Coral reef species assemblages are associated with ambient soundscapes

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ABSTRACT

Coral reefs provide a wide array of ecosystem services and harbor some of the highest levels of biodiversity on the planet, but many reefs are in decline worldwide. Tracking changes is necessary for effective resource management. Biological sounds have been suggested as a means to quantify ecosystem health and biodiversity, but this requires an understanding of natural bioacoustic variability and relationships to the taxa present. This investigation sought to characterize spatial and temporal variation in biological sound production within and among reefs that varied in their benthic and fish diversity. Multiple acoustic recorders were deployed for intensive 24-hour periods and longer term (~4-month) duty-cycled deployments on three reefs that varied in coral cover and fish density. Short-term results suggest that while there were statistically significant acoustic differences among recorders on a given reef, these differences were relatively small, indicating that a single sensor may be suitable for acoustic characterization of reefs. Analyses of sounds recorded over ~4 months indicated that the strength of diel trends in a low frequency fish band (100-1000 Hz) was correlated with coral cover and fish density but the strength of high-frequency snapping-shrimp (2-20 kHz) trends was not, suggesting that low-frequency recordings may be better indicators of the species assemblages present. Power spectra varied within reefs over the deployment periods, underscoring the need for long-duration recordings to characterize these trends. These findings suggest that, in spite of considerable spatial and temporal variability within reef soundscapes, diel trends in low-frequency sound production correlate with reef species assemblages.

Key words: bioacoustics, biodiversity, fishes, sound production

INTRODUCTION

Coral reef ecosystems can support high biodiversity and provide key habitat for many taxa (Graham & Nash 2013) as well as valuable ecosystem services (Graham et al. 2013). However, reefs are in decline worldwide as a result of multiple chronic and acute stressors (Bellwood et al. 2004, De'ath et al. 2012). Monitoring changes in reef ecosystems is a high priority, but traditional monitoring approaches can be intermittent and costly (Lammers et al. 2008). Biological sounds in the sea are utilized by a diverse array of organisms and can play a vital role in the functioning of marine communities. This is because sound production is an important component of a number of biological processes, including spawning events (Lobel 1992), courtship behaviors (Mann & Lobel 1997), feeding (Versluis 2000), and competition (Johnston & Vives 2003). Monitoring these sounds can reveal the occurrence of these behaviors, which are otherwise difficult to observe. Sounds can also be used to indicate the presence of certain taxa (e.g. Mann et al. 2009). Such information is valuable for species which are cryptic or require specific management. Unlike visual surveys, acoustic recordings can be collected without human presence, at night, and over long periods of time. However, to apply soundscape measurements as an ecological tool, it is necessary to understand the natural variability of those soundscape cues.

Biological sound production at the community level varies on multiple temporal and spatial scales. Fish sounds on Hawaiian coral reefs peak at crepuscular periods (Au et al. 2012), whereas fish calling activity on the Great Barrier Reef was found to be highest at midnight (McCauley & Cato 2000). Radford et al. (2008) measured ambient noise at a temperate reef in New Zealand over an annual period, and found that the dominant biological sound sources were contained within two frequency bands: 700-2000 Hz (fish and urchins) and 2-15 kHz (snapping shrimp), with diel and seasonal variation in amplitude. Sound production may be impacted by physical factors such as light (Staaterman et al. 2014); however, at present, the drivers of variability in sound production are mostly unknown.

Spatially, Radford et al. (2010) found spectral and temporal differences between nearby sandy, macroalgal- and urchin-dominated habitats. The frequency band associated with urchin feeding (800-2500 Hz) had much greater sound intensity at the urchin-dominated habitat compared to the other two, and the greatest differences among habitats were found at dusk (Radford et al. 2010). Similar among-site variability has been identified on coral reefs (Radford et al. 2014). Within-reef variability is also not well understood, but such an investigation is needed to determine how best to evaluate a soundscape. Given that settlement-stage fishes and invertebrates have been shown to use sound to locate and orient to settlement habitats (Tolimieri et al. 2000, Simpson et al. 2004, Tolimieri et al. 2004, Simpson et al. 2005, Vermeij et al. 2010, Radford et al. 2011), site-specific soundscapes may allow these animals to identify suitable habitats.

Despite goals of using marine soundscapes to evaluate community assemblages (McWilliam & Hawkins 2013, Staaterman et al. 2014), acoustic recordings have not typically been paired with surveys of the species present in a given habitat, making it difficult to link species or community structure to sound production. One study that collected short (120-second) recordings from coral reefs found a positive correlation between coral cover, fish density, and daytime sound intensity (Kennedy et al. 2010). A similar study using slightly longer recordings (three minutes) collected from multiple sites and times of day and paired with visual surveys found relationships between acoustic parameters and the biota present (Nedelec et al. 2015). However, the brevity of the acoustic records used in these two studies likely overlooked the high temporal variability in biotic sound production that is typically found in many locations (Radford et al. 2008, Au et al. 2012, Staaterman et al. 2013, Radford et al. 2014). This variability suggests that longer-term recordings are better suited to determine whether acoustic differences among reefs are reflective of habitat difference and whether these differences persist over longer timescales.

Because many fish species produce a range a sounds, the diversity of sound types may be indicative of fish assemblages (McWilliam & Hawkins 2013) and perhaps overall community structure. Hard corals provide key habitat for many reef fish and invertebrates, and both coral cover and architectural complexity play major roles in influencing fish assemblages (e.g. McCormick 1994, Friedlander et al. 2003, Jones et al. 2004). For example, in the Seychelles, fish species richness, functional group diversity, and abundance of corallivores decreased along a gradient of high to low coral cover and structural complexity, with very different fish assemblages at the habitat extremes (Chong-Seng et al. 2012). Evidence from a study using experimental reefs with variable numbers of coral species suggests that fish species richness, but not fish abundance or species evenness, is correlated with coral species richness (Messmer et al. 2011). Given these links between fish assemblages and coral cover/species richness, passive acoustic monitoring of the diversity and occurrence of sounds produced by coral reef fish may allow for overall habitat changes to be detected on a fine scale and over long periods of time.

To date, some effort has gone into the development of acoustic diversity indices, whereby acoustic records are used to make inferences about community biodiversity (Pijanowski et al. 2011). In theory, the use of an index allows for data reduction and improved ease of interpretation, which is desirable given that long-term acoustic monitoring produces vast quantities of data. Much of the work to date has focused on the terrestrial environment (Sueur et al. 2008, Depraetere et al. 2012, Gasc et al. 2013) but there have been some recent attempts to apply similar methods to marine bioacoustics recordings (McWilliam & Hawkins 2013, Parks et al. 2014), with mixed success.

To determine how species assemblages link to biological sound production, we deployed acoustic recorders on three reefs that varied in coral cover and fish density in the U.S. Virgin Islands National Park, a marine protected area which has been studied for several decades. Two general experiments were conducted: short-term (24 hour), high-resolution measurements within each reef type and longer-term (four month) comparisons among the reefs. Acoustic recorder deployments were carried out in coordination with visual surveys of the benthos and fish assemblages in order to investigate the links between coral cover, fish abundance and diversity, and marine biological sound production. The utility of the Acoustic Diversity Index (Sueur et al. 2008) and Acoustic Complexity Index (Pieretti et al. 2011) was then evaluated as a means of interpreting these acoustic records.

METHODS

To assess the influence that species assemblages may have on coral reef bioacoustic soundscapes, this work focused on three reefs which varied in coral cover and fish abundance. Reefs were chosen based on long-term survey data (Edmunds 2013) and a rapid, preliminary visual survey of 10 reefs in the area. Two of these – Tektite and Yawzi Point – have been studied for 25 years (see Edmunds 2013 for review). The third reef – Ram Head – was selected as a low coral cover comparison site (Fig. 1) and has been previously studied for larval settlement and current dynamics (Green & Edmunds 2011). These reefs were chosen such that they varied as much as possible from each other in coral cover and fish density. All three reefs were located in the U.S. Virgin Islands National Park and were similar in distance from shore and wave exposure. Tektite ranged from ~9-18 m depth and consisted of a large sloping reef face, Yawzi ranged from ~5-10 m depth and was composed of a large mound that sloped down to sand, and Ram Head ranged from ~8-13 m and was mostly flat, with patch reef sparsely located throughout the site. The three reefs are known to vary in coral settlement (Green & Edmunds 2011). Research was carried out under permit number VHS-2013-SCI-0005 to Mooney and Kaplan.

