illumination further quantify the effect of moon phase on snapping activity. There were significant negative relationships between moon illumination and both mean snap rates and percent daytime excess (Fig. 9). Examining the correlations between lunar phase and the daytime, nighttime, and crepuscular snap rates separately revealed that the lunar relationships with overall snap rates and percent daytime excesses result from significant decreases in daytime and crepuscular snap rates from new to full moon (Tektite: daytime $r = -0.68$, crepuscular $r = -0.61$; Yawzi: daytime $r = -0.71$, crepuscular $r = -0.38$; $p < .001$). In contrast, no significant relationships were observed between nighttime snap rate and proportion moon illumination (Fig. 9ii, dark circles).

Discussion

Passive acoustic recordings were collected with high-resolution temporal sampling (every 20 min) for a 2.5-month period at two adjacent Caribbean coral reefs and used to investigate sound production patterns of the most ubiquitous sound producers, the snapping shrimp. The relationships found between snap rates and the overall sound pressure level demonstrate that snapping shrimp acoustic activity drives the high-frequency (> 2 kHz) soundscapes of these reefs and that this activity is related to several environmental factors at different temporal scales. The high-frequency sound levels were positively correlated with snap rates, and with a doubling of snap rate, there was an approximate doubling of sound pressure, reflecting the often-close relationship between these two measurements. Yet, the use of a snap counting algorithm reveals additional

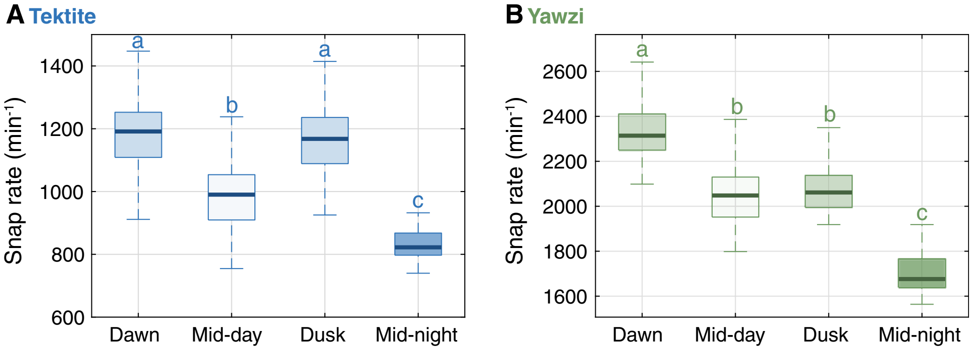

Fig. 5 Boxplot of snap rates within dawn, midday, dusk, and midnight segments of sampling days at **a** Tektite and **b** Yawzi. Box plots show median values (solid horizontal lines), 50th percentile values (box outline), and 90th percentile values (whiskers). Lowercase letters denote significant differences between snap rates for different periods of the day ($p < .05$)

