

ABSTRACT

LYON, RICHARD PATRICK. Fish biodiversity, habitat complexity, and soundscape characteristics of patch reefs in a tropical, back-reef nursery. (Under the direction of Dr. David B. Eggleston.)

Hydrophones can record the soundscapes of marine ecosystems, which helps characterize (i) habitat use by soniferous species, and, in some cases, (ii) habitat complexity, and (iii) biodiversity. Tropical back-reef, nursery areas provide essential fish habitat for juveniles moving to offshore coral reefs as they grow; yet, little is known of underwater soundscapes in these habitats. We characterized the soundscapes of seven experimental patch reefs within a seagrass-dominated, back-reef, embayment in the Bahamas. Passive acoustic recorders were deployed at each reef and recorded simultaneously for 2 min every 20 min between March and July, 2016. Sound pressure levels (SPL) and acoustic complexity (ACI) were analyzed in low (0.1 – 1.5 kHz) and high (4 – 20 kHz) frequencies to evaluate noises produced by marine organisms. Low frequency SPLs associated with fish vocalizations occasionally peaked twice per day, but showed no relationships with habitat complexity or fish biodiversity. High frequency SPLs and invertebrate snap rates peaked nightly, and correlated with structural rugosity but not fish biodiversity. High and low frequency ACI showed no associations with habitat complexity or fish biodiversity. These findings suggest that high frequency SPLs and invertebrate snap rates may be more indicative of habitat complexity in back-reef nurseries than low frequency sounds, and that neither high nor low frequency acoustic complexity correlates with biodiversity in areas dominated by juvenile fish.

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Fish Biodiversity, Habitat Complexity, and Soundscape Characteristics of Patch Reefs in a
Tropical, Back-Reef Nursery

by
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A thesis submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Master of Science

Marine, Earth, and Atmospheric Sciences

Raleigh, North Carolina

2018

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DEDICATION

To friends, family, and all of those who have supported and inspired me throughout my life.

To my dad, for all of the adventures and experiences that led to my love of the sea.

To my mom, for always being there for me and encouraging me to achieve and succeed.

BIOGRAPHY

Pat Lyon was born in California in January of 1994. At only six months of age his parents took him on his first trip to Mexico where they had a vacation home close to Cabo Pulmo Marine Reserve. At age two, he and his parents moved from California to Lake Norman, North Carolina where he was, once again, close to the water. As he got older, his love of boating and fishing only grew and after several more trips to Mexico, he obtained his open water SCUBA diving certification at age 12 in the summer of 2006. That same summer, Pat and his dad embarked on a four-day overnight diving and fishing trip to Isla Cerralvo, also known as Jacques Cousteau Island. Not surprisingly, this trip to an island named after a famous marine biologist greatly inspired Pat and ignited his love and passion for marine habitats. Eventually, Pat and his family moved to the mountains of western North Carolina where he graduated from high school as valedictorian in 2011 and started looking at colleges to pursue a degree in biology.

Pat received his bachelor's degree from Elon University near Burlington, North Carolina and while there took classes such as Wetland Ecology and Management, Aquatic Biology, and Advanced Racquetball. As a junior, and after taking guitar lessons and classes in music technology, Pat contacted Dr. Dave Gammon for a chance to carry out an undergraduate research project on the bioacoustics of Northern mockingbird birdsong. With Dave G., Pat published a paper to the journal *Ardea* and presented his research at an international ornithology conference in Nova Scotia. Upon graduating, Pat was considering his next steps when he discovered Dr. Dave Eggleston and his research projects in marine soundscape ecology. Dave E.'s soundscape work combined Pat's love and admiration for marine habitats and organisms with his experience and background in acoustics. Pat greatly

looks forward to receiving his master's degree in marine science and hopes to apply his knowledge and understanding of marine habitats to future research and careers.

ACKNOWLEDGMENTS

I would like to thank my adviser, Dr. Dave Eggleston, for his valuable time and support throughout this research project as well as for his mentorship and guidance for many things in my life. I would also like to thank Dr. DelWayne Bohnenstiehl for all of his assistance with data analysis and for his unending patience and encouragement. Special thanks are also given to Dr. Craig Layman, Enie Buhler, and Richard Appaldo for help collecting field data and hydrophones in the Bahamas.

This research would not have been possible were it not for the support, love, and inspiration from friends and family. I especially thank my mom and dad for always being there for me and for helping me achieve my dreams. This is for you.

Lastly, Bub-bub would like to thank his lab sisters: Shannon, Coon Dog, Lessum, and Stump. Thanks for being my friends throughout my years at NC State and for all of the laughs and adventures along the way.

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CHAPTER 1

INTRODUCTION

Bioacoustic research has recently moved beyond describing acoustic interactions between individuals on a species-centered level to considering the overall soundscape of a landscape (Gasc *et al.*, 2013; Sueur *et al.*, 2008; Harris *et al.*, 2016). The soundscape is comprised of all sound (biological, geophysical, and anthropogenic) within an environment (Pijanowski *et al.*, 2011). Additionally, eco-acoustic metrics such as the Acoustic Complexity Index (ACI) can reflect species diversity by measuring the variation in the acoustic spectrum in time and frequency (Pieretti *et al.*, 2011; Gasc *et al.*, 2013; Sueur *et al.*, 2014). For marine ecosystems, characterizing the underwater soundscape using passive acoustic hydrophones has identified: (i) spatiotemporal patterns in the presence of sound-producing species, (ii) impacts of natural and anthropogenic sounds on marine organisms, and (iii) habitat-specific soundscapes that are often unique to structurally complex habitats such as coral and oyster reefs (Kennedy *et al.*, 2010; Lillis *et al.*, 2014; Kaplan *et al.*, 2015; Butler *et al.*, 2016; Ricci *et al.*, 2017). Since hydrophone recordings can be taken continuously for long periods of time, acoustic data from different ecosystems have led to a new field of research -- soundscape ecology. Within coastal ecosystems, relationships between soundscape diversity, biodiversity, and habitat complexity remain relatively unfounded (Staaterman *et al.*, 2014; Harris *et al.*, 2016). Spatiotemporal variability within the marine acoustic environment must be quantified and understood before soundscape metrics can be widely applied (or new metrics developed) for use within these ecosystems.

Marine organisms rely on sound for navigation, spawning, feeding, mating, and avoiding predators (Lobel 1992; Mann and Lobel 1997; Versluis 2000; Schärer *et al.*, 2012).

For example, Nassau grouper (*Epinephelus striatus*) produce several low frequency vocalizations during spawning aggregations (Schärer *et al.*, 2012), whereas grey snapper (*Lutjanus griseus*) and French grunt (*Haemulon flavolineatum*) produce sounds when under duress (Fish and Mowbray 1970). Snapping shrimp (Family Alpheidae) create broadband, high frequency, snaps in conspecific territorial interactions, though snaps may also be used to stun prey or deter predators (Knowlton and Moulton 1963; Nolan and Salmon 1970; Versluis *et al.*, 2000). Juvenile coral reef fish rely on sound to locate habitats and occasionally demonstrate preference for either low or high frequency noises (Simpson *et al.*, 2007; Radford *et al.*, 2011). Though soundscape ecology studies have evaluated sounds produced by many different organisms in temperate, sub-tropical, and tropical habitats, recent findings emphasize the necessity for high temporal resolution of recordings to better define times of biological activity (McCauley and Cato 2000; Au *et al.*, 2012; Staaterman *et al.*, 2014; Kaplan *et al.*, 2015; Ricci *et al.*, 2016), as well as studies across a range of habitat structural complexity and biodiversity to better define the relationship between soundscape characteristics and these habitat features (e.g., Harris *et al.*, 2016; Ricci *et al.*, 2016).

Although conservation efforts have often focused on charismatic habitats that harbor the adults of a given species such as coral reefs, recent studies demonstrate that nursery habitats, such as back-reef areas that incorporate a mosaic of seagrass, mangrove, tidal creeks, and macroalgal habitats, harbor high abundances and biomass of many species, especially juveniles (see reviews by Beck *et al.*, 2001; Dahlgren and Marr 2004; Adams *et al.*, 2006). Back-reef nursery habitats are important in facilitating the growth and survival of juvenile fish and invertebrates, and these areas often support relatively high abundance and diversity of sub-adult and adult species in adjacent offshore habitats via ontogenetic

migrations from back-reef to offshore, adult habitats (Beck *et al.*, 2001; Eggleston *et al.*, 2004; Dahlgren *et al.*, 2006; Nagelkerken *et al.*, 2012). For example, Nassau grouper (*Epinephelus striatus*), a species of significant ecological and commercial importance, undergo several ontogenetic shifts from early to late juvenile development with larger juveniles (> 150 mm total length) being associated with natural and artificial patch reefs in nursery habitats (Eggleston 1995; Dahlgren and Eggleston 2000). A recent study examined the interacting effects of marine reserves and nursery habitat availability on reef fish and found that, in terms of biomass, no-take coral reef reserves had 249% higher fish biomass when adjacent to a back-reef nursery compared to no-take reserves with no nursery access (Nagelkerken *et al.*, 2012). Although these and other studies have emphasized the ecological function of back-reef systems in promoting tropical marine biodiversity and fish production (Gillanders *et al.*, 2003; Dahlgren and Marr 2004), we are unaware of any studies that have characterized the soundscape of coral patch reefs within a seagrass dominated, back-reef nursery habitat, characteristic of many tropical back-reef systems throughout the world.