Visual Surveys

Benthic cover and fish abundance and diversity at each of the study sites were characterized through SCUBA-based visual surveys prior to instrument deployment and recovery, following the standard Atlantic and Gulf Rapid Reef Assessment (AGRRA) methodology (available at http://www.agrra.org). At least three fish and benthic cover transects were carried out at each reef in both April and August 2013 (Table 1) and all surveys were carried out during daylight hours (0900-1700). Fish surveys consisted of 30 m transects (2 m wide) in which all fish along the transect were enumerated and classified to at least family level and size class. Benthic surveys consisted of 10 m long transects (1 m wide), with cover recorded at every 10 cm increment. Cover was later summarized into categories (coral, macroalgal, and other, which consisted primarily of crustose coralline algae, turf algae, other invertebrates, bare rock, dead coral, and sand). Surveys for fish and benthic cover were carried out adjacent to each other and the acoustic recorder mooring (within a few meters). Because there were no statistical differences between months, visual survey data were combined for analyses. Tests for significant differences among reefs in coral cover were conducted with a one-way ANOVA. Fish survey data were analyzed by trophic level (Herbivores, Invertivores, Consumers; data taken from

Fishbase.org) and summarized as fish density at each reef, based on the total area of transects. Visual survey data are presented as means (+/- standard error). Differences in the distributions of fish at each trophic level among reefs were examined using a Chi-square test. For both benthic and fish surveys, transects were randomized among reefs and test statistics were recalculated 1000 times for increased robustness. The probability of getting the original statistical result by chance was determined by identifying the proportion of times that the original test statistic was greater than the randomized test statistics.

Acoustic Recordings

Instrumentation

Acoustic measurements were made using the DMON (Woods Hole Oceanographic Institution, Woods Hola, MA) and the DSG (Loggerhead Instruments, Sarasota, FL) recorders. For this investigation, the DMONs were configured with a low-noise preamplifier (20 dB gain), 13.2 dB user programmable gain, a 6-pole Sallen-Key anti-alias filter, a 16-bit analog-to-digital converter, and 32 GB of FLASH memory. We programmed the DMON to record on two hydrophone (Navy type II ceramics) channels: LF (16 kHz sample rate with an anti-aliasing filter at 7.5 kHz and high pass filter at 8 Hz) and MF (120 kHz sample rate with an anti-aliasing filter at 50 kHz and high pass filter at 100 Hz). The DSG records on one channel (80 kHz sample rate) using a HTI-96 hydrophone (High-Tech Inc., Gulfport, MS) and contains a 16-bit computer board. There is a user-selectable gain setting; for these recordings, 20 dB was used, which resulted in a high-pass filter being implemented at 80 Hz.

Deployments

Two sets of deployments were made. Short-term deployments used four continuously recording DMONs spaced ~ 20m apart on each reef in both April and August for 24-hour periods at a range of depths among the three reefs (~5-14 m). Only results from August are presented here. Long-term records were collected using DMONs and DSGs recording on duty cycles at two locations per reef from April to August (~8-12 m depth). Two concrete moorings were prepared for each site. Mooring 1 consisted of a DMON with customized duty-cycling software (2.5 min/2 hours) and a DSG acoustic recorder (1 min/20 min duty cycle) for redundancy in case of equipment failure. Mooring 2 consisted of a DMON only. Moorings were deployed between 17-19 April 2013 and retrieved between 2-3 August 2013, yielding approximately 103 days of potential data collection per site.

The only instrument to record at Tektite was the DSG. The redundancy of recorders proved essential as the DSGs deployed at Yawzi and Ram Head did not successfully record. As such, acoustic comparisons between sites involve multiple recording devices. The recording durations were as follows: Tektite – 19 April – 6 July 2013; Yawzi: 17 April – 1 August 2013; Ram Head: 19 April – 2 August 2013.

Temperature data loggers (HOBO pendant model UA-002-64, Onset Computer Corporation, Bourne, MA) were deployed alongside each mooring and sampled once every 10 minutes.

Acoustic Analysis

Analysis was carried out in Matlab 8.1 (The MathWorks, Inc., Natick, MA) using customized scripts written specifically for these data. Both short- and long-term DMON recordings were cut into 60-second segments. Boat noise and any other sporadic noise was identified visually using long-term spectral average (LTSA) plots implemented in Triton version 1.90 (Scripps Whale Acoustics Lab, San Diego, CA) and confirmed aurally. LTSAs were computed with 2 s averages and in 200 Hz bins. Sound files containing these anthropogenic and transient noises were excluded from all subsequent analyses but in some cases are included in visual representations of the soundscape for illustrative purposes. These steps resulted in the exclusion of 25% and 19% (short-term and long-term) of files from Tektite, 25% and 7% of files from Yawzi, and 8% and 9% of files from Ram Head. All remaining files were corrected for calibrated hydrophone sensitivity and resampled to 44 kHz. Spectral analysis used FFT size of 880 points and a Hamming window with no overlap, yielding a spectral resolution of 50 Hz and a temporal resolution of 20 ms.

Likelihood ratio tests of the spectral density function of reef sound were used to test for temporal and spatial changes in periodograms (i.e., non-stationarity), and are described in Appendix I. For the temporal non-stationarity analysis time series were constructed separately for each hour of the day, in part to suppress diel variability.

Sound pressure level (SPL) was calculated for each minute-long file obtained in the long-term recordings by band-pass filtering sound clips using a four-pole Butterworth filter in two frequency bands: 100 – 1000 Hz and 2-20 kHz. These bands were chosen based on published frequency ranges of the majority of fish calls (Tricas & Boyle 2014) and snapping shrimp sounds (Au & Banks 1998). SPL was only calculated for DSG recordings from the same recording period as the DMONs and only for the DMON MF recordings, in order to match the DSG hydrophone frequency response more closely.

Abiotic noise such as that produced by wind can contribute substantially to SPL. In order to account for effects of wind speed, records were taken from a nearby weather buoy (NDBC

Station 41052, 18.251 N 64.763 W) and correlated with SPL in both frequency bands (averaged over the minute-long clip length) for the each clip and only for the time periods that all three reefs had operational recorders. A similar analysis was conducted to characterize the relationship between temperature and SPL.

Octave band levels (dB re 1 µPa) were calculated for each clip with centroid frequencies (F_c) at 125, 250, 500, 1000, and 2000 Hz (after Radford et al. 2014) using digital filters implemented in Matlab. Octave band levels were calculated for the new and full moon as follows. Lunar periodicity data were taken from the US Naval Observatory website (http://aa.usno.navy.mil/cgi-bin/aa_moonill2.pl). Data from two days on either side of the new and full moons that occurred during the deployment were denoted as “new” or “full” in both the fish and snapping shrimp bands and were combined for this analysis.

Power spectra were produced for all clips using Welch’s method (Welch 1967). These power spectra were used to visually characterize changes in the spectral distribution of energy over time at each reef.

Acoustic entropy (H) index values (Sueur et al. 2008) were computed using the first 15 s of each of the resampled files. Entropy was computed in three bands using band-pass filters – the full band (100-20500 Hz), the low-frequency fish band (100-1000 Hz), and the high-frequency shrimp band (2-20 kHz). In addition, the Acoustic Complexity Index (ACI; Pieretti et al. 2011) was computed for each file using a temporal step of 12 s and FFT size of 880 points. The Bonferroni correction was used to reduce the critical p-value whenever multiple comparisons were carried out.

RESULTS

Coral cover differed significantly among reefs (Fig. 2A, $F_{2,23} = 19.24$, $p<0.001$) and the results of a randomization test indicated that the probability of getting this result by chance was less than 1 in 1000. Mean proportion coral cover was highest at Tektite. Ram Head was lowest in coral cover but highest in “Other” (which included crustose coralline algae, turf algae, other invertebrates, bare rock, and sand). Fish assemblages also differed significantly among reefs (Fig. 2B, $\chi^2 = 26.573$, df = 2, $p<0.001$); however, the results of a randomization test indicated that the probability of this result arising by chance was greater than 0.05. Observed herbivore and consumer fish densities were largest at Tektike and lowest at Ram Head, with no difference in invertivore density.

Results from the spatial non-stationarity analysis (see Appendix I for methods) indicated significant differences within reefs among recorders over the 24-hour short-term deployments (Tektite: $\chi^2 = 3.99*10^5$, df = $3.1*10^5$, $p<0.0001$; Yawzi: $\chi^2 = 4.02*10^5$, df = $3.1*10^5$, $p<0.0001$; Ram Head: $\chi^2 = 4.15*10^5$, df= $3.3*10^5$, $p<0.0001$). However, these differences appeared to be very small (Fig. 3). While there was some variability among recorders at any one frequency, all power spectra following a similar shape at a given time and reef. Thus, statistical differences were likely a result of high statistical power and for all further analyses data from a single recorder was used.