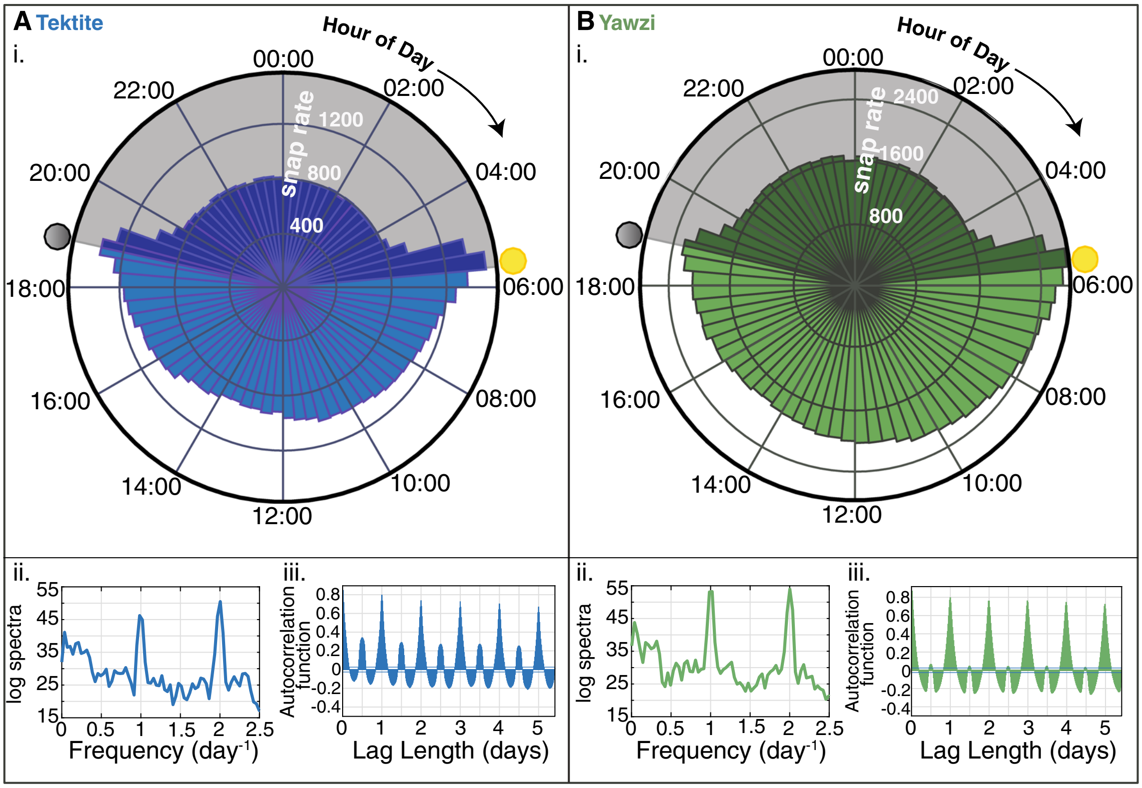

Fig. 6 Daily snap pattern trends at **a** Tektite and **b** Yawzi. (i) Angular histogram of snap rates detected for each sampling time throughout the day (every 20 min), averaged over the 2.5-month deployment. Mean sunrise and sunset are indicated by the yellow and gray circles, respectively, and nighttime hours are signified by the shaded portion of the rose plot. (ii) Snap rate periodograms showing distinct periodicities (and their relative strength) at once and twice per day, as well as a weaker periodicity at 0.035 d^{-1} ($\sim$ 29 d). (iii) Autocorrelation plots for snap rate, across lag time in days, showing high autocorrelation values at once per day intervals for both sites, and at twice per day intervals at Tektite (**a**)

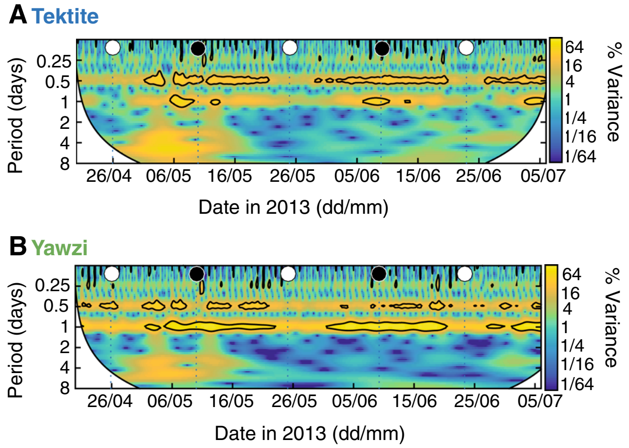

Fig. 7 Wavelet analysis. Wavelet scalograms of snap rate data at **a** Tektite and **b** Yawzi, generated using a Morlet wavelet method, illustrating the persistence and relative strength of diel periodicities throughout the monitoring period. The most intense times of diel periodicities are circled. Both time series exhibit periodicities at 0.5- and 1-d scales, strongest during new moon periods (dates of full and new moons are denoted by white and black circles, respectively); the scalogram highlights that 0.5 d is the dominant period at Tektite (**a**), whereas Yawzi is characterized by a dominant 1-d period (**b**)

spatiotemporal patterns and closer relationships to meteorological and lunar forcing than when solely examining high-frequency sound levels. These acoustic frequencies are known to have biological inputs in addition to snapping shrimp, such as urchin feeding and crab interactions with substrate (Radford et al. 2008b; Freeman et al. 2014). Our data illustrate that sound pressure level analyses might not always reflect the snapping shrimp sound production patterns. For instance, snap rates were observed to be sensitive to a short-duration weather event in early May in which wind direction switched and waves diminished, and snapping decreased by $\sim$ 50%, but the same effect was not evident in examination of the SPL data alone. This supports the use of the two complementary metrics to investigate snapping shrimp acoustic behavior and their influence on soundscapes.

