

# Fish community structure, habitat complexity, and soundscape characteristics of patch reefs in a tropical, back-reef system

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**ABSTRACT:** Marine soundscapes can provide information on the presence of soniferous species and, in some cases, habitat characteristics and biodiversity of certain marine organisms. Tropical back-reefs functioning as nursery areas provide essential fish habitat for juveniles and sub-adults moving to offshore coral reefs as they grow; yet little is known of underwater soundscapes in these habitats. We characterized the soundscapes of 7 artificial patch reefs within a seagrass-dominated, back-reef embayment in The Bahamas. Hydrophones were deployed at each reef and recorded simultaneously for 2 min every 20 min from March to July 2016. Sound pressure levels (SPLs) and acoustic complexity (ACI) were analyzed for low (0.1–1.5 kHz) and high (4–20 kHz) frequency bands to evaluate sounds produced by marine organisms. Low frequency SPLs associated with fish vocalizations peaked twice per day for some reefs, but showed no relationship with habitat complexity or fish community structure. High frequency SPLs and invertebrate snap rates peaked nightly and were positively correlated with structural rugosity of reefs but not fish community structure. ACI values for both high and low frequency bands showed no associations with habitat complexity or fish community structure. 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 SPLs, and that neither ACI values for low or high frequency bands correlate with fish community structure in areas dominated by juvenile and sub-adult fish.

**KEY WORDS:** Soundscapes · Fish community structure · Habitat complexity · Nursery

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## 1. INTRODUCTION

Hydrophones can detect the presence of sound-producing organisms over extended time periods at high sampling rates that are not possible when using traditional survey techniques such as nets, traps, and visual surveys (Lammers et al. 2008, Sueur et al. 2008). Therefore, monitoring the soundscapes of marine habitats can be a complementary tool for sampling fish and invertebrates (Ricci et al. 2017). Though marine soundscape studies have evaluated sounds

produced by many fish and invertebrates 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 for sound-producing organisms (McCauley & Cato 2000, Au et al. 2012, Staatterman et al. 2014, Kaplan et al. 2015, Ricci et al. 2016). Additionally, connections between underwater soundscape characteristics and fish community variables such as diversity and evenness have been investigated to assess the use of acoustic recordings as a non-invasive

and long-term method of monitoring marine organisms and habitats (Kennedy et al. 2010, Kaplan et al. 2015, Nedelec et al. 2015, Harris et al. 2016). Furthermore, marine soundscape studies show that soundscape characteristics vary among reefs based on habitat quality or benthic composition (i.e. coral and macroalgal cover) (Kennedy et al. 2010, Kaplan et al. 2015, Nedelec et al. 2015, Butler et al. 2017). Though recent studies have found linkages between underwater soundscapes, fish communities, and habitat characteristics for predominantly coral reefs, it is still unclear whether these relationships are present in other marine ecosystems, where a range of habitat structural complexities and different fish communities exist.

Back-reef habitats with a mosaic of seagrass, mangroves, tidal creeks, macroalgal habitats, and patch reefs can act as nurseries facilitating the growth and survival of juvenile fish and invertebrates. These areas often support a relatively high abundance and diversity of sub-adult and adult species in adjacent offshore habitats via ontogenetic migrations from back-reef to offshore habitats (Beck et al. 2001, Eggleston et al. 2004, Adams et al. 2006, Dahlgren et al. 2006, Nagelkerken et al. 2012). Marine soundscape ecology studies looking to attribute acoustic variables with habitat composition have focused on coral reefs and have found increased low frequency sound production with an increase in coral cover (Kaplan et al. 2015, Nedelec et al. 2015). Only recently, however, have related studies examined the relationship between habitat characteristics such as structural rugosity and associated soundscapes (Kaplan et al. 2018). Artificial patch reefs, consisting of concrete blocks, have been used to evaluate fish community responses to variations in habitat composition and complexity (Hixon & Beets 1989, Beets & Hixon 1994, Eggleston et al. 1997). Additionally, fish of significant ecological and commercial importance like Nassau grouper *Epinephelus striatus* are associated with both natural and artificial patch reefs while undergoing several ontogenetic shifts from early to late juvenile development (Eggleston 1995, Eggleston et al. 1997). We are unaware of any studies that have characterized the soundscapes of patch reefs within a seagrass dominated, back-reef habitat that is used as a nursery.