Passive acoustic recorders can indicate the presence and persistence of sound-producing organisms in marine habitats over extended periods of time with high temporal resolution (Lammers *et al.*, 2008; Sueur *et al.*, 2008), and provide a complementary tool for sampling fish and invertebrates in back-reef habitats to more traditional gear such as nets, traps, and visual surveys (Ricci *et al.*, 2017). The goals of this study were to: 1) characterize temporal diel variation in soundscapes associated with experimental patch reefs of varying structural complexity (see below), as well as 2) determine potential relationships between several soundscape variables and measures of habitat complexity and fish biodiversity. The system consisted of concrete-block patch reefs of varying structural complexity that were

located within an expansive seagrass meadow within the Bight of Old Robinson, Abaco Island, the Bahamas.

METHODS

Overview

Seven concrete block patch reefs of varying structural complexity served as the experimental units in this study. Fish biodiversity, habitat characteristics, and the underwater soundscape were quantified at each patch reef over a five-month period between March and July, 2016. Habitat characteristics consisted of measures of structural rugosity of each concrete block patch reef, as well as the density of the seagrass surrounding each patch reef. Fish biodiversity measures consisted of: (i) fish species diversity, (ii) evenness, (iii) biomass, (iv) abundance, and (v) size. Soundscape characterization consisted of measures of sound pressure levels (in dB re 1 μ Pa), invertebrate snap rates, and acoustic complexity.

Study Site

Habitat characteristics, fish biodiversity, and soundscape patterns were characterized within the Bight of Old Robinson: a semi-enclosed, seagrass-dominated embayment on Abaco Island, the Bahamas (Figure 1). Habitats within the Bight of Old Robinson are comprised of seagrass, sand, hard-bottom, rocky outcroppings, and patch reefs (Allgeier *et al.*, 2011; Layman and Allgeier 2012). Concrete block patch reefs were built for research purposes over four years before the beginning of this study, and are made of concrete blocks that are either well-stacked or haphazardly piled – water depths at low tide varied from 1.3 to 3.9 meters (Allgeier *et al.*, 2011; Yeager *et al.*, 2011). Concrete block patch reefs ranged in

number of blocks from 8 to 84. Reef soundscapes were treated as acoustically independent as they were interspersed among seagrass beds and separated by distances of > 400 meters (Lillis *et al.*, 2014). Of the seagrass species found around these reefs, *Thalassia testudinum* was by far the most abundant, followed by *Syringodium filiforme* and *Halodule wrightii* (Layman *et al.*, 2013; Layman *et al.*, 2016; C. A. Layman *unpublished data*). Some sites were subjected to nutrient addition studies in prior years which resulted in increased seagrass density surrounding certain patch reefs (C. A. Layman *unpublished data*). Reefs that were selected for this study are located 1.2 - 2.3 km northwest of Little Harbour and directly east of a mosaic of tidal creeks and mangroves that provide essential habitat for juvenile fish making ontogenetic shifts to offshore reefs (Zapata *et al.*, 2014; Huijbers *et al.*, 2015).

Patch Reef Rugosity and Seagrass Characteristics

The rugosity of each patch reef was measured using a chain method to estimate the ratio of reef width and length to chain width and length (Luckhurst and Luckhurst 1978; Gratwicke and Speight 2005). Divers measured the length and width of each individual patch reef using a straight rope suspended over the concrete blocks. A jack-chain (1 link = 2 cm) was then placed over the blocks and allowed to conform to all contours and crevices (Luckhurst and Luckhurst 1978). Rugosity was calculated as the ratio of the contoured, chain length to the straight, rope length. Both length and width measurements of rugosity were made for each patch reef and the average of length and width rugosity was used to characterize overall rugosity for each reef. Seagrass density was calculated by counting the number of short-shoots within three, 0.1 m² quadrats at distances of 1 meter and 4 meters away from each reef. These counts were repeated in three randomly chosen directions from a

given reef, such that mean counts were based on a sample size of three. Distances of 1 and 4-meters from each reef were chosen because, in previous studies on seagrass characteristics surrounding reefs in the same system, seagrass blade length was significantly higher directly adjacent to the reef (0 to 1 meter away) compared to 3 to 4 meters away (Layman *et al.*, 2013). Reef rugosity and seagrass densities were characterized during May, 2016.

Differences in the mean density of seagrass between 1 meter and 4 meters away from patch reefs were tested with a one-way analysis of variance model. When evaluating the relationship between habitat complexity and high frequency acoustic variables, only structural rugosity was used as previous research has suggested that soniferous marine invertebrates like snapping shrimp that contribute to the high frequency aspect of marine soundscapes prefer hard-bottom structure such as oyster reefs over seagrass meadows (Glancy *et al.*, 2003).

Fish Biodiversity

Visual surveys of reef fish residing on experimental patch reefs were conducted by SCUBA divers during seven different sampling days between February and May, 2016. During each visual survey, fish were counted by a diver that was positioned approximately 3 meters away from the reef, with counts made during daylight when water visibility was greater than 10 meters. Fish total length (in cm) was estimated by comparing fish to a PVC-pipe marked in 1-cm increments. Species abundances above 20 per reef (common with *Haemulidae* spp. recruits) were grouped to the nearest 5 or 10 individuals. Due to the relatively small size of the reefs, divers were able to count the total number of fish during each ~15 minute survey. Data from visual fish surveys were used to generate the following

response variables: (i) Shannon diversity, (ii) Pielou's evenness, (iii) abundance, and (iv) biomass. The following equation was used to determine the relationship between fish length and biomass:

$$W=aL^b$$

where a and b values are species-specific constants derived from online databases (fishbase.com), L is fish total length, and W is weight in grams (Andradi-Brown *et al.*, 2016). If data for the a and b constants for species observed during visual surveys were not present in online databases, these parameters were selected from fish of similar body shape and phylogeny as a proxy. For a given fish response variable, the data from each patch reef was averaged over the seven visual surveys. The relationship between fish response variables, habitat characteristics, and soundscape metrics was tested with linear least-squares regression models. Fish biodiversity metrics among reefs of varying habitat complexity were evaluated with a one-way analysis of variance model, and Tukey's post-hoc tests were used to identify differences among specific patch reefs.

Acoustic Sampling

Underwater sounds associated with each experimental patch reef were recorded using passive acoustic recording hydrophones (SoundTrap, Ocean Instruments New Zealand). Hydrophones were secured vertically on metal poles ~0.5 meters above the seafloor and ~1.5 meters away from the base of each patch reef. Hydrophones were submerged at least 0.5 meters below the surface of the water at all times while recording. Recordings were collected in two deployments: (1) February 29th to May 24th and (2) May 31st to August 1st, 2016, with

gaps in the data representing times where hydrophones were not recording due to maintenance and data downloading (from May 25th to May 30th). Hydrophones were set to record two minutes every 20 minutes with a sampling rate of 96 kHz throughout both deployments to enhance characterization of temporal acoustic patterns, such as diurnal trends for each site. The analog signal of the SoundTrap hydrophone is digitized at a fixed rate of 288 kHz. A digital anti-alias filter, with a cutoff frequency of 0.45 times the desired sample rate, is then applied before decimation. Consequently, the useable (-3 dB) bandwidth of these recordings is 0.020-43.0 kHz.

Acoustic Analysis

Each two-minute recording was processed in MATLAB using purpose-written code. These recordings were analyzed into low (0.1 – 1.5 kHz) and high (4 – 20 kHz) frequency bands. The low frequency band was selected to capture noises from tropical reef fish, such as those from the families Haemulidae, Lutjanidae, and Serranidae (Fish and Mowbray 1970; Kennedy *et al.*, 2010). The high frequency band was chosen to isolate frequencies associated with marine invertebrate snaps (primarily Alpheid snapping shrimp) while limiting acoustic input from soniferous fish and wind energy (Cato & Bell 1992).

The mean spectrum was calculated for each 2-minute recording (NFFT = 32,768, 0% overlap). Spectral amplitudes for each file were then summed to generate a time series of sound pressure levels (SPLs) within the low and high frequency bands. SPLs among sites were compared using non-parametric Kruskal-Wallis tests, and Wilcoxon rank sum tests were used for temporal comparisons, such as nighttime versus daytime SPLs.

Snap rates for invertebrate snaps were assessed for each recording using an envelope correlation and amplitude evaluation method developed by Bohnenstiehl *et al.*, 2016. The snap detection procedure operated in the 4 – 20 kHz frequency band, where these arrivals exhibited the highest signal levels relative to the background noise. It used a correlation coefficient cutoff of 0.70 and a 102 dB re 1 μ Pa (peak-to-peak) amplitude threshold, which corresponds to the 90% quantile of the background sound levels observed throughout the recording period. The detection kernel was derived from the local recordings and left-padded to suppress the possible detection of sea surface reflected arrivals at short time delays. Kruskal-Wallis tests were used to evaluate differences in median invertebrate snap rate among sites while Wilcoxon rank-sum tests were used for temporal comparisons of snap rates.

The Acoustic Complexity Index (ACI) has been previously used in marine soundscape research as an eco-acoustic metric for call diversity and measures the variation in the acoustic spectrum in time and frequency (Sueur *et al.*, 2014; Staaterman *et al.*, 2014; Harris *et al.*, 2016). ACI was calculated for four, 30-second duration segments, which were then averaged for each two-minute recording. These calculations used a window length of 4096 points with 0% overlap ($\Delta f = 23.44$ Hz, $\Delta t = 0.043$ sec), and were performed in the two frequency bands: low (0.1 – 1.5 kHz) and high (4 – 20 kHz). To determine if ACI values varied significantly among experimental reefs, Kruskal-Wallis tests were utilized.

Potential relationships between habitat complexity, fish biodiversity, and soundscape data were evaluated with correlation models. For example, low frequency (0.1 – 1.5 kHz) soundscape metrics from vocalizing fish, such as SPLs and ACI, were correlated with fish biodiversity metrics, as well as potential relationships between high frequency (4 – 20 kHz)

soundscape metrics, such as SPL and ACI, and snap rates. Other potential relationships were explored using correlation models, such as between snap rates and fish biodiversity, or between soundscape metrics and habitat complexity.