Differences between the two reef sites were detected in the magnitudes of snap rates, as well as in snap rate periodicities and the strengths of correlations with temperature, light, and lunar phase. The considerably lower snap rate at Tektite suggests a lower abundance of resident snapping shrimp, assuming that the number of snaps relates to the

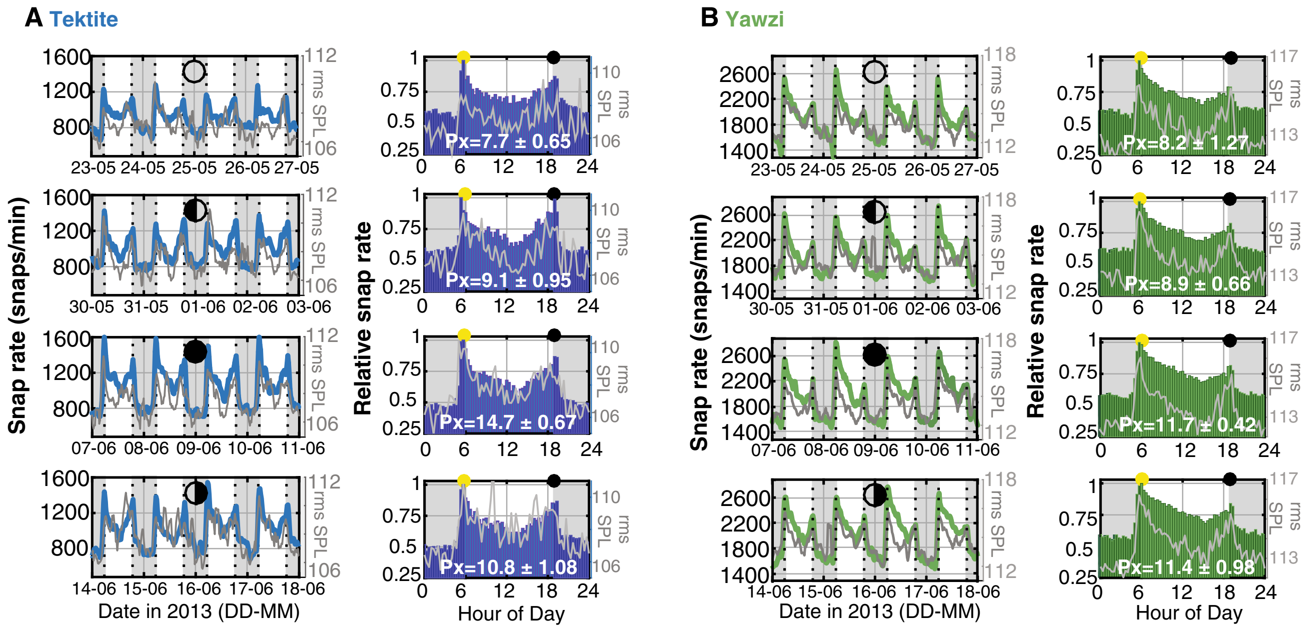

Fig. 8 Snap and time of day patterns by lunar phase. Left plots show 4 d of snap rates and rms SPL (2–20 kHz analysis band) around each lunar phase (top to bottom: full, last quarter, new, and first quarter moons). Histograms show the distribution of relative snap rate by hour of day for the corresponding lunar phase, with yellow and black circles indicating sunrise and sunset, respectively. *Px* values displayed on histograms are the percent excess daytime snaps calculated for each lunar phase sample