Median sound pressure levels in the low-frequency fish band were typically highest at Tektite and differences among reefs were most pronounced at ca. dusk and dawn (Fig. 4A). At other times, the differences were often marginal. Ram Head typically showed the lowest median sound pressure, with considerably reduced levels during the day, and only slightly reduced compared to the other reefs at night. The median SPL in the high-frequency shrimp band was greatest at Yawzi, followed by Ram Head and then Tektite (Fig. 4B). Elevated median sound production was apparent at dawn but not dusk. Unlike in the fish band, the shrimp band seemed to follow a similar daily pattern at all reefs with differences mainly in sound intensity.

The magnitude of the diel trend in low-frequency fish sounds (i.e., the difference between median low-frequency SPL at dusk (~18:00) and midnight and dawn (~06:00) and midnight) was significantly but weakly correlated with percent coral cover and fish density (Table 2), with the strongest trend apparent at Tektite, followed by Yawzi and Ram Head (Fig. 5). There was only one significant correlation in the high-frequency snapping shrimp band (between the strength of the dawn peak in sound production and fish density). This correlation was weaker than all of the correlations between peaks in low-frequency fish-sound production and species assemblages,

Temperature increased over the deployment period across all three reefs from ~26.7 ˚C in mid-April to ~29.4 ˚C in early August, with limited variation among reefs. There were no significant correlations between temperature and SPL in the fish band at any of the three reefs. Correlations in the shrimp band were significant at both Tektite and Ram Head but not Yawzi (TK: $R^2 = 0.025$, $F_{1,720} = 18.273$, $p< 0.0001$; RH: $R^2 = 0.07$, $F_{1,819} = 58.261$, $p< 0.0001$; YA: $R^2 = 0.001$, $F_{1,836} = 0.815$, p=NS). Wind speed was not significantly correlated with SPL in either frequency band at any site except for Ram Head in the shrimp band ($R^2=0.03$, $F_{1,756} = 21.668$, $p<0.0001$).

The low-frequency fish band was separated into octaves (125, 250, 500, 1000, 2000 Hz) to identify the frequencies at which sound levels were elevated. While the distribution of energy did not differ consistently among sites or between the new or full moon, there were differences at certain frequencies. In particular, octave band levels were elevated at 500 Hz at Tektite at dusk and dawn compared to other reefs during the new moon, and at dusk during the full moon (Fig.

6). Octave band levels were elevated at 2000 Hz for all times of day at Yawzi and Ram Head, likely as a result of higher shrimp snapping amplitudes at those reefs compared to Tektite.

Power spectral density estimates were combined to produce heat maps showing changes in the distribution of energy by frequency over a 24-hour period for each site in July 2013 (Fig. 7). These plots indicate that spectral and temporal variability was greatest at Tektite, with diel trends in sound increases at dusk and dawn. The crepuscular trend was present but difficult to discern for Yawzi, and largely absent for Ram Head. The noon peak at Ram Head was a result of some incidental (likely anthropogenic) impulse noise that was recorded, reflecting the intrusion of abiotic sounds into the coral reef soundscape.

Results from the temporal non-stationarity analysis indicated that power spectra for each reef changed over the deployment period (Tektite: $\chi^2 = 1.56*10^7$, df = $3.7*10^5$, $p<0.0001$; Yawzi: $\chi^2 = 1.94*10^7$, df = $3.7*10^5$, $p<0.0001$; Ram Head: $\chi^2 = 1.92*10^7$, df = $3.7*10^5$, $p<0.0001$). Results were similar when this analysis was carried out separately for each time of day (i.e., power spectra for each time of day changed over the course of the deployment). However, there was no clear trend over time; rather, spectra varied on short time scales throughout the deployment period within each reef (Fig. 8).

To test what kind of sounds drive the acoustic entropy index, we partitioned the entropy into both fish and shrimp bands and compared them to the full bands. Acoustic entropy values pooled over the deployments were largely driven by the 2-20 kHz (shrimp) frequency range (Fig. 9). Correlations between entropy calculated in just the shrimp band and in the full band were strong (Fig. 9A2) or very strong (Figs. 9B2, 9C2) for all three reefs. However, correlations between entropy in the fish band and the total band were very weak at all three reefs. There were significant differences among reefs in the mean entropy values in the fish band ($F_{2,3068} = 151.56$,

$p<0.0001$) and the results of a post hoc test indicated that the fish entropy values at Yawzi and Ram Head were significantly higher than those at Tektite. This result is divergent from visual data and the finding that the strength of the diel trend in sound production in the fish band correlates with coral cover and fish density, as fish band entropy did not correlate with either of these biological attributes of the reefs. Furthermore, mean Acoustic Complexity Index (ACI) values (Tektite – 341.4; Yawzi – 355.1; Ram Head – 354.2) did not follow a discernable pattern and were not correlated with species assemblages at each reef. Similarly, the diel trend in ACI did not correlate with the diel trend in SPL.

DISCUSSION

Marine soundscapes are increasingly being studied as a means to identify differences among habitats. This is the first study, to our knowledge, which pairs a detailed assessment of the soundscape with traditional visual surveys of coral reef benthos and fish communities. The goals were to both evaluate the spatiotemporal variation of the soundscapes of three reefs and address how these differing acoustic environments may be representative of different habitats or community structure. Acoustic differences among reefs were evident but were relatively small in magnitude. For example, there were differences between sites in the low-frequency fish band at crepuscular times, when fish and invertebrates may be more acoustically active (Lammers et al. 2008, Radford et al. 2014, Staaterman et al. 2014), but not at many other times of day. These differences at low frequencies were associated with similar but also relatively small differences in coral cover and fish density. While there were significant differences in fish assemblages among reefs, these were not sufficiently large enough in magnitude to withstand a randomization test. The reduced SPL during the day in the fish band at Ram Head but not at the other reefs could result from among-reef differences in the acoustically active fishes. Subsequent investigations should attempt to identify the individual sound types present at each reef to better address this question. Overall, results suggest that the species assemblages present at each reef were associated with the localized bioacoustic soundscape. However, data collected from reefs that vary more in fish density and coral cover would likely better elucidate this trend. The regression based methods used here (Fig. 5) suggest that there are soundscape gradients relative to some measures of community structure. While more reefs were recorded here than in other studies (e.g. Staaterman et al. 2013, Staaterman et al. 2014), investigations that address additional reefs could provide further data on these links.

Notably, there were fewer differences between sites and soundscapes in the higher-frequency snapping shrimp band. While overall shrimp sound pressure levels varied in intensity, the temporal trends did not differ between reefs of varying species assemblages (Fig 5). This suggests that while shrimp were potentially more abundant at Yawzi, their snapping patterns followed the same diel trends. This is perhaps reflective of the relative similarity of physical conditions between sites (e.g., light, depth, and temperature). Snapping shrimp patterns were not related to coral cover (Fig 6), which suggests that this portion of the soundscape, while often dominant in intensity, may not be reflective of benthic cover and associated fish assemblages. Indeed, snapping shrimp sounds are abundant in a variety of habitats (Lammers et al. 2008). Unlike many fish, snapping shrimp are not similarly reliant on live coral for shelter and nutrition; instead they select habitat that provides shelter such as rocky outcrops, live or dead coral, and sponges (Cato & Bell 1992). Accordingly, their abundance (and by extension, sound production) are likely not driven by live coral cover per se, which could explain the lack of relationship between reef coral cover and shrimp sound production. If coral reef sounds are used for settlement, this discrepancy suggests that the higher-frequency snapping shrimp band may be a less reliable indicator of suitable habitat.

Results from the short-term deployment indicated that there were significant spectral differences among recorders on a reef at a given time of day; however, a visual assessment of a subset of these spectra confirms only limited inter-recorder variability (Fig. 3). The biological relevance of these small differences is unknown. Animals may be able to discern these fine-scale acoustic differences when searching for suitable settlement habitat, but given the overall consistency in power spectra within reefs, it is likely that a single sensor deployed on a reef would be adequate to record the broad trends in sound production.

The presence of diel trends in both frequency bands suggests that snapshot-type recordings likely miss substantial temporal trends. Given that differences among reefs may only be evident when sound production increases (i.e., during crepuscular times), these results reflect the importance of collecting recordings over at least a diel cycle to capture these natural trends. For example, a recording collected at noon would not necessarily indicate any difference in sound production at low frequency between Tektite and Yawzi whereas a recording collected at dusk would (Fig. 4).

There was considerable variability in power spectral density at 500 Hz and 5 kHz at each reef over the course of the deployments (Fig. 8), but these changes were not associated with the temporal or physical characteristics measured (lunar cycles, changes in temperature or wind speed). Because of this variability within reefs over time, recordings collected over longer durations (i.e., weeks to months) may be best suited to characterizing trends in sound production and for comparing among reefs.