The goals of this study were to (1) characterize diel variation in soundscapes associated with artificial patch reefs of varying habitat complexity to determine times of biological activity, and (2) determine potential relationships between artificial patch reef soundscape variables and habitat complexity and fish community structure.

## 2. MATERIALS AND METHODS

### 2.1. Overview

A total of 7 artificial patch reefs of varying structural complexity served as the experimental units in this study. Fish community structure, habitat complexity characteristics, and the underwater soundscape were quantified at each artificial patch reef between March and July 2016. Habitat characteristics consisted of measures of structural rugosity of each artificial patch reef, as well as the density of the seagrass surrounding each reef. Fish community structure measures consisted of (1) fish species diversity, (2) evenness, (3) total biomass, and (4) abundance. Soundscape characterization consisted of measures of sound pressure levels (in dB re 1  $\mu$ Pa), invertebrate snap rates, and acoustic complexity. All statistical analyses were performed in MATLAB 2014a (MathWorks) with  $\alpha = 0.05$  for all statistical tests.

### 2.2. Study site

Habitat characteristics, fish community structure, and soundscape patterns were characterized at 7 artificial patch reefs within the Bight of Old Robinson, a semi-enclosed seagrass-dominated embayment on Abaco Island, The Bahamas (Fig. 1). Habitats within the Bight of Old Robinson are comprised of seagrass, sand, hard-bottom, rocky outcroppings, and patch reefs (Allgeier et al. 2011, Yeager et al. 2011, Layman & Allgeier 2012). Artificial patch reefs were built for research purposes more than 4 yr before the beginning of this study, and were made of concrete blocks that were either well-stacked or haphazardly piled (Yeager et al. 2011, Allgeier et al. 2013, 2018, Layman et al. 2013, 2016) (Fig. 2). Water depths at low tide varied from 1.3 to 3.9 m with tides varying water depth by  $\sim 0.5$  m (Table 1). Artificial patch reefs ranged in number of blocks from 8 to 84 (Table 1). Reef soundscape recordings were considered acoustically independent when  $>400$  m apart (Lillis et al. 2014). Of the seagrass species found around these reefs, *Thalassia testudinum* was the most abundant, followed by *Syringodium filiforme* and *Halodule wrightii* (Allgeier et al. 2013, 2018, Layman et al. 2013, 2016). Reefs 6 and 7 had been subjected to nutrient addition studies in prior years which resulted in increased seagrass density (Allgeier et al. 2018). Artificial patch reefs selected for this study were located approximately 1.2 to 2.3 km

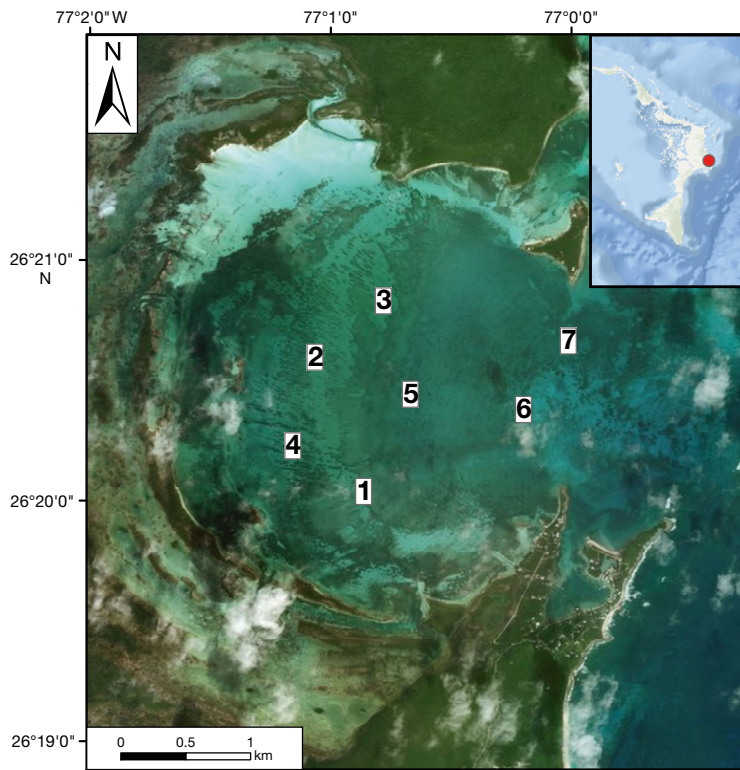


Fig. 1. Locations of 7 artificial patch reefs situated within the Bight of Old Robinson, Abaco Island, The Bahamas. Patch reefs are numbered 1 to 7 in order of least to most structurally complex

northwest of Little Harbour and directly east of a mosaic of tidal creeks and mangroves (Fig. 1) that provide essential habitat for sub-adult and juvenile fish making ontogenetic shifts to offshore reefs (Zapata et al. 2014, Huijbers et al. 2015).