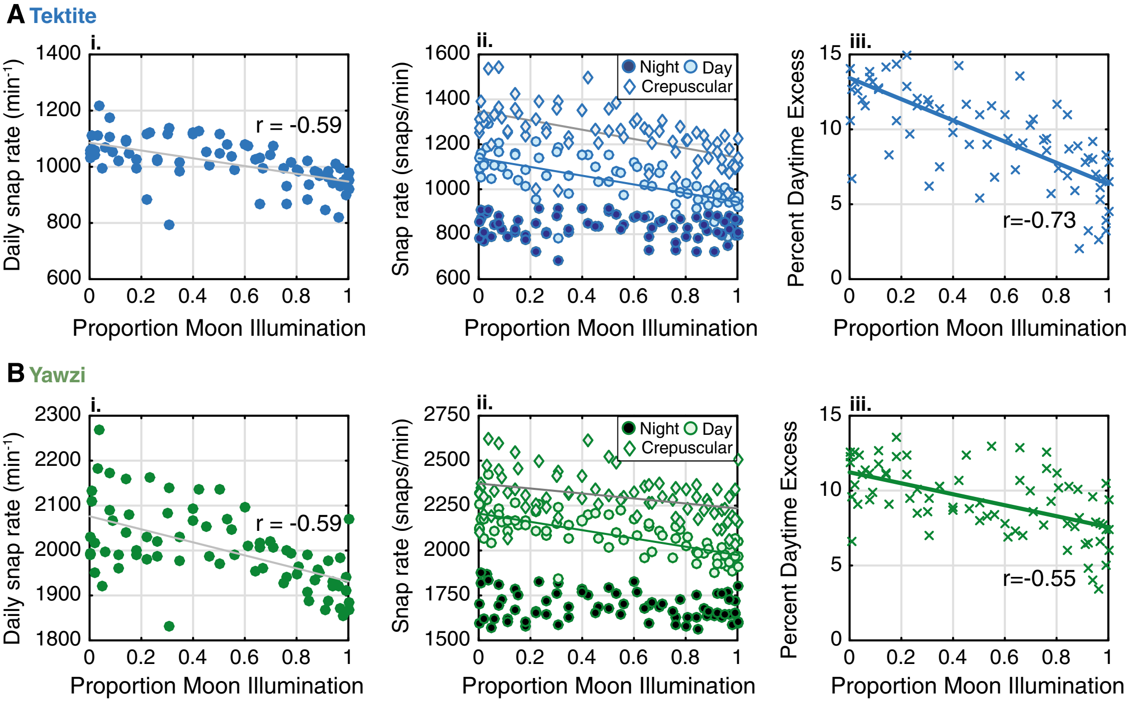

Fig. 9 Relationships between snap rates and lunar phase. Correlations between lunar phase (proportion of moon illuminated) and (i) mean snap rate, (ii) daytime and nighttime snap rates, and (iii) percent daytime excess snaps, at **a** Tektite and **b** Yawzi reef sites. Significant correlation coefficients are shown for panels (i) and (iii). In panel (ii), correlations were significant between snap rate and lunar phase for daytime samples (Tektite $r = -0.68$, Yawzi $r = -0.71$; $p < .001$) and crepuscular samples (Tektite $r = -0.61$; Yawzi $r = -0.38$; $p < .001$)

number of shrimp and could result from disparities in the extent of the two reefs, composition and density of benthic shrimp habitat, or other biological variables such as shrimp predator or food abundance. Visual surveys during the study period documented higher fish densities and percent coral cover at Tektite compared to the Yawzi sites (Kaplan et al. 2015), but the relationship between such habitat health metrics and snapping shrimp is uncertain. It is important to consider also that in shallow environments such as coral reefs, overall site differences in SPL and snap rates could result from small bathymetric and depth differences between locations, possibly causing differences in sound propagation and reflections. It is important to consider also that in shallow environments such as coral reefs, overall site differences in SPL and snap rates could result from even small bathymetric and depth differences between locations, possibly causing differences in sound propagation and reflections. Indeed, propagation of individual snaps is extremely complex in these three-dimensional habitats, where shrimp are at high densities within a mosaic of substrates. Because measured sound levels and snap detections result from the interaction of such physical, acoustic, and biological factors, ecologically interpreting spatial differences in their magnitudes is a challenge. However, this underscores the need to further investigate the significance of relative measures such as day/night anomalies or diel pattern in snap rates, as intersite variation in these metrics could be more reliably indicative of ecological differences (e.g., species composition, shrimp/host diversity).