Coral cover and reef architectural complexity play a major role in influencing fish assemblages (e.g. McCormick 1994, Friedlander et al. 2003, Jones et al. 2004). Thus, the greater magnitude trend in low-frequency diel sound production at Tektite may be driven by links between elevated coral cover at that site and higher fish density, which was observed on that reef. Because many fish species produce sound during spawning, which often occurs around the new moon (D'Alessandro et al. 2007), elevated levels of low-frequency SPL at Tektite during the new moon could be linked to spawning activity, which has been shown to occur around the time of year that these instruments were deployed (D'Alessandro et al. 2007).

Several behavioral experiments have suggested that larval fish may use reef sound to identify a suitable settlement habitat (e.g. Tolimieri et al. 2000, Simpson et al. 2004, Tolimieri et al. 2004, Simpson et al. 2005, Radford et al. 2011). Most fishes without specialized morphological adaptations cannot hear frequencies higher than around 1000 Hz (Popper & Fay 2011), and the majority of fish calls are often below 1000 Hz (Tricas & Boyle 2014). Thus, low-frequency sounds on reefs will likely be of higher relevance as a settlement cue than high frequencies (cf. Simpson et al. 2008), where sound production may not be as closely linked to habitat quality. Accordingly, passive acoustic recordings of these lower frequency fish bands may provide a better evaluation of community assemblages. Ocean noise levels are increasing at low frequencies as a result of commercial shipping activities (Andrew et al. 2002, McDonald et al. 2006, Chapman & Price 2011). While most of these increases are below 300 Hz, an elevated low-frequency noise floor could have adverse effects on acoustic communication in fishes and, by extension, larval recruitment to reefs.

If differences in low-frequency sound production were a result of differences in fish species assemblages, why was only limited difference in fish density detected through the visual surveys? Many soniferous species, such as squirrelfishes (Amorim 2006), are cryptic and nocturnal. Other species may also shy away from divers and human observers. Thus, visual fish surveys conducted during daylight hours may largely miss these and similar species (Brock 1982). As far as possible, further studies should ensure that efforts are taken to identify cryptic species, which may disproportionately contribute to acoustic recordings. Similar analyses may also benefit from comparing reefs with larger differences in fish assemblages. Acoustic data have the benefit of recording fishes that may be missed by visual surveys; however, the number of soniferous fishes is not well known. Out of approximately 30,000 extant fish species, 700 are known to produce sound across at least 30 families (Luczkovich et al. 2008). Additional efforts to determine the distribution of sound production across unstudied fishes is needed.

Acoustic entropy values were largely driven by snapping shrimp activity. Shrimp snaps are broadband and were ubiquitous in the acoustic records obtained at all three reefs. However, they represent only one type of sound. Accordingly, high values of acoustic entropy from snapping shrimp sounds are not reflective of overall acoustic diversity. To address this fundamental limitation of this index, we compared the entropy calculated in a low frequency fish band to visual survey data and observed trends in amplitude at each reef, but no relationship was observed. While it is possible that this index is correctly identifying Yawzi as the reef with highest call diversity, that finding is not supported by either the visual survey data or the sound amplitude data.

Similarly, the ACI did not yield results that were consistent with the other analyses presented here. There are a few reasons why this might be the case. ACI values could be higher in recordings with lots of variability (i.e., large amplitude differences between adjacent frequency and time bins) but this variability could result from a small number of vocalizations spaced throughout a recording. Conversely, in a soundscape with high bioacoustic activity, ACI values could be low because of a high density of calling activity (i.e., chorusing) and corresponding small differences in intensity between frequency and time bins. Thus, more work is needed to develop an index that is effective for marine soundscapes.

CONCLUSION

Assessments of extended acoustic records from reefs that vary in species assemblages reflect trends in biological sound production that correlate with coral cover and fish density. In particular, low frequency sound, which is dominated by fish calls, and crepuscular soniferous activity, when fish are most acoustically active, provided the strongest links to visual characterizations of the reef. Conversely, high frequency acoustic recordings of snapping shrimp did not correlate with the species present. Acoustic and biological differences among reefs were small and further work on a broader range of reefs is needed to better elucidate these relationships. Additional work is needed to develop acoustic diversity indices that are suitable for the marine environment. Overall, these results strengthen the basis for using acoustic recordings to help guide monitoring and conservation efforts.

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Table 1. Summary of visual survey transects undertaken in 2013 on three reefs in the US Virgin Islands National Park.

	Site					
	Tektite		Yawzi		Ram Head	
Survey Month	April	August	April	August	April	August
Number of fish transects	8	3	9	4	5	4
Number of benthic transects	4	4	4	5	4	5

Table 2. Statistical results from the correlation of the strength of diel trends in sound production in low-frequency (LF) and high frequency (HF) at dawn and dusk with coral cover and fish density from each reef. Alpha was reduced using the Bonferroni correction to 0.0063

	Coral cover			Fish density		
	R^2	$F_{1,236}$	p	R^2	$F_{1,236}$	p
LF-dawn	0.087	22.400	0.000	0.062	15.642	<0.001
LF-dusk	0.060	15.125	0.000	0.046	11.535	<0.001
HF-dawn	0.023	5.458	0.020	0.031	6.53	0.006
HF-dusk	0.024	5.773	0.017	0.025	6.075	0.014

Fig. 1. Deployment map (A) showing locations of three reefs located within the U.S. Virgin Islands National Park on which acoustic recording devices were deployed (TK – Tektite, YA – Yawzi, RH – Ram Head). Example of acoustic recorder moorings (B) showing a DMON deployed for a 24-hour period (left) and for 4-month dutycycled period (right).

Fig. 2. Proportion of benthic cover (A, mean +/- SEM) and fish density by trophic level (B, mean density m^{-2} +/- SEM) for each reef. Fish density was split into functional groups (herbivores, invertivores, and consumers).

Fig. 3. Power spectra from each of four recorders (different colors) at dusk (18:00) for (A) Tektite, (B) Yawzi, and (C) Ram Head. Recordings were collected over 24-hour periods in August 2013. Power spectra have been smoothed using convolution. The shapes of the spectra at a given reef and time of day are similar, with some variation among recorders at certain frequencies.

Fig. 4. Sound pressure level (rms) in (A) 100-1000 Hz band and (B) 2-20 kHz band, pooled across ~4-month recording duration at each reef (median with 25-75 percentiles). The greatest peaks in SPL in the low frequency fish band (A) were at Tektite at dawn (06:00) and after dusk (20:00), with smaller peaks at Yawzi, and no observable peaks at Ram Head. Overall high frequency SPL (B) was highest at Yawzi, followed by Ram Head and then Tektite for all times of day, with a stronger peak at dawn than dusk at all three reefs.