### 2.3. Patch reef rugosity and seagrass characteristics

Reef rugosity and seagrass densities were measured during May 2016. The rugosity of each artificial patch reef was measured using a chain method (Luckhurst & Luckhurst 1978, Gratwicke & Speight 2005). Divers measured the length and width of each individual 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 & 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 reef and the average of length and width rugosity was used.

Seagrass density was calculated by counting the number of short-shoots within three 0.1 m<sup>2</sup> quadrats

at distances of 1 and 4 m away from each reef. These counts were repeated in 3 randomly chosen directions from a given reef, such that mean counts were based on  $n = 3$ . Distances of 1 and 4 m 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 m away) compared to 3 to 4 m away (Layman et al. 2013, 2016).

Differences in the mean density of seagrass between 1 and 4 m away from patch reefs, which could influence the presence of fish on a reef, were tested with a 1-way ANOVA model. Seagrass density measures were normally distributed with equal variances (Bartlett's test,  $T > 14.1$ ,  $p < 0.028$ ). 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 (Family Alpheidae) that contribute to the high frequency aspect of marine soundscapes prefer hard-bottom structure such as coral and oyster reefs over seagrass meadows and unstructured bottom (Williams 1984, Glancy et al.

2003, Lillis et al. 2014). Artificial patch reefs were ordered from least to most complex based on the mean ranks of structural rugosity, seagrass density at 1 m, and seagrass density at 4 m (Table 1). We initially used principal component analysis (PCA) to determine the variation among habitat variables (rugosity, seagrass density, etc.) in an attempt to find which habitat variables accounted for the most variation among reefs. After running the PCA, we found that seagrass density at both distances and rugosity contributed similarly in defining the first principal component, and subsequently used these 3 variables to rank habitat complexity.

### 2.4. Fish biodiversity

Visual surveys of reef fish residing on artificial patch reefs were conducted by SCUBA divers during 7 different sampling days between February and May 2016 ( $n = 7$  for each reef) (see Table 2). During each visual survey, fish were counted by a diver that was positioned approximately 3 m away from the reef, with counts made during daylight (12:00 to 15:00 h EST) when water visibility was greater than 10 m.

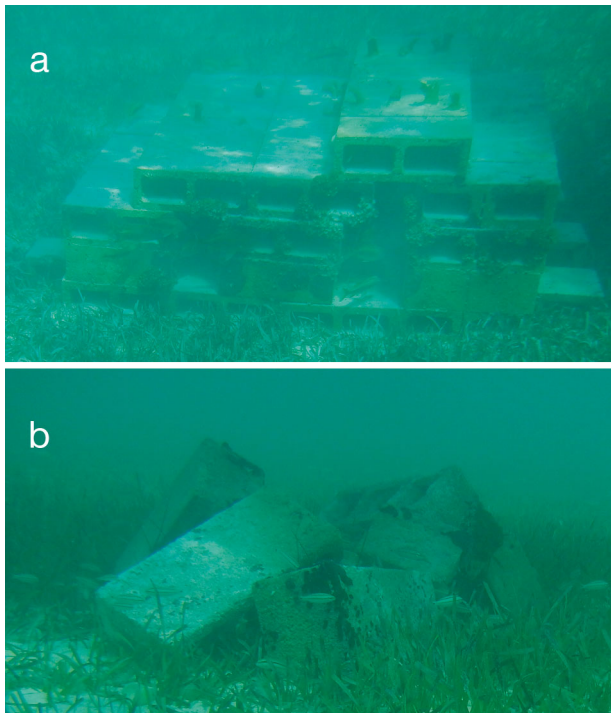


Fig. 2. Examples of 2 artificial patch reefs used in this study. (a) Reef 1 is less structurally complex, whereas (b) reef 5 is a more structurally complex reef