Several studies have attempted to implement acoustic diversity indices as a measure of coral reef diversity or health (Staaterman et al. 2014; Bertucci et al. 2016), but tests of these indices have found them to be disproportionally influenced by the snapping shrimp acoustic component (McWilliam and Hawkins 2013; Kaplan et al. 2015; Pieretti et al. 2017) and thus unlikely to accurately reflect coral reef community structure. Some studies have suggested that high snap rates (or high-frequency acoustic energy) reflect higher habitat quality (Rossi et al. 2016; Butler et al. 2017), while other works have found negative or null relationships between snap rates and metrics of habitat health such as coral cover and fish density (Nedelec et al. 2015; Kaplan et al. 2015; Freeman and Freeman 2016). In combination with these inconsistent relationships between snapping and reef health metrics, the snap rate differences measured at our adjacent reefs highlight the importance of understanding the relevant scales and biophysical causes of variation to validate ongoing ecoacoustic assessments of coral reefs.

Water temperature correlated significantly with snap rates, averaged at a daily scale, despite a relatively small change in temperature throughout the 84-d monitoring period (< 2 °C). Several previous studies of snapping shrimp sound patterns, which examined the high-frequency "snapping band" sound levels, reported no apparent influence of temperature on tropical habitats (Johnson et al. 1947; Everest 1948; Knowlton and Moulton 1963), citing the lack of substantial seasonal variation, but our findings indicate that even small changes in water temperature can affect snap rates and by extension affect the overall soundscape. This relationship could have important implications for predicting future soundscapes in changing environments with increasing coral reef water temperatures. It has been suggested that ocean acidification could diminish soundscape cues in marine environments due to snap rate decreases in response to lower pH (Rossi et al. 2016), but the relative importance or combinatory effects of temperature and pH have yet to be examined.

Light levels were also significantly linked to snap rates at multiple scales, not only due to day/night differences, but also during daylight hours when snap rates showed a negative relationship with irradiance. This suggests that shrimp are more active in the daylight hours when light levels are lower. Accordingly, both reef sites demonstrated substantial dawn and dusk peaks in snap rate and SPL, showing sharp increases in snap rate immediately prior to sunrise and following sunset. However, the two sites differed slightly in the relative strength of the peaks (higher dawn snap rate compared to dusk snap rate at Yawzi, opposite at Tektite), further indicative of intriguing biological differences between sites. Snap rates measured at both sites showed consistently dominant daytime snapping compared to nighttime. This is in contrast to most reports of elevated nighttime snap activity in a variety of other geographical locations (Johnson et al. 1947; Everest 1948; Knowlton and Moulton 1963; Radford et al. 2008a, 2014; Pieretti et al. 2017), but these studies typically examine only a small number of acoustic samples. Detection of the unexpected daytime snapping tendency observed is in part the result of our close examination of snapping patterns using a high-temporal resolution dataset and a fine-scale snap detection routine, but also is consistent with recent evidence of higher spatial variation in snapping shrimp sound production patterns than previously assumed (Lammers et al. 2008; Lillis and Mooney 2016).

Snap rates and their temporal rhythms are clearly the result of a complex combination of biological and environmental factors, and the causal mechanisms of these relationships remain an open question. Ecological or evolutionary drivers of the apparent circadian rhythms in snapping (e.g., the timing of feeding, mating, depredation) remain speculative at this point due to our inability to make visual observations of these animals. Shrimp are generally reported to snap primarily during agonistic intra- and interspecific interactions (Nolan and Salmon 1970; Schein

1975, 1977), but more recently have been observed to also snap without external provocation suggesting additional communicative snap functions (Rossi et al. 2016; Lillis et al. 2017). These studies, however, examined only socially monogamous species, and many coral reef snapping shrimp species are highly social, living in large eusocial colonies or in multi-species symbiotic configurations, which would be expected to influence their snapping habits. A single study of social shrimp snapping behavior described short-term coordinated snapping in response to nest intruders (Tóth and Duffy 2005). Given that coral reefs harbor a great diversity of snapping shrimp species, with a variety of social structures and microhabitat (Anker et al. 2006), our finding that their combined acoustic activity on a reef has a complicated rhythm is not surprising. A reef soundscape integrates the activity of myriad species, and it is likely that observed snapping patterns reflect both direct and indirect effects of environmental factors (e.g., light, temperature) and the presence or behavior of other animals (e.g., intruders, predators, symbionts). Documenting spatiotemporal snapping patterns exposes cryptic variation in the reef community and its acoustic environment and underscores the need for additional study of the relevant sound producers in marine habitats to interpret the ecological meaning of soundscape variation.

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