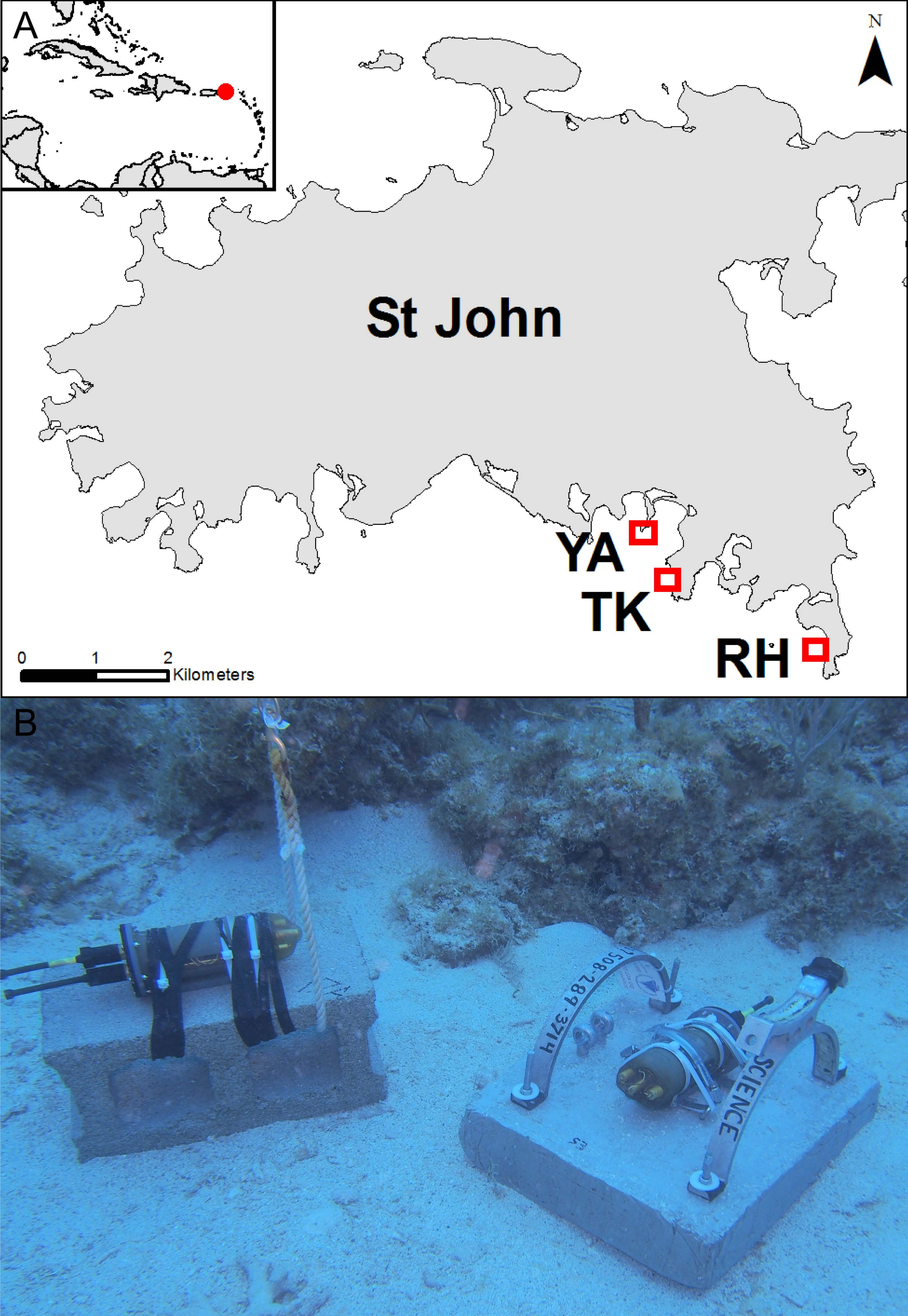
Fig. 5. Correlation between the mean coral cover (A-B) and mean fish density (C-D) at each reef and the strength of diel trend, measured as the difference in median SPL between dusk (~18:00) and midnight, and dawn (~06:00) and midnight, in 100-1000 Hz (A, C) and 2-20 kHz (B, D) bands over the four-month dutycycled recording period (differences shown with 25-75 percentiles). R-squared values are shown adjacent to the linear regressions.

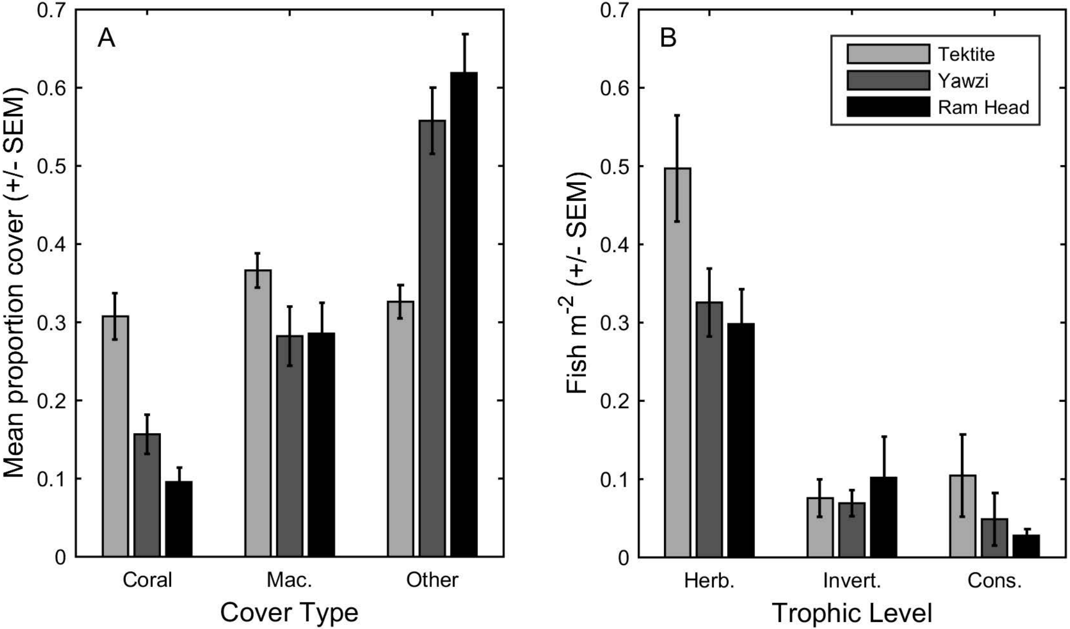
Fig. 6. Octave band levels (F_C = 125, 250, 500, 1000, 2000) at four times of day (00:00, 06:00, 12:00, 18:00) at the new and full moons, pooled over the four-month recording period (median with 25-75 percentiles). Low frequency octave band levels (500 Hz) are elevated at Tektite compared to other sites at dusk and dawn during both new moon and at dusk during the full moon (black arrows).

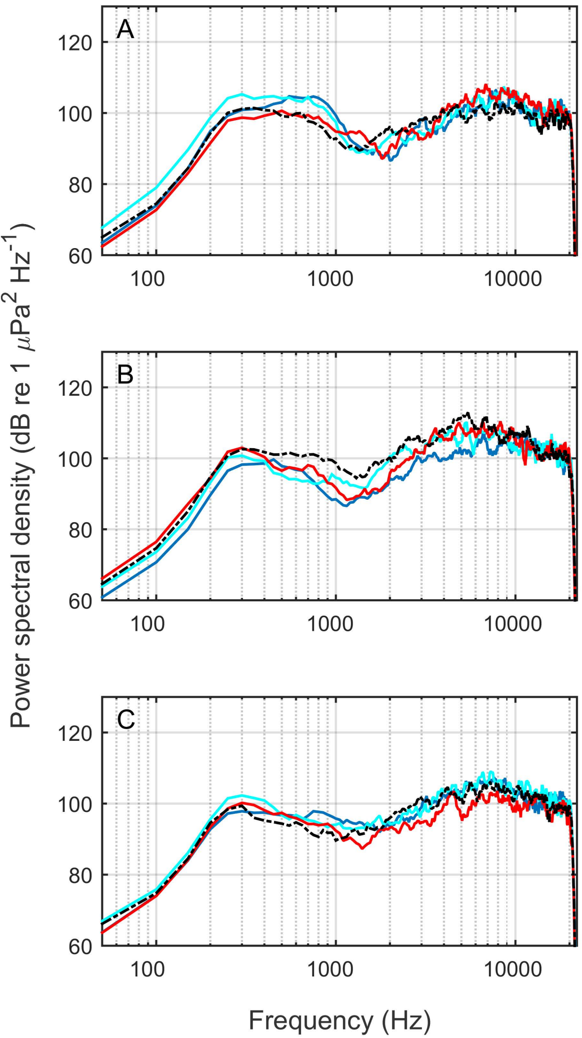
Fig. 7. Power spectral density estimates over a 24-hour period from 4-5 July 2013 at (A) Tektite, (B) Yawzi, and (C) Ram Head, displayed up to 20 kHz. Colorbars indicate power spectral density (dB/Hz). Peaks in sound production are apparent at Tektite at dusk and dawn. Smaller peaks are apparent at dusk at Yawzi and Ram Head, with less energy at dusk. This period of time was exclusive of boat noise at all reefs but a series of five consecutive high amplitude impulsive sounds (likely physical contact with the hydrophone) is the cause of the elevated energy at noon at Ram Head.