Fish total length (TL; 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 min survey. Data from visual fish surveys were used to generate the following fish community variables: (1) Shannon diversity, (2) Pielou's evenness, (3) abundance, and (4) total biomass. The following equation was used to determine the relationship between fish length and biomass:

$$W = aL^b \quad (1)$$

where  $a$  and  $b$  values are species-specific constants derived from online databases ([www.fishbase.de/](http://www.fishbase.de/)),  $L$  is fish total length, and  $W$  is weight (in g) (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 community variable, the data from each artificial patch reef were averaged over the 7 visual surveys. The relationship between fish community variables, habitat complexity characteristics, and soundscape metrics was tested with linear least-squares regression models. Fish community structure among reefs of varying habitat complexity was evaluated with Kruskal-Wallis tests, and Tukey-Kramer post hoc tests were used to identify differences among individual patch reefs.

## 2.5 Acoustic sampling

Underwater sounds associated with each artificial patch reef were monitored simultaneously using hydrophones (SoundTrap ST300; Ocean Instruments New Zealand). Hydrophones were secured vertically on metal poles ~0.5 m above the seafloor and positioned 1.5 m away from the base of each patch reef, which represents a small (1 to 2 m diameter) isolated area of relief within the embayment (Table 1, Figs. 1 & 2). Standardizing the position of each hydrophone at such a short range from the structure (1.5 m = 1 acoustic wavelength at 1000 Hz) minimized any impact variable water depths may have had on the transmission of sound between the reef and the hydrophone.

Recordings were collected in 2 deployments: (1) 29 February to 24 May, and (2) 31 May to 1 August 2016, with gaps in the data representing times where hydrophones were not recording due to maintenance

Table 1. Habitat complexity variables and reef characteristics for 7 concrete block artificial patch reefs. Values for rugosity and seagrass density were evaluated between 24 and 31 May 2016. Seagrass density ( $n = 3$ ) is reported as mean ( $\pm$  SE) number of shoots  $m^{-2}$ . Mean ranks were calculated based on rugosity, seagrass density at 1 m, and seagrass density at 4 m

Reef	Latitude (°N)	Longitude (°W)	Depth (m)	Length $\times$ width (m)	No. of blocks	Rugosity	Seagrass density at 1 m ( $m^{-2}$ )	Seagrass density at 4 m ( $m^{-2}$ )	Mean rank
1	26.3324	77.0154	1.3	2.5 $\times$ 1.25	9	0.95	567 $\pm$ 51	456 $\pm$ 62	1.3
2	26.3432	77.0166	2.0	2 $\times$ 1.75	27	1.13	656 $\pm$ 106	444 $\pm$ 222	2.0
3	26.3458	77.0141	2.2	1 $\times$ 1.25	8	1.75	622 $\pm$ 44	578 $\pm$ 40	3.7
4	26.3387	77.0183	1.7	2 $\times$ 1.75	36	1.40	733 $\pm$ 77	611 $\pm$ 87	4.0
5	26.3423	77.0103	3.1	2 $\times$ 1.25	84	1.98	867 $\pm$ 217	500 $\pm$ 51	4.7
6	26.3410	77.0043	3.9	1 $\times$ 1	20	1.50	1011 $\pm$ 11	656 $\pm$ 73	5.3
7	26.3458	77.0012	3.6	1 $\times$ 0.75	30	2.50	1256 $\pm$ 139	867 $\pm$ 102	7.0



and data downloading (from 25 to 30 May). Hydrophones were set to record for 2 min every 20 min with a sample rate of 96 kHz throughout both deployments. 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, was then applied before decimation. Therefore, the useable (−3 dB) bandwidth of these recordings was 0.020 to 43.0 kHz.

## 2.6. Acoustic analysis

All 2 min recordings were processed in MATLAB 2014a using purpose-written code. These recordings were analyzed into low (0.1 to 1.5 kHz) and high (4 to 20 kHz) frequency bands. The low frequency band was selected to capture sounds from tropical reef fish, such as those from the families Haemulidae, Lutjanidae, and Serranidae (Fish & 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 (Cato & Bell 1992).

The mean spectrum was calculated for each 2 min recording (number of points used in the fast Fourier transform [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 artificial patch reefs 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 to 20 kHz frequency band, where snaps 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  $\mu$ 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 zero-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 reefs while Wilcoxon rank-sum tests were used for temporal comparisons of snap rates.