Values for sunrise and sunset were obtained from the United States Naval Observatory website (<http://www.usno.navy.mil/USNO/>). For each deployment day, median nighttime (sunset to sunrise) and daytime (sunrise to sunset) SPLs, snap rates, and ACI values were determined. Low frequency (0.1 – 1.5 kHz) SPLs and ACI pertaining to crepuscular hours bracketed the period of one hour before and one hour after sunset or sunrise. All times were set to Eastern Standard Time for the entirety of this analysis.

RESULTS

For the results below, we focus first on temporal patterns in the soundscape, which is necessary to identify what soundscape data to use in analyzing spatial patterns. For example, peaks in low frequency (0.1 – 1.5 kHz) sound pressure levels were observed around periods of sunrise and sunset for some reefs. Thus, for all spatial comparisons involving low frequency sounds associated with fish vocalizations, we used soundscape variables during crepuscular periods. For spatial comparisons involving high frequency (4 – 20 kHz) acoustic variables and invertebrate snap rates, soundscape variables were considered separately for nighttime and daytime recording periods. In each section below, we describe the relationships among habitat complexity, fish biodiversity, and the soundscape.

Temporal Patterns in Acoustic Time Series

Crepuscular peaks in low frequency (0.1 – 1.5 kHz) sound pressure levels were present for some reefs, such as reefs 6 and 7 (Figure 2A), and nightly peaks in high frequency (4 – 20 kHz) sound pressure levels were present at all reefs (Figure 2B). Three of seven reefs displayed significantly higher SPLs at low frequencies during crepuscular periods compared to all other times (Wilcoxon Rank-Sum, $Z > 2.9$, $p < 0.004$) (Figure 3A). High frequency SPLs were significantly higher at night than during the day for all reefs (Wilcoxon Rank-Sum, $Z > 4.5$, $p < 0.001$) (Figure 3B).

Median invertebrate snap rates varied by reef, and were consistently higher at night than during the day, with pronounced shifts in snap rates occurring during crepuscular periods (Wilcoxon Rank-Sum, $Z > 4.8$, $p < 0.001$) (Figure 4). High frequency (4 – 20 kHz) SPLs were positively correlated with snap rates for all reefs ($r = 0.27 - 0.66$, $p < 0.001$), suggesting that changes in high frequency SPLs can be described by invertebrate snapping activity (Figure 5A). High frequency ACI was also correlated with snap rate, though only at relatively low rates (Linear Regression, $r = 0.18 - 0.89$, $p < 0.001$), and as can be seen in Figure 5b, the relationship is clearly non-linear, with the ACI values saturating and leveling off at rates above ~750 snaps/minute.

Spatial Variation in Habitat Complexity, Fish Biodiversity, and Soundscape Metrics

Habitat Complexity - Experimental patch reefs varied in their rugosity, as well as the surrounding mean density of seagrass (1 and 4-meter distances from the reef), with seagrass density generally increasing with reef rugosity (Figure 6). There was a positive and statistically significant increase in seagrass density with reef rugosity – this pattern was

stronger for seagrass measured at 1 meter from the reef ($r = 0.72 \pm 0.26$, $p = 0.033$) than at 4 meters from the reef ($r = 0.67 \pm 0.36$, $p = 0.041$). Mean seagrass density was significantly higher at 1-meter distances from the reef compared to 4-meters (nested, one-way ANOVA: $F_{7,28} = 2.88$, $p = 0.021$). Experimental reefs 3, 6, and 7 had the highest rugosity (Figure 6A), and mean seagrass densities were significantly highest at reef 7 at 1 meter distances from the reef (one-way ANOVA: $F_{6,20} = 4.84$, $p = 0.007$) (Figure 6B). Conversely, reef 1 had the second lowest rugosity and some of the lowest mean seagrass densities at 1 meter distances (Figure 6). Seagrass densities at 4 meter distances were not significantly different among reefs (one-way ANOVA: $F_{6,20} = 1.86$, $p = 0.1572$).

Fish Biodiversity - Fish biodiversity variables varied significantly among reefs, though more complex reefs tended to have higher fish diversity and biomass while less complex reefs had higher fish abundances. Average Shannon diversity at reefs 4, 5, and 7 was significantly higher than average diversity at reefs 2 and 3 (one-way ANOVA: $F_{6,48} = 17.56$, $p < 0.001$) (Table 1). Average fish evenness was highest for reefs 1, 4, 5, and 7, yet was lowest for reefs 2 and 3 (one-way ANOVA: $F_{6,48} = 13.02$, $p < 0.001$) (Table 1). Average fish abundance showed inverse patterns to diversity, wherein reefs 2 and 3 had higher average fish abundance than reefs 5, 6, and 7 (one-way ANOVA: $F_{6,48} = 6.52$, $p < 0.001$) (Table 1). Reef 6 had the highest average biomass and there was no significant difference in average biomass among all other reefs (one-way ANOVA: $F_{6,28} = 18.02$, $p < 0.001$) (Table 1).

Soundscape Variables – Generally, more complex patch reefs had higher median values for all soundscape variables; this pattern was stronger for high frequency variables compared to low frequency. In terms of spatial variation in the soundscape, reefs 4, 6, and 7

had the highest crepuscular, low frequency SPLs (0.1 – 1.5 kHz) compared to other reefs (Kruskal-Wallis, $\chi^2 = 516.85$, $p < 0.001$) (Figure 7A). At all other times, reef 6 had the highest, low frequency SPLs (Kruskal-Wallis, $\chi^2 = 6311.35$, $p < 0.001$). For crepuscular, low frequency ACI, reef 6 had the highest values with reefs 2, 4, and 7 having the second highest values (Figure 7B). Nighttime high frequency (4 – 20 kHz) SPLs were highest for reefs 5, 6, and 7 (Kruskal-Wallis, $\chi^2 = 673.68$, $p < 0.001$) (Figure 8A). Daytime high frequency SPLs showed similar spatial patterns between reefs as nighttime high frequency SPLs (Kruskal-Wallis, $\chi^2 = 823.09$, $p < 0.001$). Reefs 4, 6, and 7 had the highest nighttime ACI in high frequencies among reefs (Kruskal-Wallis, $\chi^2 = 602.61$, $p < 0.001$) (Figure 8B). Nighttime snap rates were highest for reefs 5, 6, and 7 compared to others (Kruskal-Wallis, $\chi^2 = 624.18$, $p < 0.001$) (Figure 8C). Daytime snap rates were also highest for reefs 5, 6, and 7 compared to others (Kruskal-Wallis, $\chi^2 = 586.70$, $p < 0.001$).

Relationships between Fish Biodiversity and Habitat Complexity

There was a negative and statistically significant correlation between mean fish abundance per patch reef, and seagrass density at 1 meter distance from the reefs ($r = -0.87 \pm 0.08$, $p = 0.017$). Mean fish abundance was not significantly correlated with any other habitat variables (Linear regression, $p > 0.221$). There were no significant correlations between average fish diversity, evenness or biomass and any habitat variables (Linear regression, $p > 0.110$).

Relationships between Habitat Complexity, Fish Biodiversity, and Acoustic Variables

Some marine soundscape studies have suggested that acoustic variables may be positively correlated with habitat complexity and fish biodiversity (e.g., Harris et al., 2016; Bertucci et al., 2016). In contrast to expectations, neither median, crepuscular, low frequency (0.1 – 1.5 kHz) sound pressure levels nor ACI were correlated with any habitat complexity or fish biodiversity variables (Linear regression, $p > 0.072$) (Figure 10). There were, however, significant correlations between habitat complexity and high frequency (4 – 20 kHz) soundscape variables. For example, at high frequencies, median, nighttime SPLs were positively correlated with reef rugosity ($r = 0.86 \pm 0.14$, $p = 0.015$) (Figure 9A). Median, nighttime high frequency SPLs were not correlated with average fish diversity, evenness, or biomass (Linear regression, $p > 0.145$). Nighttime, high frequency ACI values were not correlated with any of the habitat complexity or fish biodiversity variables (Linear regression, $p > 0.068$) (Figure 10).

Median nighttime snap rates were positively correlated with rugosity ($r = 0.79 \pm 0.26$, $p = 0.013$) (Figure 9B). Nighttime invertebrate snap rate was not significantly correlated with average fish diversity, evenness, abundance or biomass (Linear regression, $p > 0.064$).

DISCUSSION

This study explored relationships between spatiotemporal variation in the soundscape of experimental patch reefs, and the structural complexity and associated fish diversity on patch reefs in a back-reef nursery habitat. It addressed a fundamental question in the emerging field of underwater soundscape ecology – do the variety and abundance of sounds

recorded in a given habitat accurately reflect the complexity of the habitat and biodiversity of its inhabitants? For the seagrass-dominated back-reef habitat examined in this study, there are two general answers: (i) no, the low frequency sounds that might be produced by juvenile fish did not correlate with the diversity of fish on or habitat complexity of experimental patch reefs, and (ii) yes, invertebrate snaps likely associated with snapping shrimp were positively correlated with reef habitat complexity. Specifically, sound pressure levels in the low frequency band (0.1 – 1.5 kHz), indicative of reef fish vocalizations, occasionally peaked twice per day at three of the most complex sites around crepuscular times; however, the relationships between habitat and low frequency SPL and ACI were not significant. Sound pressure levels in the high frequency band (4 – 20 kHz), as well as invertebrate snap rates, peaked at night. Acoustic variables collected at these biologically relevant temporal periods were compared with habitat complexity and fish biodiversity. High frequency SPLs and snap rates were significantly correlated with structural rugosity, although not fish biodiversity. Low frequency sound pressure levels showed no relationships with habitat complexity or fish biodiversity. Acoustic complexity values were not related to fish biodiversity or habitat complexity for neither low nor high frequencies.