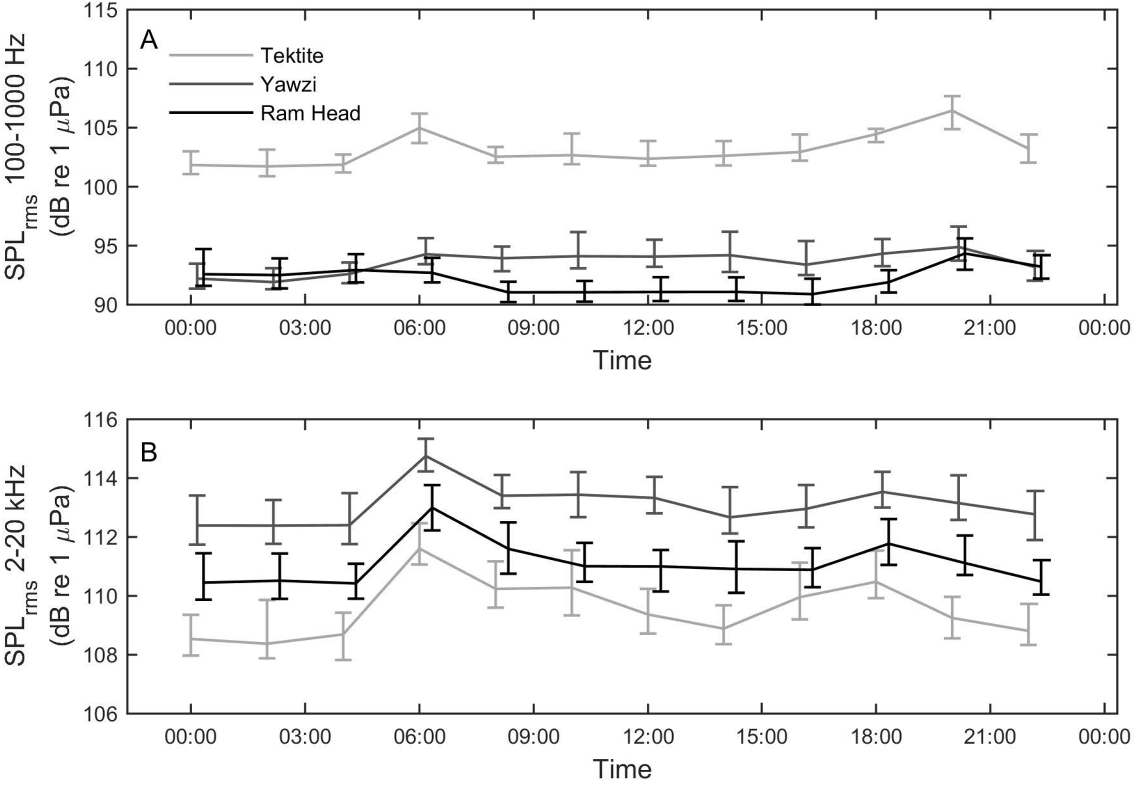
Fig. 8. Power spectral density at (A) 500 Hz and (B) 5 kHz for three reefs from the entire long-term deployment period. Missing data (white space) is a result of files containing boat noise being removed and/or recorder failure (e.g. end of blue line). Results from the non-stationarity analysis indicate that the periodograms changed over the course of the deployment period; however, there is no clear temporal trend at any site. Rather, there is constant variability.

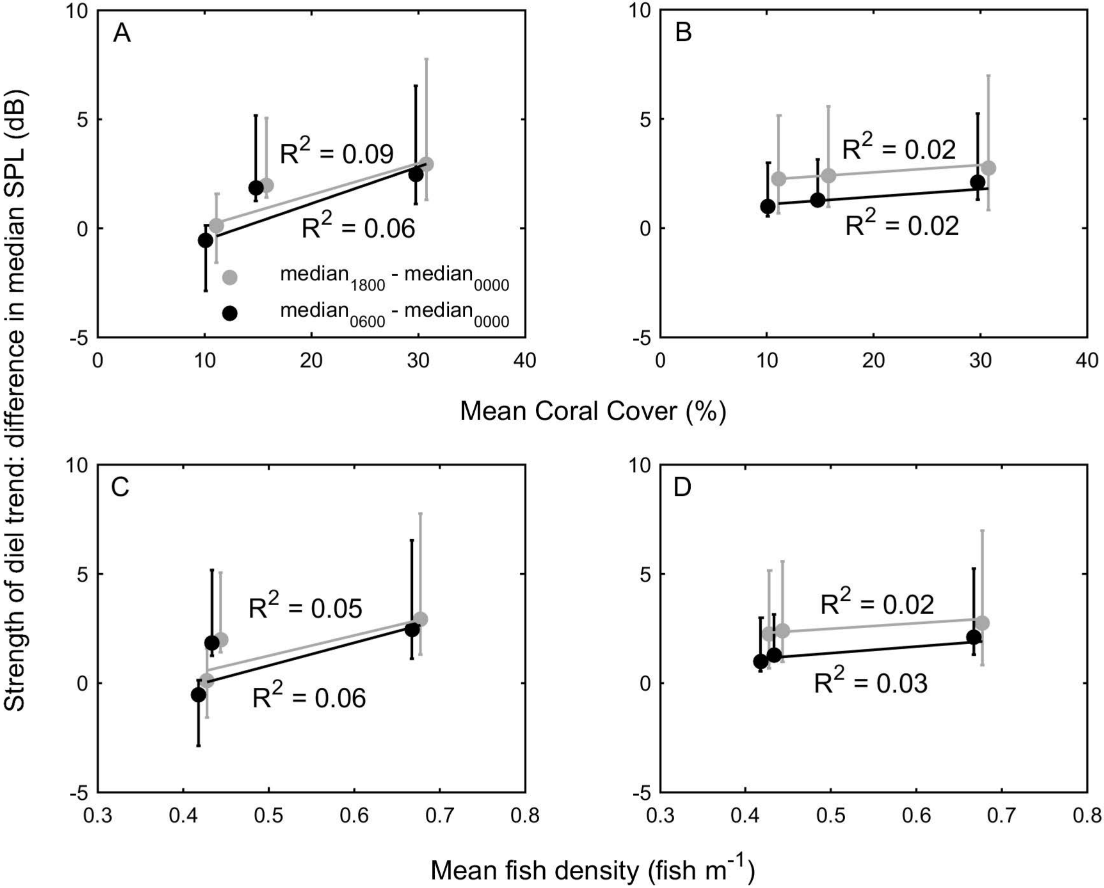
Fig. 9. Top graphs: relationships between entropy (H) calculated in a low-frequency fish band (100-1000 Hz) and the full band (100 Hz – 20 kHz) and boxplots of the range of low-frequency H at (A1) Tektite, (B1) Yawzi, and (C1) Ram Head (central mark is the median and the edges of the box are 25th and 75th percentiles). Bottom graphs: the relationship between H in a high-frequency shrimp band (2-20 kHz) and the full band at each of those three sites (A2, B2, C2). Linear regressions are shown in red and R-squared values are included for each relationship.