The acoustic complexity index (ACI) has been used previously in marine soundscape research as an eco-acoustic metric for call diversity of fishes, and it measures the variation in the acoustic spectrum in time and frequency (Pieretti et al. 2011, McWilliam & Hawkins 2013, Staatterman et al. 2014, Sueur et al. 2014, Harris et al. 2016). ACI was calculated for four 30 s duration segments, which were then averaged for each 2 min recording. These calculations used a window length of 4096 points with 0 % overlap ( $\Delta f = 23.44$  Hz,  $\Delta t = 0.043$  s), and were performed in the 2 frequency bands: low (0.1 to 1.5 kHz) and high (4 to 20 kHz). Kruskal-Wallis tests determined if ACI values varied significantly among artificial patch reefs.

Potential relationships between habitat complexity, fish community structure, and soundscape data were evaluated with correlation models. For example, low frequency (0.1 to 1.5 kHz) soundscape metrics from vocalizing fish, such as SPLs and ACI, were correlated with fish community variables, as well as potential relationships between high frequency (4 to 20 kHz) soundscape metrics, such as SPL and ACI, and snap rates. Correlation models were used to determine potential relationships between snap rates and fish community, as well as between soundscape metrics and habitat complexity.

Hourly water temperature data were collected from a single recorder (HOBO Pendant) mounted on a PVC pipe at reef 5. Sunrise and sunset times were obtained from the United States Naval Observatory website ([www.usno.navy.mil/USNO/](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 to 1.5 kHz) SPLs and ACI pertaining to crepuscular hours bracketed the period of 1 h before and 1 h after sunset or sunrise. Lunar phase information was derived from percent illumination data obtained from the United States Naval Observatory website. All times were set to Eastern Standard Time for this analysis.

## 3. RESULTS

For the results below, we focused first on temporal patterns in the soundscape, which are necessary to identify what soundscape data to use in analyzing spatial patterns. For example, peaks in low frequency (0.1 to 1.5 kHz) SPLs were observed around sunrise and sunset for some reefs. Thus, for all spatial comparisons involving low frequency sounds associated with fish vocalizations, we analyzed SPLs

and ACI for soundscape recordings during crepuscular periods. Spatial comparisons involving high frequency (4 to 20 kHz) SPLs, ACI, and invertebrate snap rates were considered separately for nighttime and daytime recording periods. In each section below, we describe the relationships among habitat complexity, fish community structure, and the soundscape.

### 3.1. Temporal patterns in acoustic time series

Crepuscular peaks in low frequency (0.1 to 1.5 kHz) SPLs were present at reefs 5 and 7 (Fig. 3a), and nightly peaks in high frequency (4 to 20 kHz) SPLs were present at all reefs (Fig. 3b). In total, 3 of 7 reefs displayed significantly higher SPLs at low frequencies during crepuscular periods compared to all other times (Wilcoxon rank sum,  $Z > 2.9$ ,  $p < 0.004$ ) (Fig. 4a). High frequency SPLs were significantly higher at

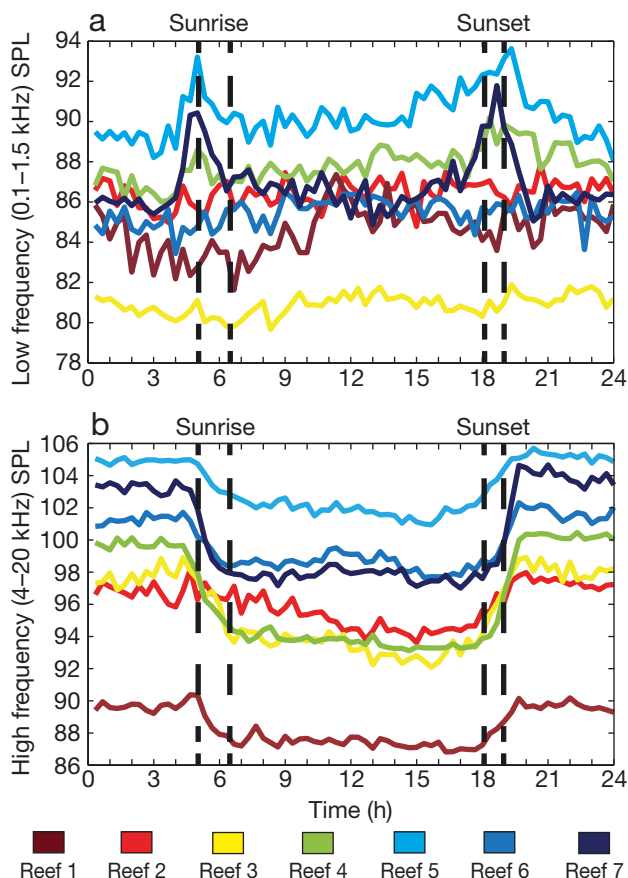


Fig. 3. Median daily sound pressure levels (SPLs) (dB re 1  $\mu$ Pa) in the (a) low (0.1–1.5 kHz) and (b) high (4–20 kHz) frequency bands for each patch reef. Vertical dashed lines: ranges of sunset and sunrise times