Temporal Soundscape Characteristics

For each experimental patch reef, high frequency (4 – 20 kHz) sound pressure levels and invertebrate snap rates were highest at night compared to during the day. Related studies of underwater soundscapes in tropical Caribbean habitats found similar peaks in high frequency sound pressure levels, likely associated with snapping shrimp, that were highest around crepuscular periods (Staaterman *et al.*, 2014; Kaplan *et al.*, 2015). Conversely, high

frequency snapping shrimp sounds in more temperate waters indicate significant fluctuations in temporal snapping activity, with activity being predominantly at night during summer months (Radford *et al.*, 2008; Bohnenstiehl *et al.*, 2016; Ricci *et al.*, 2016). It is also possible that snapping shrimp prefer to be more active during periods of darkness to avoid predation (Radford *et al.*, 2008; R. P. Lyon *unpublished data*).

As reported in other studies (e.g., Bohnenstiehl *et al.* 2016; Ricci *et al.*, 2016), high frequency SPLs were significantly and positively correlated with invertebrate snap rates. Although high frequency ACI also responded positively with increased snapping, the metric leveled off at moderate rates of activity (Figure 5). Similarly, many papers have identified changes in ACI based on the broadband signals associated with a single organism: snapping shrimp (e.g., Kaplan *et al.*, 2015; Butler *et al.*, 2016). At one particular reef in this study, ACI varied approximately 40% in response to changes in invertebrate snap rate, and this percentile change in ACI from a soundscape with predominantly one soniferous species in high frequencies is greater than the percentile change in ACI in other studies attributing ACI in high frequencies to organism diversity (Bertucci *et al.*, 2016). Based on this evidence, temporal changes in ACI may simply be due to fluctuations in activity from one, soniferous species and ACI may not be robust to variations in call rate. This may also be true when evaluating ACI at low frequencies in an attempt to estimate fish biodiversity as other studies have indicated that ACI may vary temporally based on fish call rate, not necessarily fish call diversity (Desjonqueres *et al.*, 2015; Buscaino *et al.*, 2016).

Low frequency (0.1 – 1.5 kHz) sound pressure levels showed only occasional crepuscular or diurnal patterns for three reefs (4, 6, and 7) with relatively high complexity compared to others. More seasonal patterns in low frequency SPLs and ACI, such as

relationships with lunar phase or temperature, were not observed at these experimental patch reefs. For coral reef habitats in the Florida Keys, USA, low frequency sound pressure levels were elevated during periods of the new moon when many soniferous marine organisms are acoustically active (McCauley and Cato 2000; McCauley 2012; Staaterman *et al.*, 2014). In the US Virgin Islands, low frequency SPLs were higher around times of dusk and dawn than other times (Kaplan *et al.*, 2015). Though these studies were performed in similar tropical reef areas, they did not focus on back-reef, nursery habitats containing predominantly juvenile fish.

Spatial Soundscape Characteristics

In this study, high frequency SPLs and invertebrate snap rates were significantly correlated with structural rugosity, whereas low frequency SPLs were not correlated with either rugosity or seagrass density. ACI in both high and low frequencies was not significantly correlated with any measures of habitat complexity or fish biodiversity. Recently, studies have found potential relationships between habitat health and composition and underwater soundscapes. In sponge-dominated hard-bottom habitats in the Florida Keys, snapping shrimp snaps were considerably higher in healthy areas as opposed to degraded ones (Butler *et al.*, 2017). In the US Virgin Islands, the soundscapes of three reefs with varying coral and macroalgal cover were correlated significantly with coral cover, whereas high frequency sound pressure levels showed no relationship with habitat composition (Kaplan *et al.*, 2015). Previous research, however, has shown that snapping shrimp are not dependent on live coral cover for essential habitat and preferentially select habitat that provides high amounts of interstitial space, such as oyster reefs, rocky outcroppings, sponge

cavities, and coral rubble (Williams 1984; Cato and Bell 1992). This study, as well as others evaluating differences in the soundscape based on habitat, indicate that high frequency sound pressure levels or invertebrate snaps, such as snapping shrimp snaps, have the potential to indicate benthic composition, quality, and complexity (Lillis *et al.*, 2014; Bohnenstiehl *et al.*, 2016; Butler *et al.*, 2016; Butler *et al.*, 2017).

Neither high nor low frequency ACI, was correlated with fish diversity, evenness, abundance, or biomass. Both terrestrial and marine soundscape ecology studies strive to link traditional methods of measuring biodiversity with acoustic metrics such as ACI which evaluate the spectral and temporal variation in animal vocalizations (Sueur *et al.*, 2008; Sueur *et al.*, 2014; Kaplan *et al.*, 2015; Harris *et al.*, 2016). Though these metrics were developed and have been well tested for use in terrestrial soundscapes as a proxy for biodiversity, recent attempts to correlate biodiversity with acoustic characteristics in the marine realm have yielded mixed results (Pieretti *et al.*, 2011; Gasc *et al.*, 2013; Sueur *et al.*, 2014; Harris *et al.*, 2016). In many instances, elevated sound pressure levels and acoustic complexity in low frequency bands have been significantly correlated with higher fish diversity and abundance (Kennedy *et al.*, 2010; Nedelec *et al.*, 2015; Kaplan *et al.*, 2015; Harris *et al.*, 2016), although our results do not support the same findings in back-reef, nursery habitats. ACI and sound pressure levels may prove ineffective for evaluating fish biodiversity or presence in back-reef nursery habitats predominantly inhabited by juvenile organisms. For example, although vocalizations from juvenile fish species have been documented in the past (Lanzig 1974; Fine *et al.*, 1997; Loesser *et al.*, 1997), this study did not show increased ACI or sound pressure levels in low frequencies with a higher abundance or diversity of juvenile organisms. Sound production as a result of spawning is unlikely in

back-reef, nursery habitats such as the Bight of Old Robinson, as a majority of the fish seen during visual surveys were not sexually mature. It may also be adaptive to remain somewhat silent as a juvenile in a nursery area: a previous study demonstrated that spawning groups of silver perch (*Bairdiella chrysoura*) reduce their mating calls by an average of 9 dB when in the presence of bottlenose dolphin vocalizations, suggesting the possibility for prey adaptive silence in marine soundscapes (Curio 1976; Luczkovich *et al.*, 2000). This prey adaptive silence is unconfirmed in juvenile fish species in back-reef nurseries. Conversely, vocalizations from juvenile fish may simply be too quiet to be recorded using passive acoustic monitoring. Further research into sound production by juvenile organisms may be needed to better understand the acoustic ecology of back-reef habitats.

Study Implications

Though there is strong evidence that larval and juvenile coral reef fish rely on reef noise for settlement and locating habitats (Simpson *et al.*, 2005; Simpson *et al.*, 2007; Radford *et al.*, 2011; Lillis *et al.*, 2013), the results from the present study suggest that for back-reef nursery areas, the low frequency soundscape is relatively quiet, and that soundscape metrics like acoustic complexity are not related to fish abundance or biodiversity. Playback experiments from patch reefs have elicited responses from both juvenile and adult reef fish suggesting that sound does play a role in fish movement, yet the soundscape of patch reef habitats themselves have not been recorded (Radford *et al.*, 2011). Other studies in the Caribbean that have recorded the soundscapes of coral reefs have found low frequency (0.1 – 1 kHz) SPLs range from ~90 to 105 dB re 1 μ Pa, whereas in this study, low frequency (0.1 – 1.5 kHz) SPLs ranged from ~80 to 94 dB re 1 μ Pa (Kaplan *et al.*, 2015). Though it is

likely that juvenile fish locate deeper, offshore coral reefs using a myriad of different cues, including acoustics, it is still unclear if juvenile fish differentiate between patch reefs of varying complexity using sound as sound production from the juvenile fish inhabiting these sites may be limited.

Our results show that data derived from passive acoustic recorders may potentially indicate habitat complexity in back-reef nursery areas through evaluating the sounds produced by cryptic, soniferous, and resident invertebrates. Passive recorders can help elucidate when and where organisms like snapping shrimp are active when traditional sampling methods would be otherwise ineffective (Bohnenstiehl *et al.*, 2016; Ricci *et al.*, 2016). Though results focusing on the relationship between live coral cover and invertebrate snapping noise are relatively mixed (Kennedy *et al.*, 2010; Kaplan *et al.*, 2015), recent findings suggest healthy hard-bottom areas contain higher invertebrate snaps compared to degraded ones (Butler *et al.*, 2017). Since snapping shrimp live in habitats with considerable interstitial space (Cato and Bell 1992), monitoring invertebrate snaps using acoustics may prove effective in predicting habitat complexity variables like structural rugosity

Conclusions

Although soundscapes can indicate the presence of soniferous organisms in marine habitats over extended periods of time, they may not effectively signify abundance or biodiversity of fish in habitats that are dominated by juvenile stages. The results from this study suggest that invertebrate snaps relate to the structural rugosity of patch reefs in a tropical back-reef nursery. The notion that back-reef nurseries dominated by juvenile stages

may be relatively quiet in low frequency sounds compared to off-shore reefs harboring more adults requires further testing.

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Table 1. Mean values for fish diversity, evenness, abundance, biomass, and total length (cm) for each reef with standard errors. Values were derived from seven visual fish surveys between February and June, 2016.