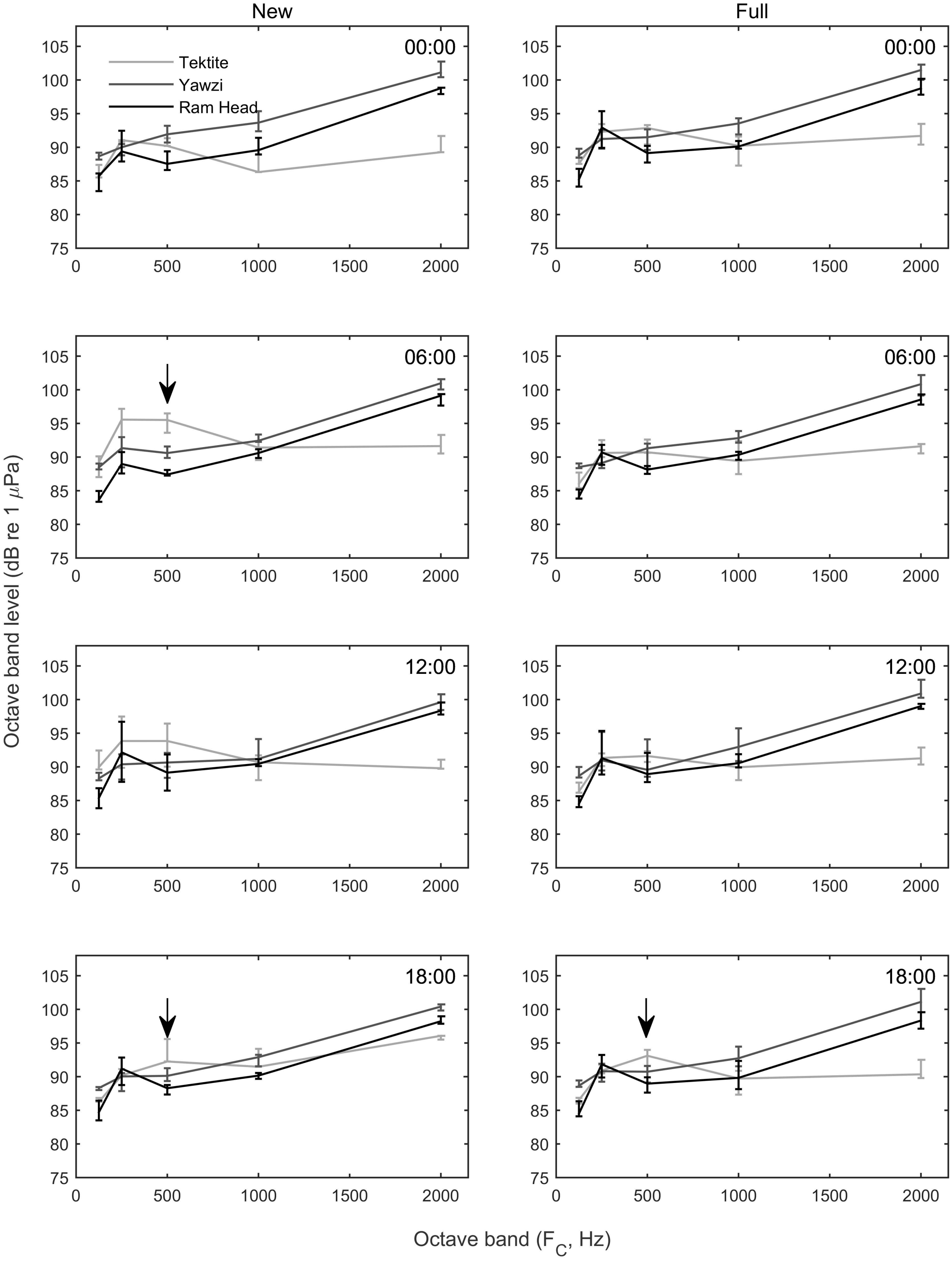

A
N
St John
YA
TK
RH
0
1
2
Kilometers
B
508-289-3714
SCIENCE

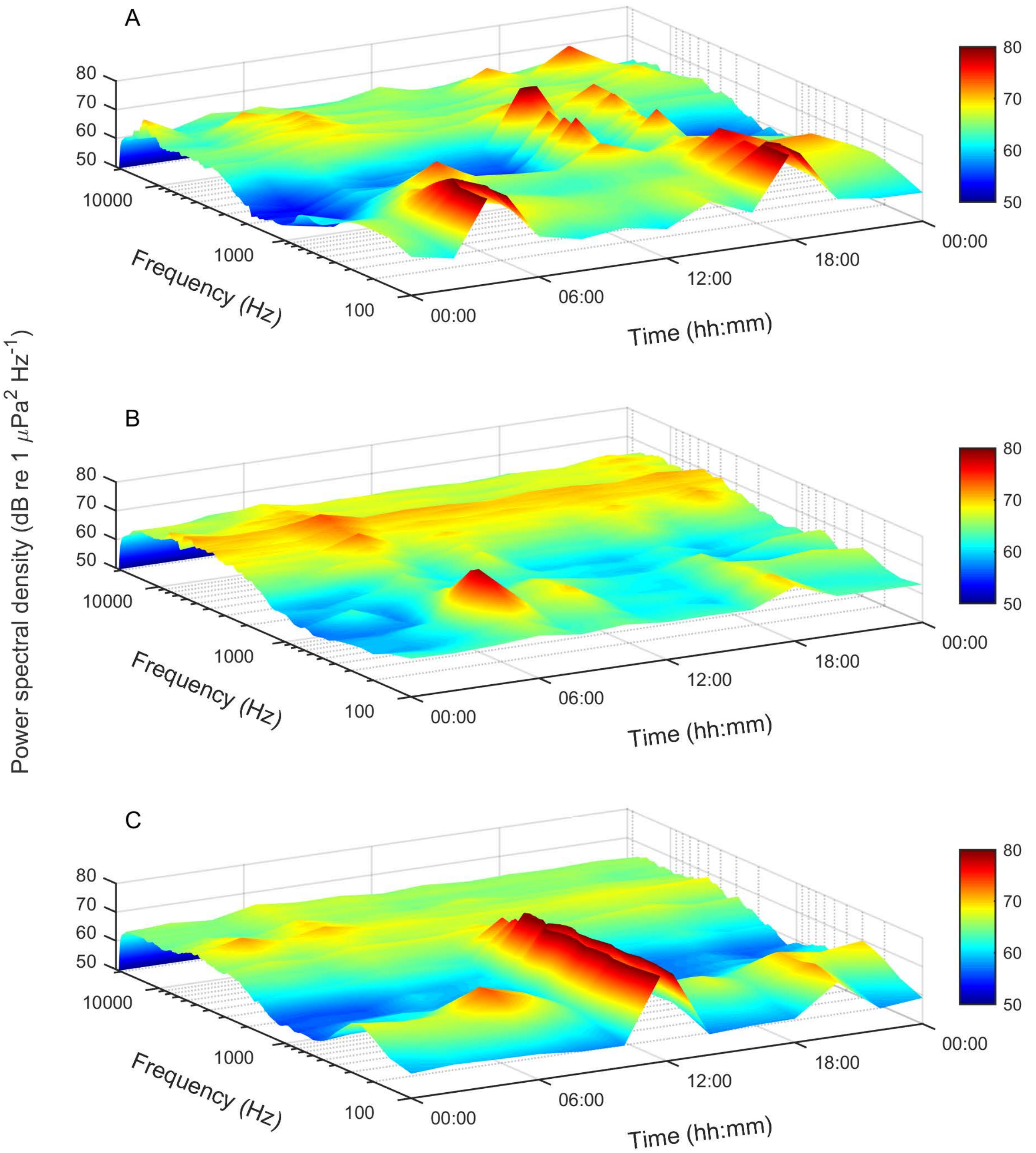

A
B
Mean proportion cover (+/- SEM)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Coral
Mac.
Other
Cover Type
Fish m-2 (+/- SEM)
Herb.
Invert.
Cons.
Trophic Level
Tektite
Yawzi
Ram Head

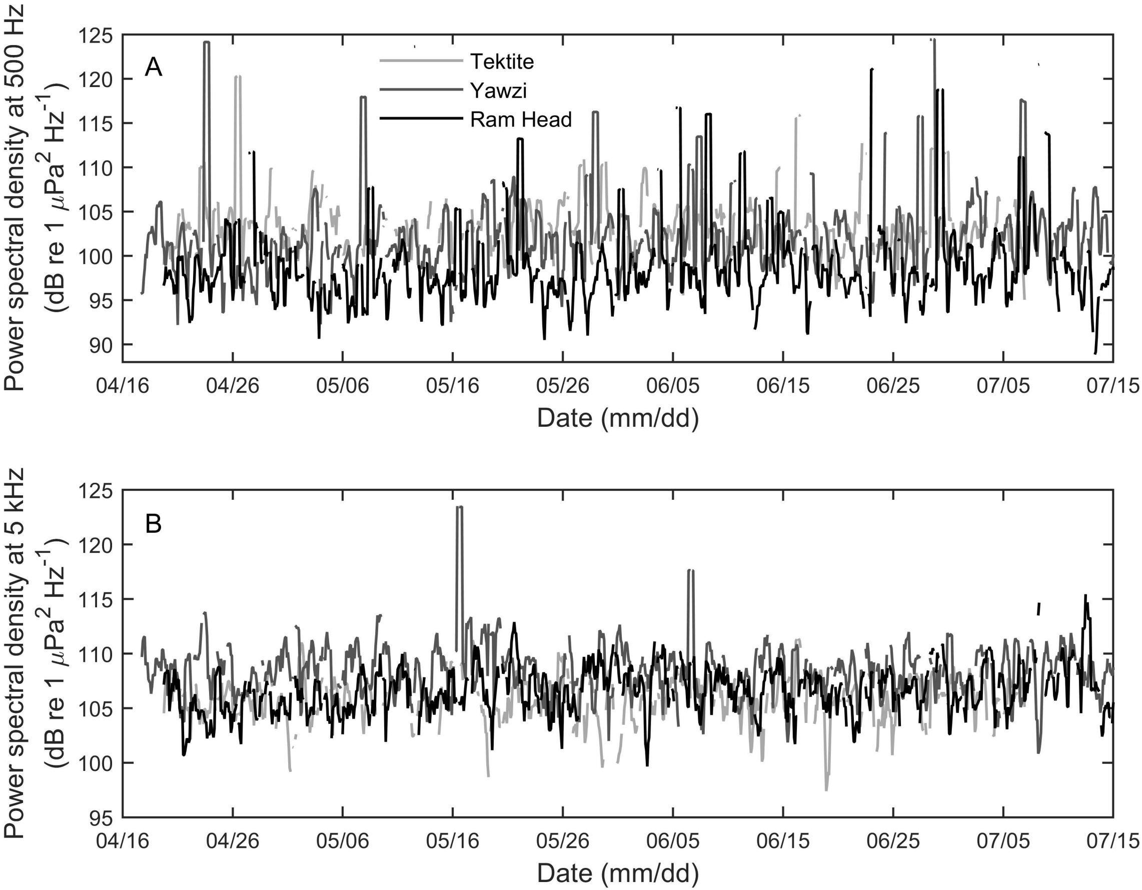

A
B
C
120
100
80
60
100
1000
10000
Power spectral density (dB re 1 μPa^2 Hz^{-1})
Frequency (Hz)