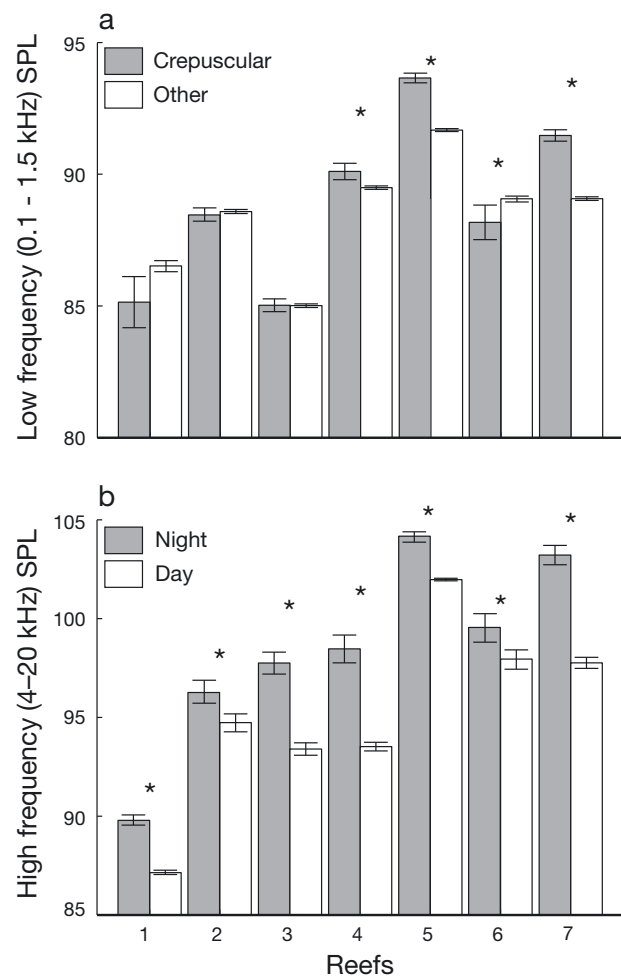


Fig. 4. Median sound pressure level (SPL) (dB re 1  $\mu$ Pa) in the (a) low (0.1–1.5 kHz) and (b) high (4–20 kHz) frequency bands at specific times of day for each reef. SPLs during 2 different time periods for each reef were compared using Wilcoxon rank-sum tests. Error bars: uncertainty in the median SPL estimated from 10 000 bootstrap samples. Significant differences between time periods for each reef are represented by asterisks

night than during the day for all reefs (Wilcoxon rank sum,  $Z > 4.5$ ,  $p < 0.001$ ) (Fig. 4b). Low frequency SPLs did not vary significantly with lunar cycle (Kruskal-Wallis,  $p = 0.47$ ) (Fig. S1a in the Supplement at [www.int-res.com/articles/suppl/m609p033\\_supp.pdf](http://www.int-res.com/articles/suppl/m609p033_supp.pdf)) and exhibited little ( $< 1$  dB re 1  $\mu$ Pa) seasonal (March to July) change (linear regression,  $p < 0.001$ ) (Fig. S2a).

Snap rates also were consistently higher at night than during the day, with pronounced shifts in snap rates occurring during crepuscular periods (Wilcoxon rank sum,  $Z > 4.8$ ,  $p < 0.001$ ) (Fig. 5). High frequency (4 to 20 kHz) SPLs were positively correlated with snap rates for all reefs ( $r = 0.27$ – $0.66$ ,  $p < 0.001$ )