Reef	Shannon Diversity	Pielou's Evenness	Abundance	Biomass (grams)	Average Length (cm)
1	1.32 +/- 0.06	0.74 +/- 0.04	89.71 +/- 21.22	3533.79 +/- 1482.97	20.19 +/- 0.30
2	0.58 +/- 0.09	0.35 +/- 0.04	176.86 +/- 44.58	897.81 +/- 166.93	4.93 +/- 0.06
3	0.68 +/- 0.11	0.44 +/- 0.08	165.29 +/- 33.56	374.12 +/- 58.30	8.85 +/- 0.20
4	1.81 +/- 0.09	0.72 +/- 0.03	115.14 +/- 12.44	2738.37 +/- 676.11	10.75 +/- 0.23
5	1.57 +/- 0.05	0.80 +/- 0.03	24.00 +/- 2.42	312.96 +/- 76.67	6.77 +/- 0.06
6	1.11 +/- 0.21	0.60 +/- 0.07	59.86 +/- 9.72	9900.02 +/- 1376.84	7.17 +/- 0.31
7	1.50 +/- 0.07	0.78 +/- 0.02	39.86 +/- 3.26	632.40 +/- 125.21	7.10 +/- 0.30

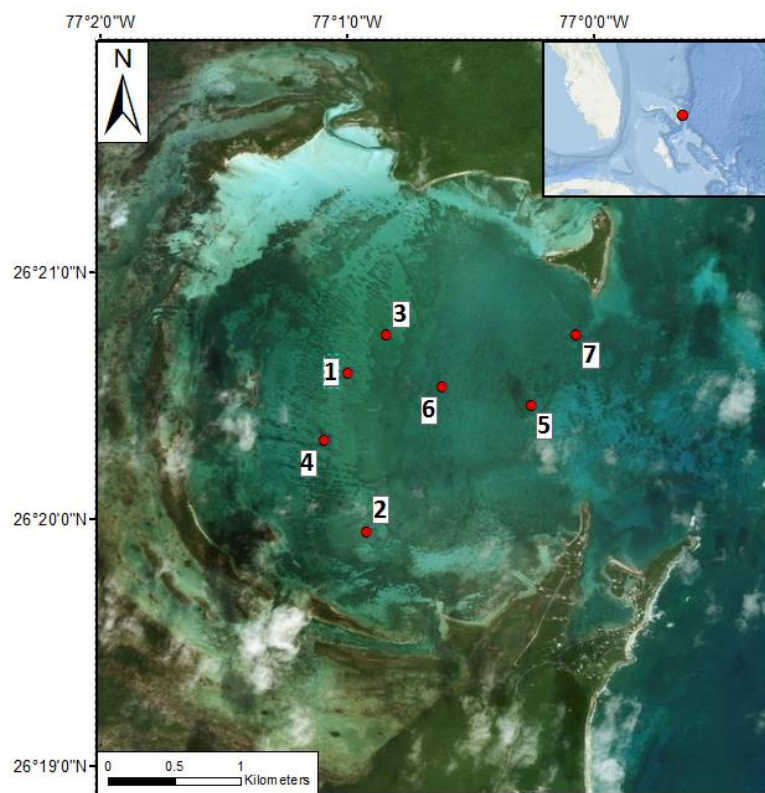


Figure 1. Locations of seven concrete block experimental patch reefs situated within the Bight of Old Robinson, Abaco Island, the Bahamas. Patch reefs are numbered 1 to 7 in order of least to most structurally complex.

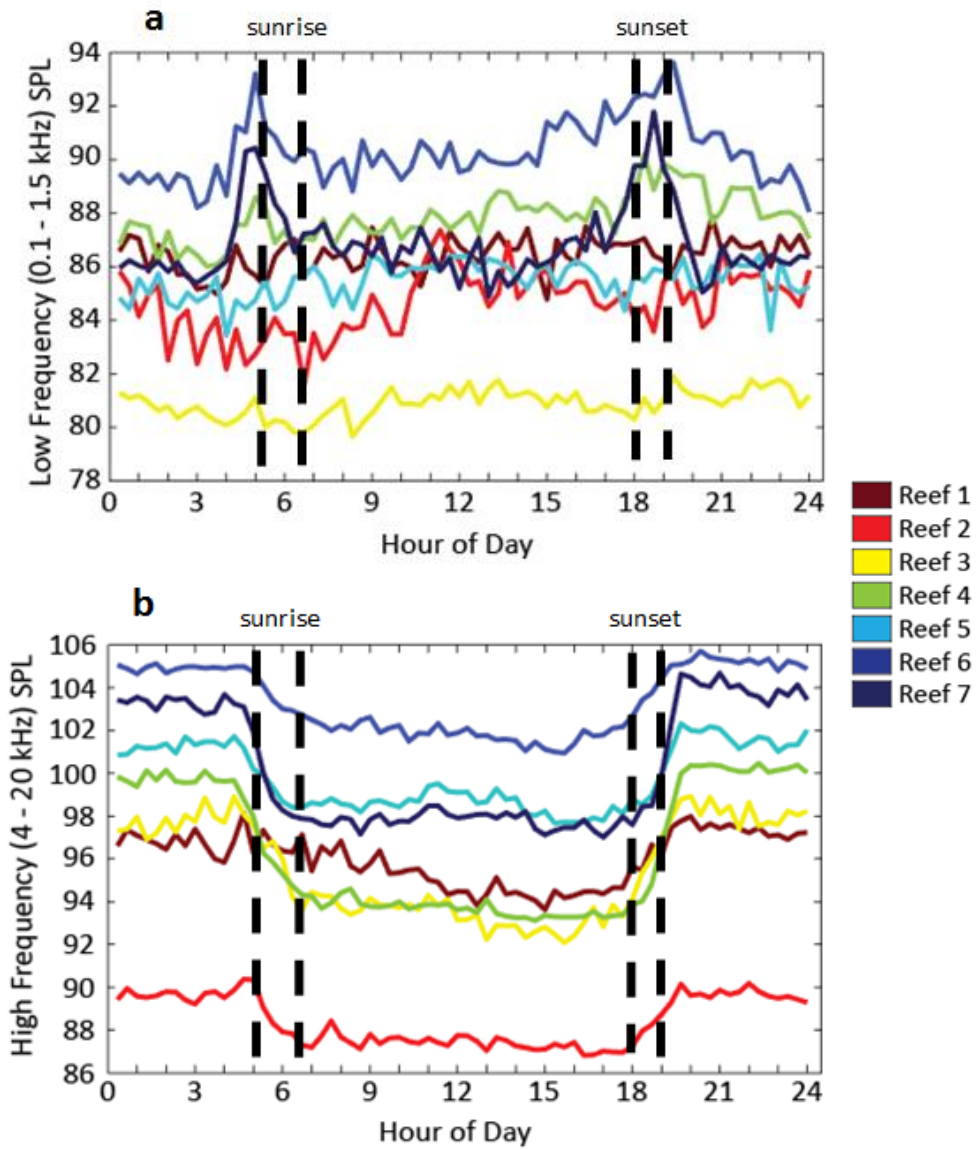


Figure 2. Median daily SPLs (dB re 1 μ Pa) in the low (0.1 – 1.5 kHz) (a) and median daily SPLs (dB re 1 μ Pa) in the high (4 – 20 kHz) (b) frequency bands for each site. Vertical dashed lines correspond to the ranges of sunset and sunrise times.

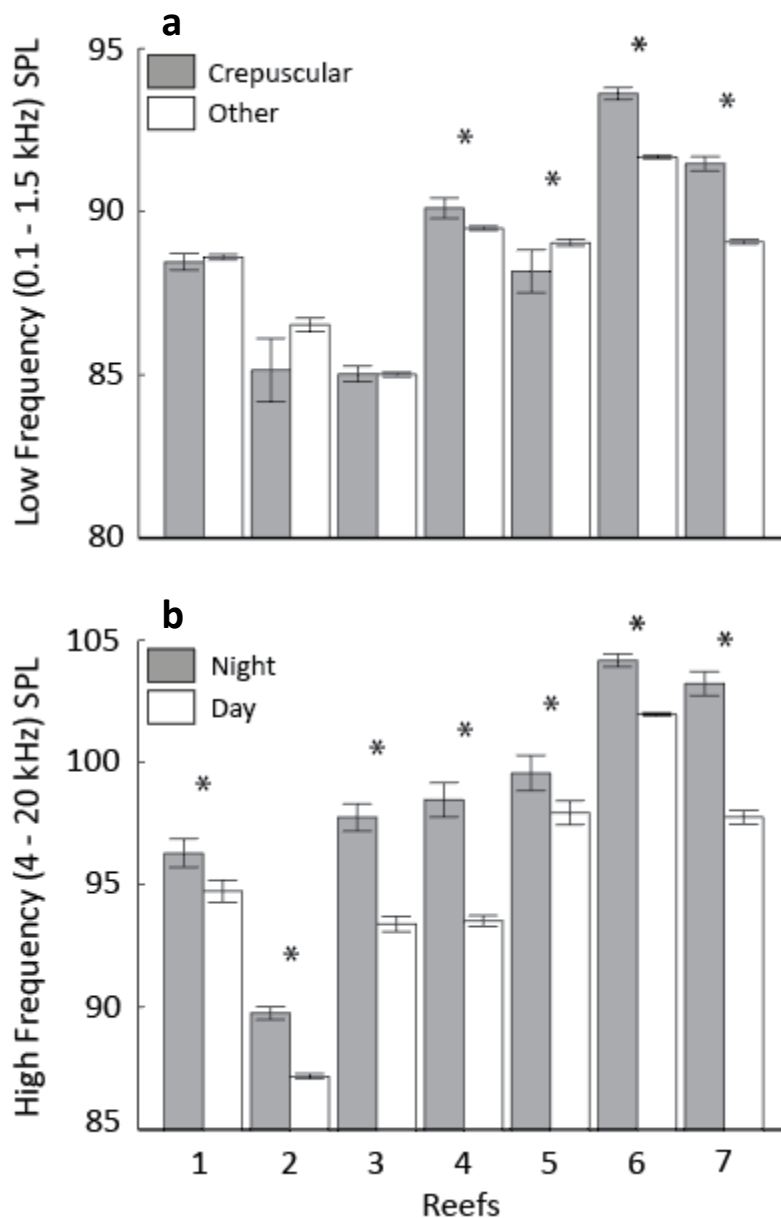


Figure 3. Median SPL (in dB re 1 μ Pa) in the low (a) (0.1 – 1.5 kHz) and high (b) (4 – 20 kHz) frequency bands at specific times of day for each reef. SPLs during two different time periods for each reef were compared using Wilcoxon Rank-Sum tests. Error bars are the uncertainty in the median SPL estimated from 10,000 bootstrap samples. Significant differences between each reef are represented by asterisks.