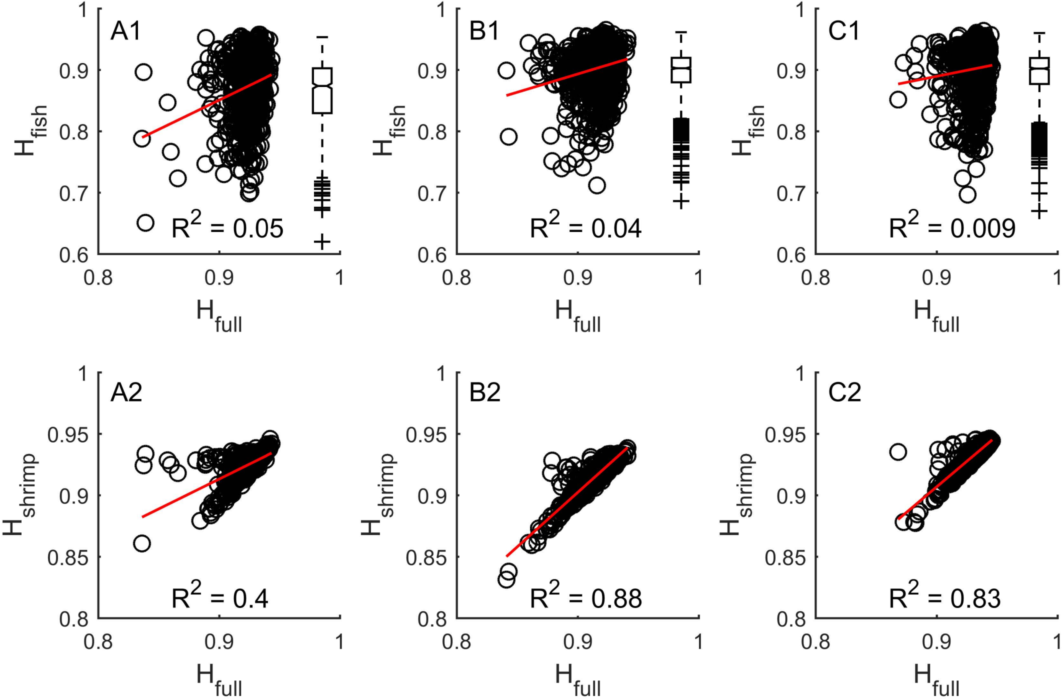

A
Tektite
Yawzi
Ram Head
SPL$_{rms}$ 100-1000 Hz (dB re 1 μPa)
115
110
105
100
95
90
00:00
03:00
06:00
09:00
12:00
15:00
18:00
21:00
00:00
Time
B
SPL$_{rms}$ 2-20 kHz (dB re 1 μPa)
116
114
112
110
108
106
00:00
03:00
06:00
09:00
12:00
15:00
18:00
21:00
00:00
Time

A
B
C
D
R^2 = 0.09
R^2 = 0.06
R^2 = 0.02
R^2 = 0.02
R^2 = 0.05
R^2 = 0.06
R^2 = 0.02
R^2 = 0.03
median1800 - median0000
median0600 - median0000
Strength of diel trend: difference in median SPL (dB)
Mean Coral Cover (%)
Mean fish density (fish m^-1)
10
5
0
-5
0
10
20
30
40
0.3
0.4
0.5
0.6
0.7
0.8


New
Full
00:00
06:00
12:00
18:00
Tektite
Yawzi
Ram Head
105
100
95
90
85
80
75
0
500
1000
1500
2000
Octave band level (dB re 1 μPa)
Octave band (F_C, Hz)


A
B
C
Power spectral density (dB re 1 μPa^2 Hz^{-1})
80
70
60
50
10000
1000
100
Frequency (Hz)
00:00
06:00
12:00
18:00
00:00
Time (hh:mm)
80
70
60
50


A
Tektite
Yawzi
Ram Head
Power spectral density at 500 Hz
(dB re 1 μPa² Hz⁻¹)
125
120
115
110
105
100
95
90
04/16
04/26
05/06
05/16
05/26
06/05
06/15
06/25
07/05
07/15
Date (mm/dd)
B
Power spectral density at 5 kHz
(dB re 1 μPa² Hz⁻¹)
125
120
115
110
105
100
95
04/16
04/26
05/06
05/16
05/26
06/05
06/15
06/25
07/05
07/15
Date (mm/dd)


A1
R^2 = 0.05
B1
R^2 = 0.04
C1
R^2 = 0.009
A2
R^2 = 0.4
B2
R^2 = 0.88
C2
R^2 = 0.83
H_fish
H_shrimp
H_full
0.6
0.7
0.8
0.85
0.9
0.95
1

APPENDIX I

This appendix outlines periodogram-based likelihood ratio (LR) tests for temporal and spatial non-stationarity of the spectral density function (sdf) of reef sound. The statistical results underlying these tests are available in Dzhaparidze (1986).

Let X_{th}, $t = 1, 2, \ldots, T$, be a collection of T independent time series each of length n recorded at times of day $h = 1, 2, \ldots, H$ on days $t = 1, 2, \ldots, T$ and let $f_{th}(\omega)$ be the unknown sdf at time of day h on day t. Interest centers on testing the null hypothesis $H_o\colon f_{th}(\omega) = f_h(\omega)$ for all h and t that the sdf at each time of day is stationary over time against the general alternative hypothesis H_1 that it is not.

Let $I_{th}(\omega_j)$ be the periodogram ordinate for X_{th} at Fourier frequency $\omega_j, j = 1, 2, \ldots, J$. It is a standard result that $I_{th}(\omega_j)$ is approximately independent of $I_{th}(\omega_k)$ and has an approximate exponential distribution with mean $f_{th}(\omega_j)$ and probability density function:

$$g\left(I_{th}(\omega_j)\right) = \frac{1}{f_{th}(\omega_j)} exp\left(-\frac{I_{th}(\omega_j)}{f_{th}(\omega_j)}\right)$$

The log likelihood is given by:

$$\log L = -\sum_{t=1}^{T}\sum_{h=1}^{H}\sum_{j=1}^{J}\left(\log f_{th}(\omega_j) + \frac{I_{th}(\omega_j)}{f_{th}(\omega_j)}\right)$$

The maximum likelihood (ML) estimate of $f_{th}(\omega_j)$ under H_1 is simply $I_{th}(\omega_j)$ and the corresponding maximized value of the log likelihood is:

$$\log L_1 = -THJ - \sum_{t=1}^{T} \sum_{h=1}^{H} \sum_{j=1}^{J} \log I_{th}(\omega_j)$$

The ML estimate of the common sdf $f_h(\omega_j)$ under H_o is the periodogram average:

$$\hat{f}_h(\omega_j) = \frac{1}{T} \sum_{t=1}^{T} I_{th}(\omega_j)$$

and the corresponding maximized value of the log likelihood is:

$$\log L_o = -THJ - T \sum_{h=1}^{H} \sum_{j=1}^{J} \log \hat{f}_h(\omega_j)$$

Finally, the LR statistic for testing H_o against H_1 is:

$$LR = 2\ (\log L_1 - \log L_o\ )$$

which, under H_o, has an approximate chi squared distribution with degrees of freedom given by $(T-1)HJ$.

The same general approach can be used to test for spatial non-stationarity. Let X_{tk}, *t* = 1, 2, …, *T* be a collection of *T* independent time series each of length *n* recorded at locations *k* = 1, 2, …, *K* at times *t* = 1, 2, …, *T* and let $f_{tk}(\omega_j)$ be the unknown sdf at location *k* at time *t*. Interest centers on testing the null hypothesis $H_o\colon f_{tk}(\omega_j) = c_{tk}\ f_t(\omega_j)$ that at each time the sdf's at the different locations are the same up to a multiplicative scaling against the general alternative hypothesis H_1 that they are not. For definiteness, under H_o, take $c_{t1} = 1$ for all *t*.

As before, the maximized value of the log likelihood under H_1 is:

$$\log L_1 = -TKJ - \sum_{t=1}^{T}\sum_{k=1}^{K}\sum_{j=1}^{J} \log I_{tk}(\omega_j)$$

where $I_{tk}(\omega_j)$ is the value of the peridogram at time *t* and location *k* for Fourier frequency ω_j. Maximizing the log likelihood under H_o must be done numerically. In doing so, it is helpful to note that for fixed values of the scaling parameters $c_1 = 1, c_2, \dots, c_K$, the ML estimate of $f_t(\omega_j)$ is the weighted average:

$$\hat{f}_t(\omega_j) = \frac{1}{K}\sum_{j=1}^{J}(I_{tk}(\omega_j)/c_k)$$

As before, the LR statistic for testing H_o against $H_1$is:

$$LR = 2\ (\log L_1 - \log L_o)$$

where $\log L_o$ is the numerically maximized log likelihood under H_o. Under H_o, LR has an approximate chi squared distribution with degrees of freedom given by $T(KJ - (K + J - 1))$.

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