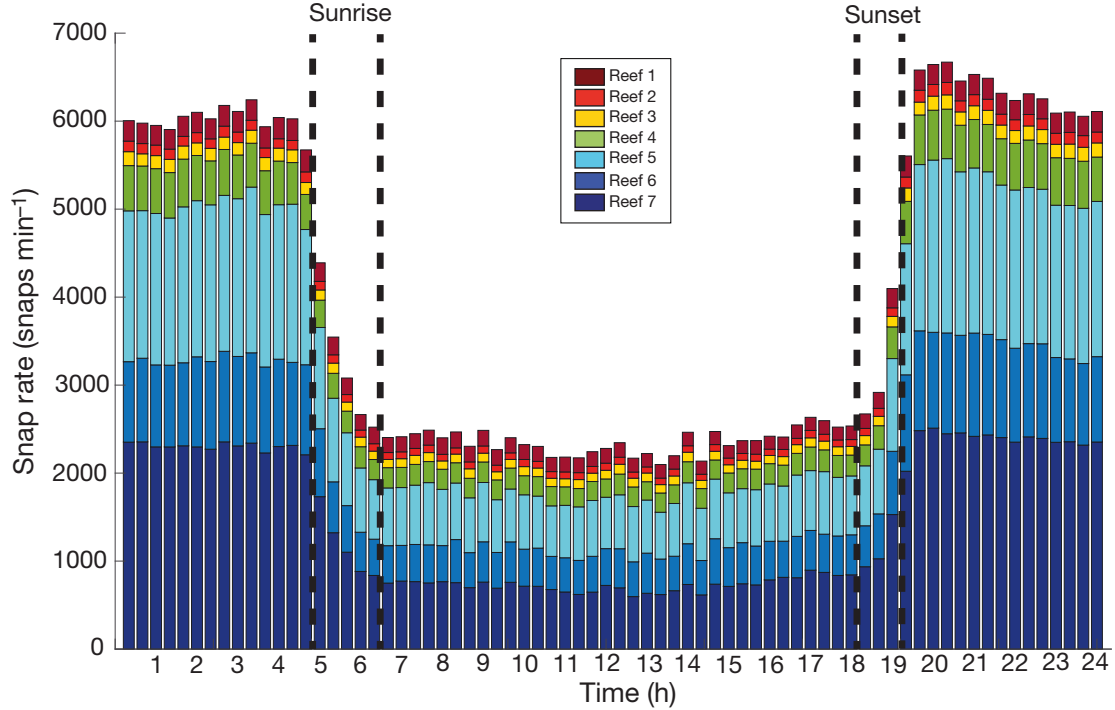


Fig. 5. Median invertebrate snap rate for each patch reef based on the times of each recording in a day. Bars: median snap rates for each recording time over each day; vertical dashed lines: ranges of sunset and sunrise times

(Fig. 6a). High frequency ACIs also were correlated positively with rates  $< \sim 750$  snaps  $\text{min}^{-1}$  (linear regression,  $r = 0.49\text{--}0.84$ ,  $p < 0.001$ ); however, the relationship saturates and then rolls off at higher rates—and is better modeled empirically as a convex second order polynomial (Fig. 6b).

The high frequency band SPLs did not vary significantly with lunar cycle (Kruskal-Wallis,  $p = 0.85$ ) (Fig. S1b) but did increase slightly ( $< \sim 3$  dB re  $1 \mu\text{Pa}$ )

over the period between May and July 2016 (linear regression,  $p < 0.001$ ) (Fig. S2b). This long-term increase is consistent with higher snap rates in response to a seasonal increase in water temperature (e.g. Bohnenstiehl et al. 2016, Lillis & Mooney 2018); however, given that the sites were separated by  $< 2$  km (Fig. 1), sustained difference in water temperatures are unlikely and therefore this environmental variable cannot explain spatial variation in SPLs.