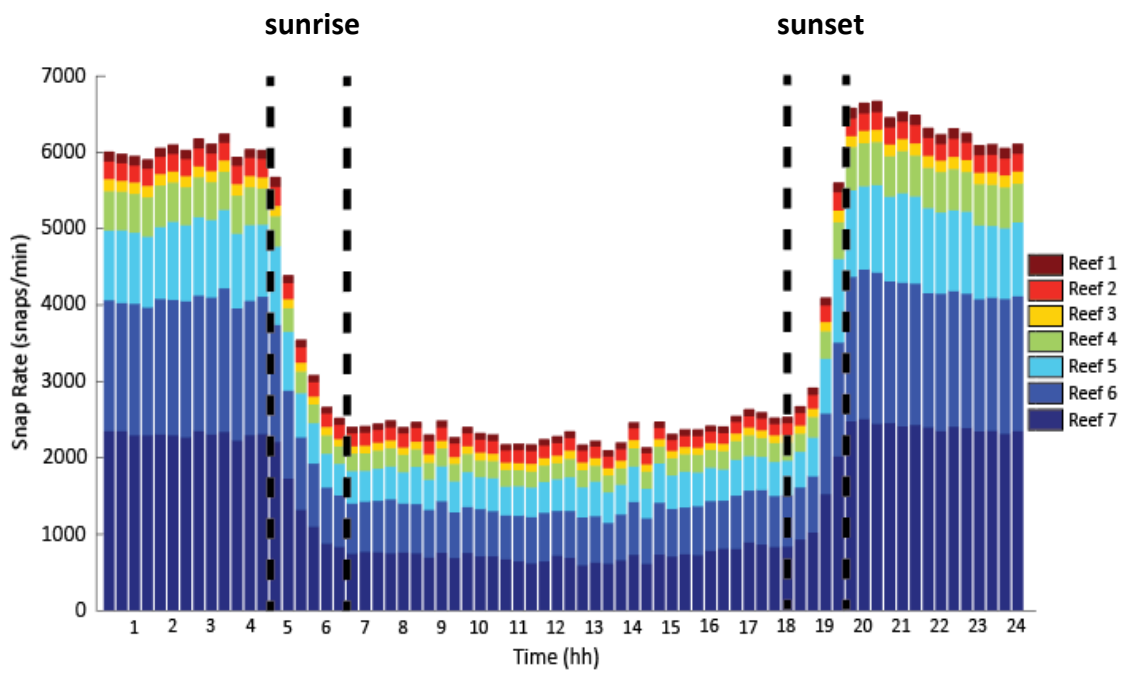


Figure 4. Median invertebrate snap rate for each site based on the times of each recording in a day. Bars represent median snap rates for each recording time over each day. Vertical dashed lines correspond to ranges of

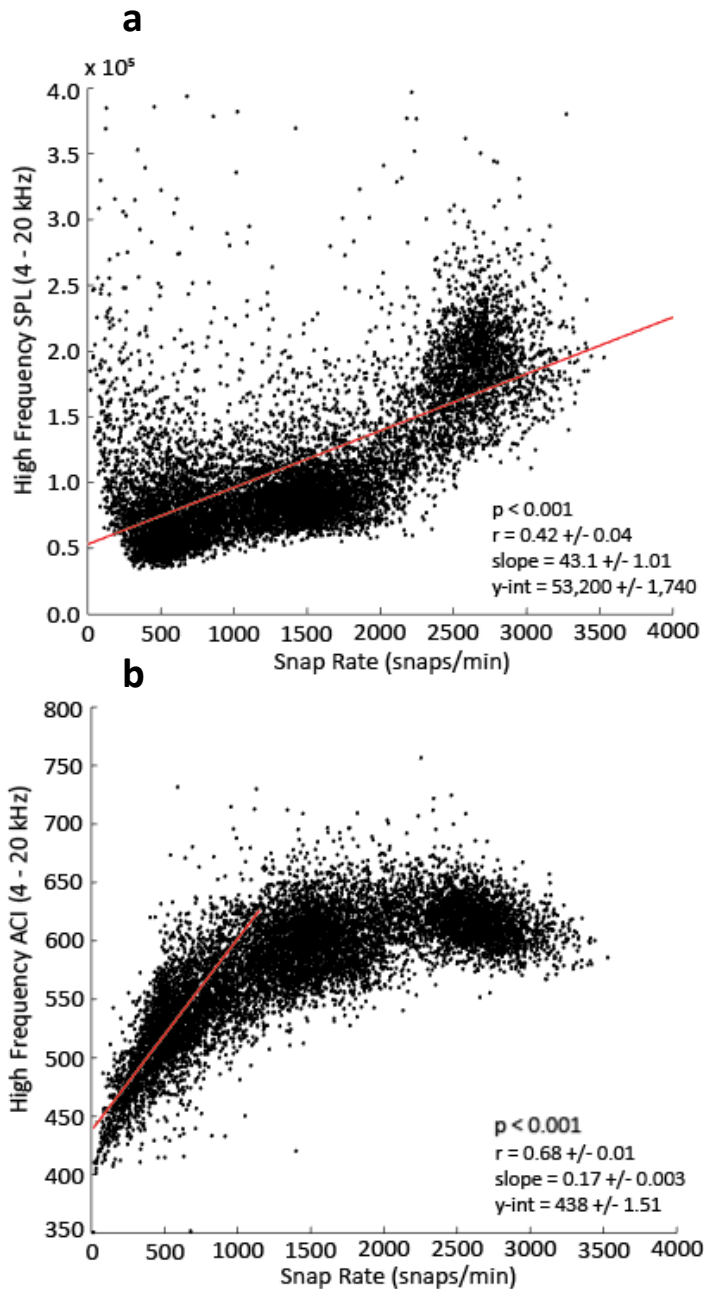


Figure 5. Relationship between invertebrate snap rates from each recording and high frequency (4 – 20 kHz) root-mean-square sound pressure levels (μPa) (a) and acoustic complexity (b) for reef 7. Linear regressions for panel (b) were performed on snap rates between 0 and 750 snaps/min to describe the strength of the trend before leveling off. Statistical analysis was performed using linear regression models. Uncertainty in the correlation coefficient, slope, and intercept were determined from 10,000 bootstrap samples.

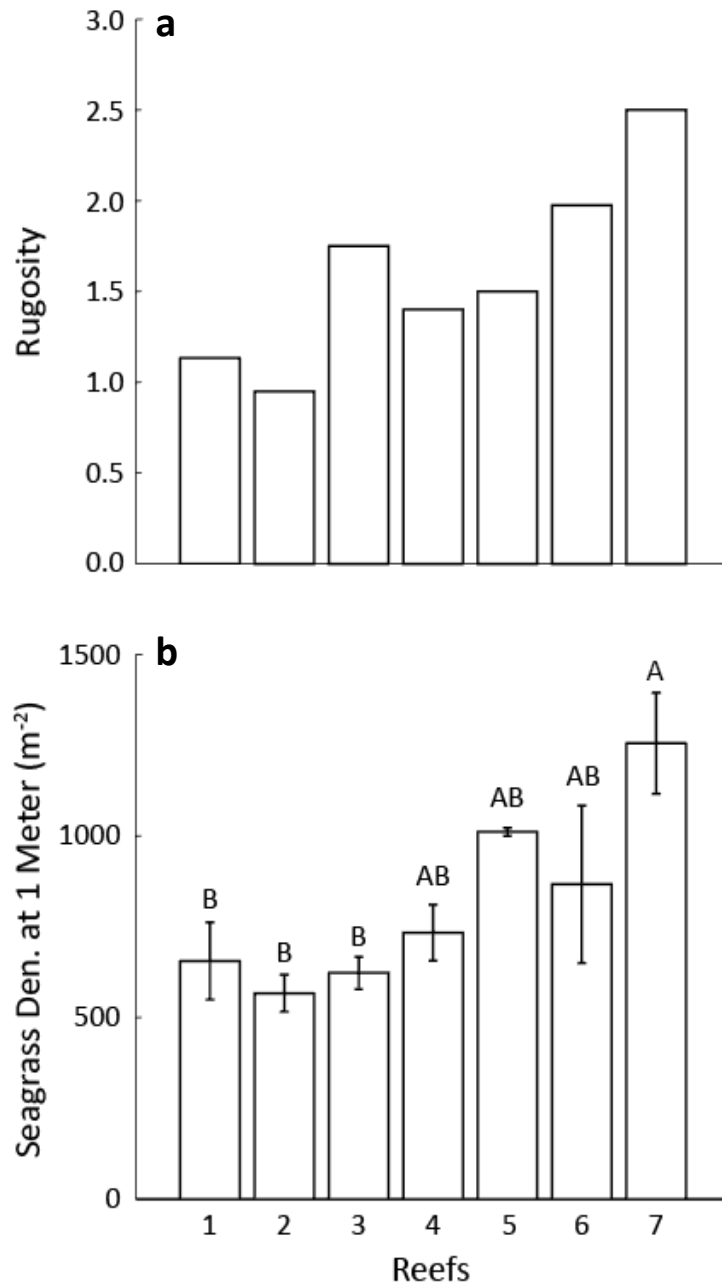


Figure 6. Rugosity (a) and mean seagrass density at 1 meter (b) for each reef. Error bars indicate standard error for seagrass density at 1 meter (N=3). A one-way ANOVA with Tukey post-hoc tests was used to differentiate reefs based on seagrass density. Letters above each bar indicate statistical differences between reefs (from one-way ANOVA and Tukey's post hoc test); reefs that do not share the same letter are significantly different from each other.

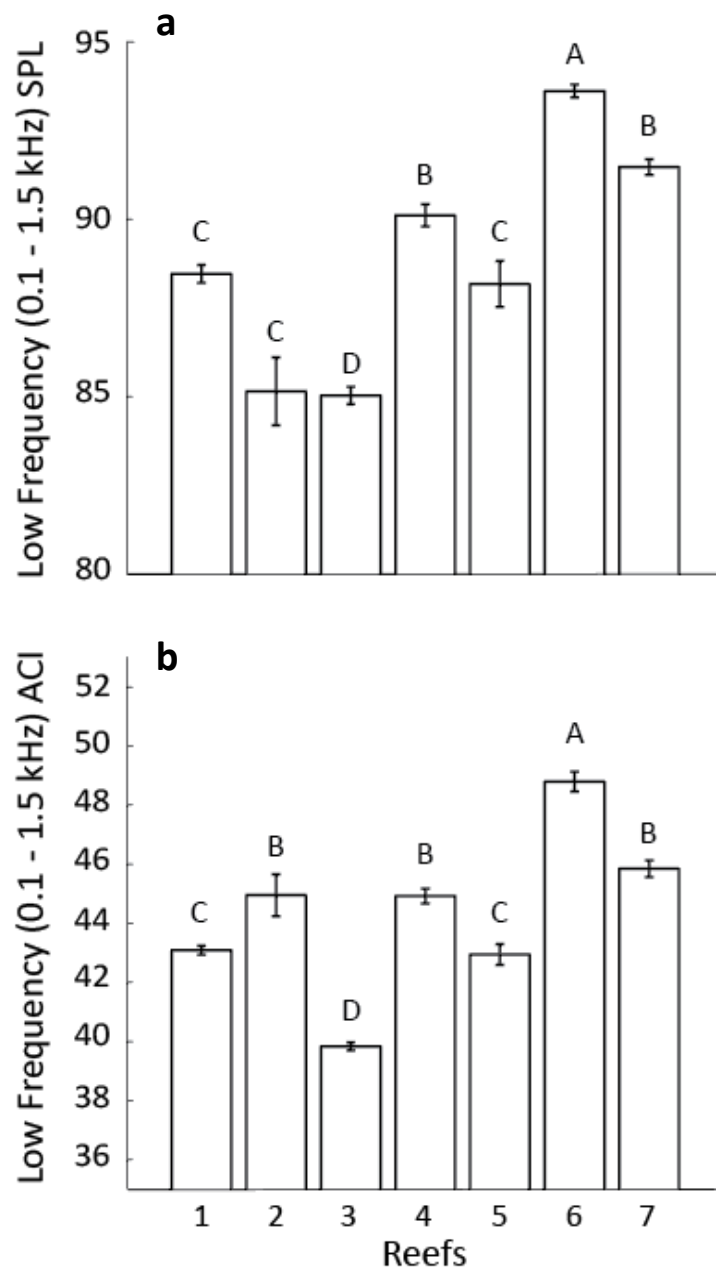


Figure 7. Median, crepuscular, low frequency (0.1 – 1.5 kHz) SPLs (dB re 1 μPa) (a) and ACI (b) for each reef. Soundscape metrics at crepuscular hours were chosen because acoustic biological activity was highest for low frequencies at these times. Error bars are the uncertainty in the median SPL and ACI estimated from 10,000 bootstrap samples. Differences among sites were evaluated using Kruskal-Wallis tests. Letters above each bar indicate statistical differences between reefs; reefs that do not share the same letter are significantly different from each other.

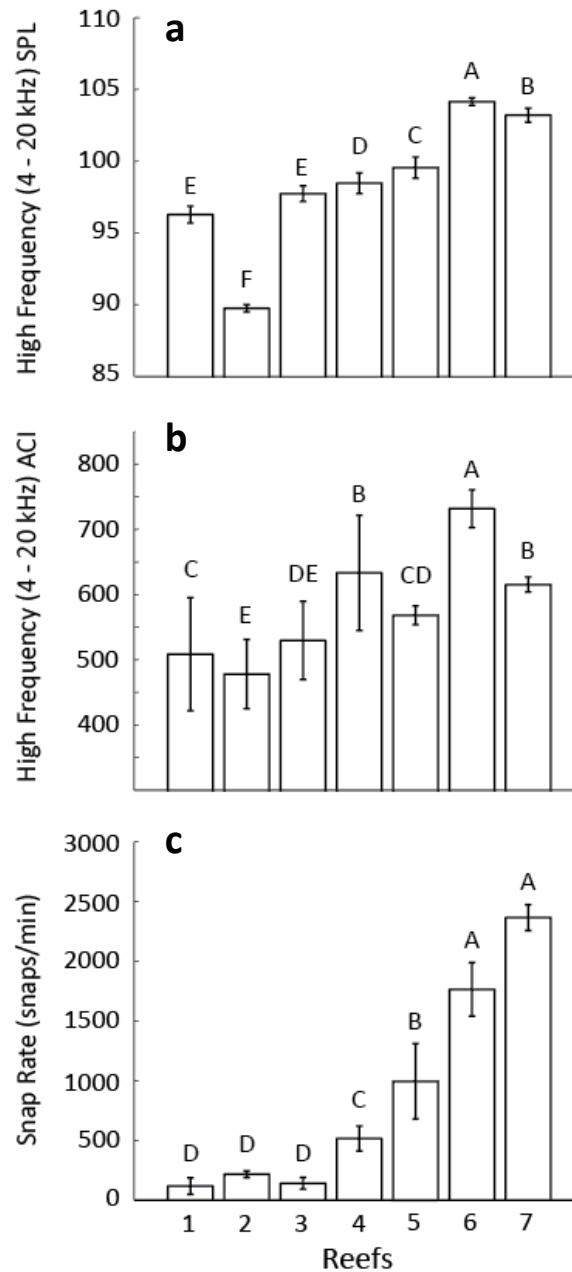


Figure 8. Median nighttime, high frequency (4 – 20 kHz) SPLs (dB re 1 μ Pa) (a) ACI (b), and snap rate (c) for each reef. Soundscape metrics at nighttime were chosen because acoustic biological activity was highest for high frequencies at these times. Error bars are the uncertainty in the median SPL, ACI, and snap rate estimated from 10,000 bootstrap samples. Differences among sites were evaluated using Kruskal-Wallis tests. Letters above each bar indicate statistical differences between reefs; reefs that do not share the same letter are significantly different from each other.

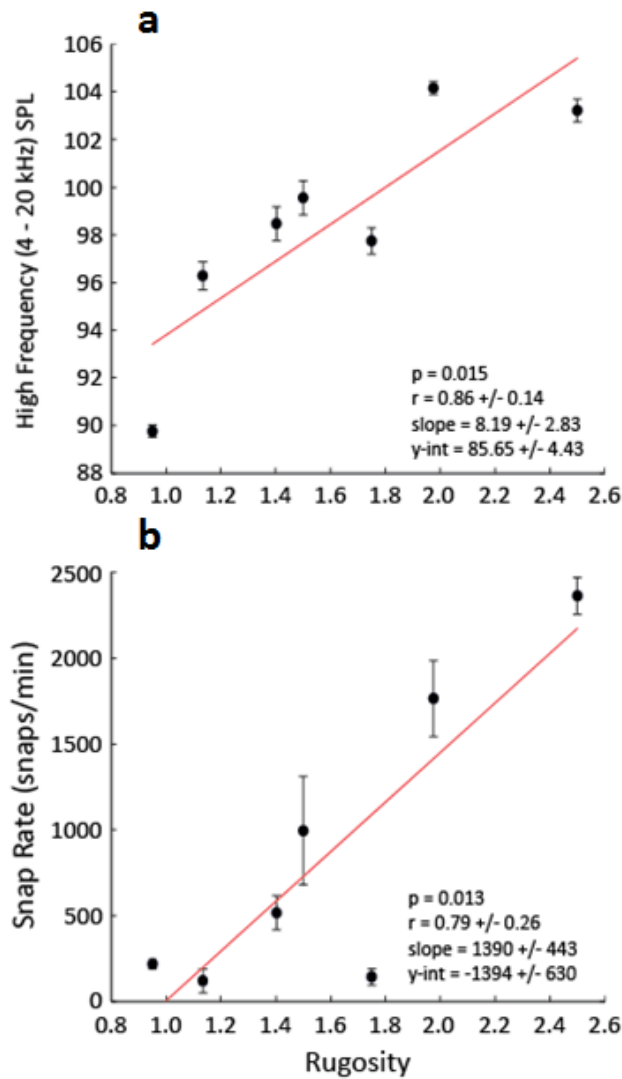
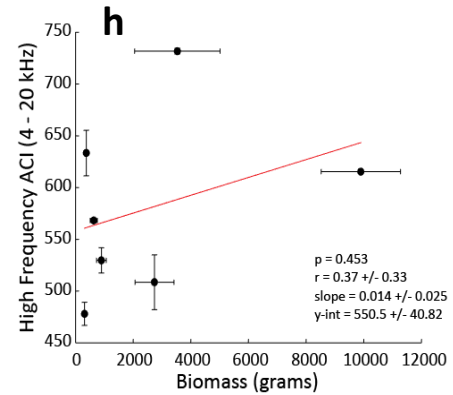
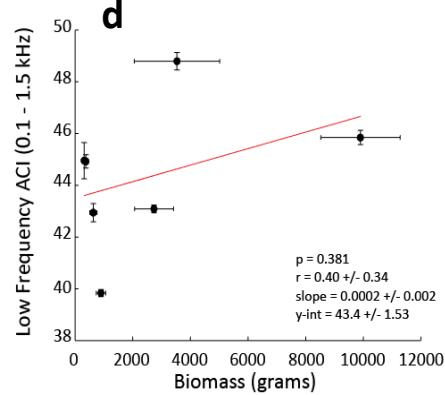
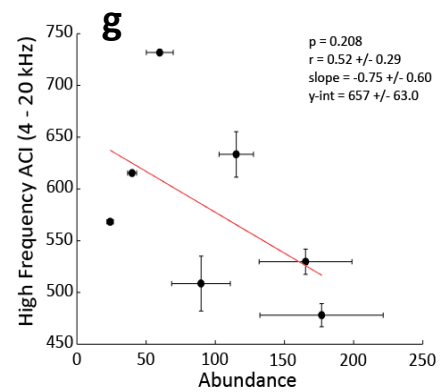
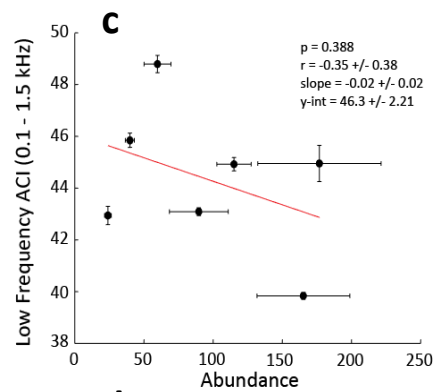
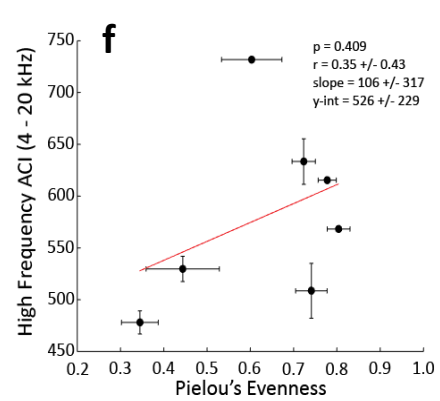
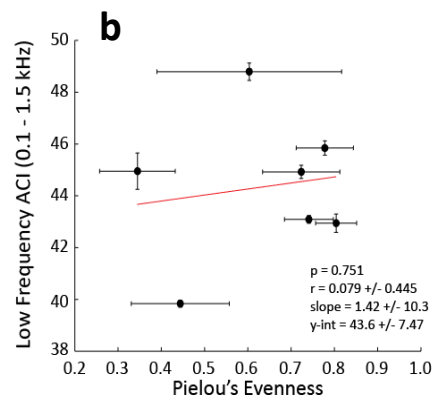
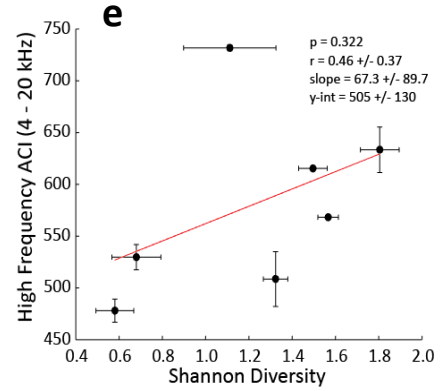
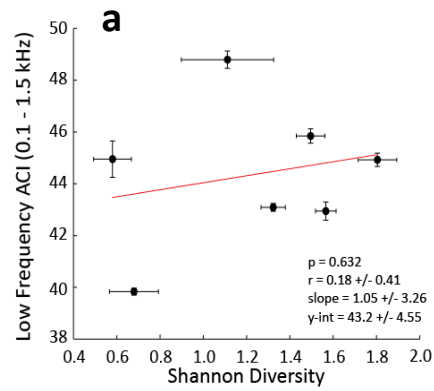


Figure 9. Relationship between median nighttime high frequency (4 – 20 kHz) SPL (dB re 1 μ Pa) (a) and invertebrate snap rate (b) with rugosity for each reef. Error bars represent the uncertainty in the median SPL and snap rate estimated from 10,000 bootstrap samples. Statistical analysis was performed using linear regression models, with uncertainty in correlation coefficient, slope, and intercept determined by bootstrap procedure.

Figure 10. Relationship between median crepuscular low frequency (0.1 – 1.5 kHz) ACI (a – d), median nighttime high frequency (4 – 20 kHz) ACI (e – h), and fish diversity, evenness, abundance, and biomass. Vertical error bars represent the uncertainty in the median ACI estimated from 10,000 bootstrap samples. Horizontal error bars represent the standard error for each fish biodiversity variable. Statistical analysis was performed using linear regression models, with uncertainty in correlation coefficient, slope, and intercept determined by bootstrap procedure.



APPENDIX

Appendix A



Figure A.A.1: Examples of experimental patch reefs used in this study.

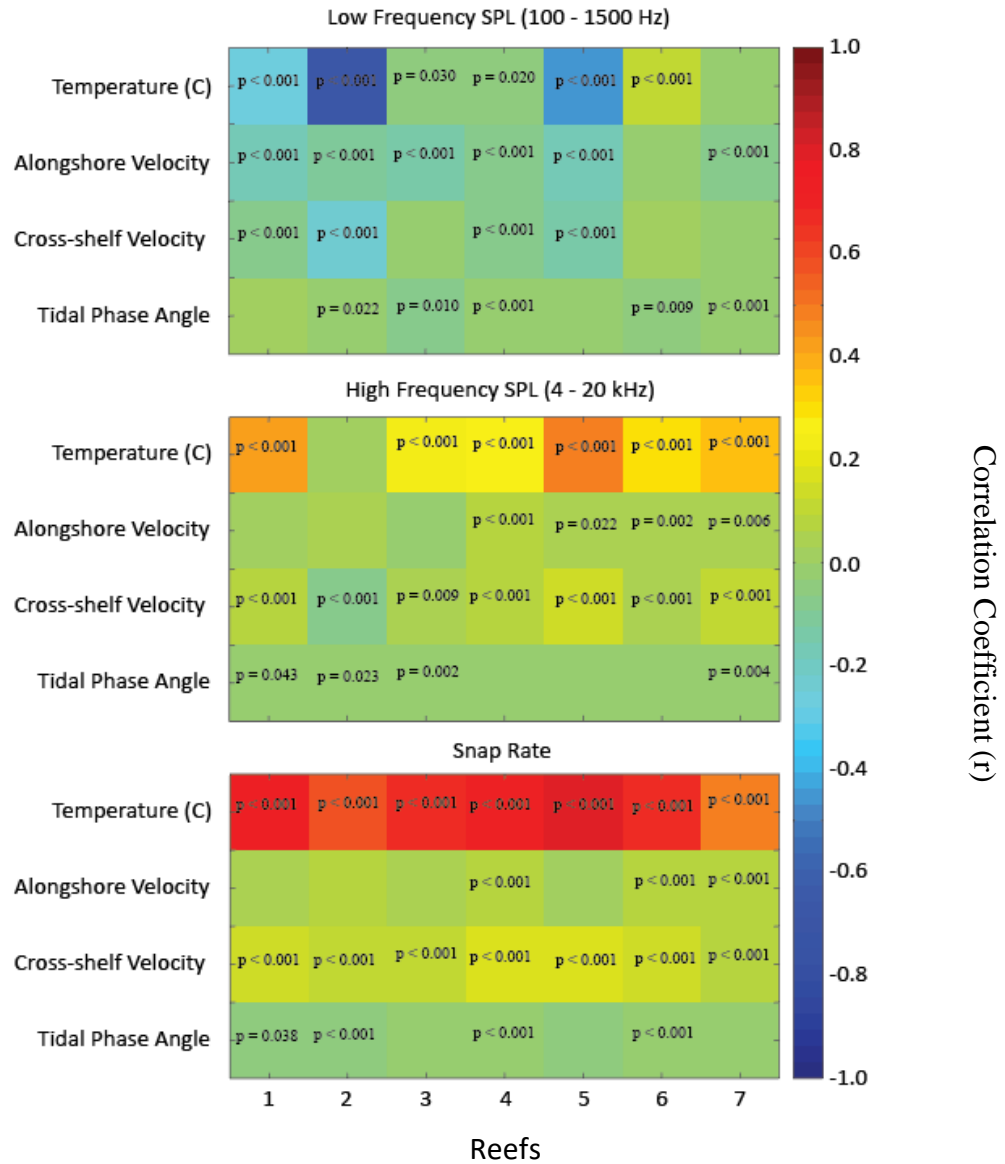


Figure A.A.2: Correlations between environmental variables recorded at or near selected sites and acoustic variables. Water temperature (in °C) was collected from recorders situated at a patch reef located within the Bight of Old Robinson. Wind velocities and tidal data were collected from data recorders in Pelican Harbour, Abaco Island about 3 km away from the Bight of Old Robinson.