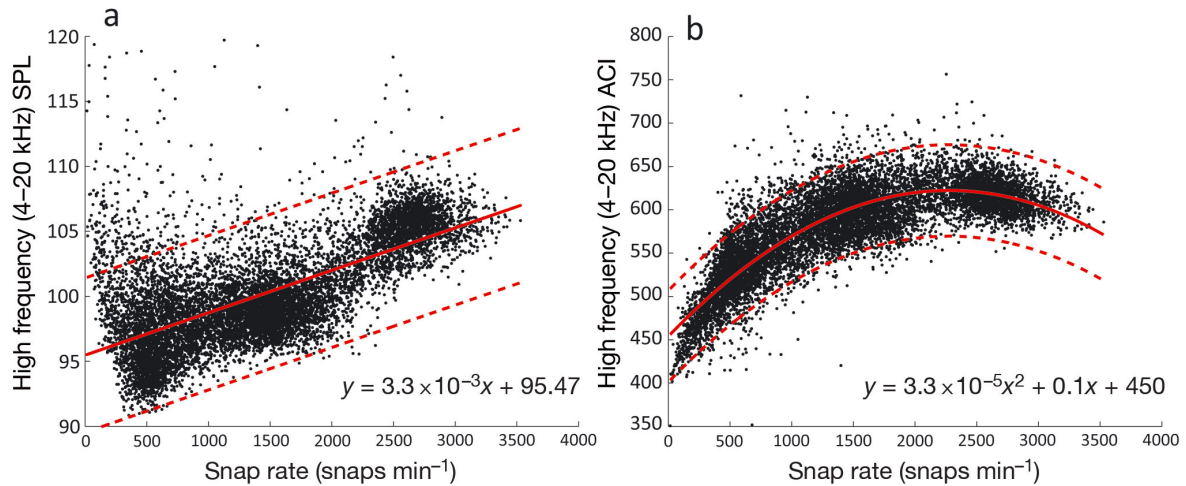


Fig. 6. Relationship between invertebrate snap rates from each recording and (a) high frequency (4–20 kHz) sound pressure levels (dB re  $1 \mu\text{Pa}$ ) and (b) acoustic complexity for reef 7. Statistical analysis was performed using linear regression models for (a) and second order polynomial models for (b). Dashed lines are 95% CI for the fitted models. Uncertainty in the model parameters was calculated using 10 000 bootstrap samples. Uncertainty for model parameters in (a):  $4.1 \times 10^{-5}$ , 0.076. Uncertainty for model parameters in (b):  $4.0 \times 10^{-7}$ , 0.001, 0.958

### 3.2. Spatial variation in habitat complexity, fish biodiversity, and soundscape metrics

#### 3.2.1. Habitat complexity

Artificial patch reefs varied in their rugosity, as well as the surrounding mean density of seagrass (1 and 4 m distances from the reef). Seagrass density increased in a statistically significant manner with increasing reef rugosity—this pattern was slightly stronger for seagrass measured at 1 m from the reef ( $r = 0.72 \pm 0.26$ ,  $p = 0.033$ ) than at 4 m ( $r = 0.67 \pm 0.36$ ,  $p = 0.041$ ) (Fig. 7). Mean seagrass density was significantly higher at 1 m distances from the reef compared to 4 m (nested, 1-way ANOVA,  $F_{7,28} = 2.88$ ,  $p = 0.021$ ). Reefs 3, 5, and 7 had the highest rugosity (Fig. 7a), and mean seagrass densities varied significantly based on reef complexity (1-way ANOVA,  $F_{6,20} = 4.84$ ,  $p = 0.007$ ) with the highest seagrass density at reef 7 at 1 m distance from the reef (Tukey-Kramer,  $p < 0.05$ ) (Fig. 7b). Conversely, reef 1 had the lowest rugosity and the lowest mean seagrass density at 1 m distance (Fig. 7). Seagrass densities at 4 m distances were not significantly different among reefs (1-way ANOVA,  $F_{6,20} = 1.86$ ,  $p = 0.1572$ ).

#### 3.2.2. Fish community structure

Fish community variables varied significantly among reefs, with more complex reefs tending to have higher Shannon diversity and biomass, while less complex reefs had higher fish abundances. The most abundant fish species were from families Haemulidae, Scaridae, and Labridae with large schools (>100 ind.) of small (<5 cm TL) French and tomtate grunts (*Haemulon flavolineatum* and *H. aurolineatum*, respectively) being frequently observed. Average Shannon diversity varied significantly from reef to reef (Kruskal-Wallis,  $F_{6,48} = 35.32$ ,  $p < 0.001$ ), with reefs 4, 6, and 7 having higher average diversity than reefs 1 and 3 (Tukey-Kramer,  $p < 0.05$ ) (Table 2). Average fish evenness also varied significantly (Kruskal-Wallis,  $F_{6,48} = 29.62$ ,  $p < 0.001$ ) and was highest for reefs 6 and 7, and lowest for reefs 1 and 3 (Tukey-Kramer,  $p < 0.05$ ) (Table 2). Average fish abundance varied significantly among reefs (Kruskal-Wallis,  $F_{6,48} = 34.32$ ,  $p < 0.001$ ) and varied in-

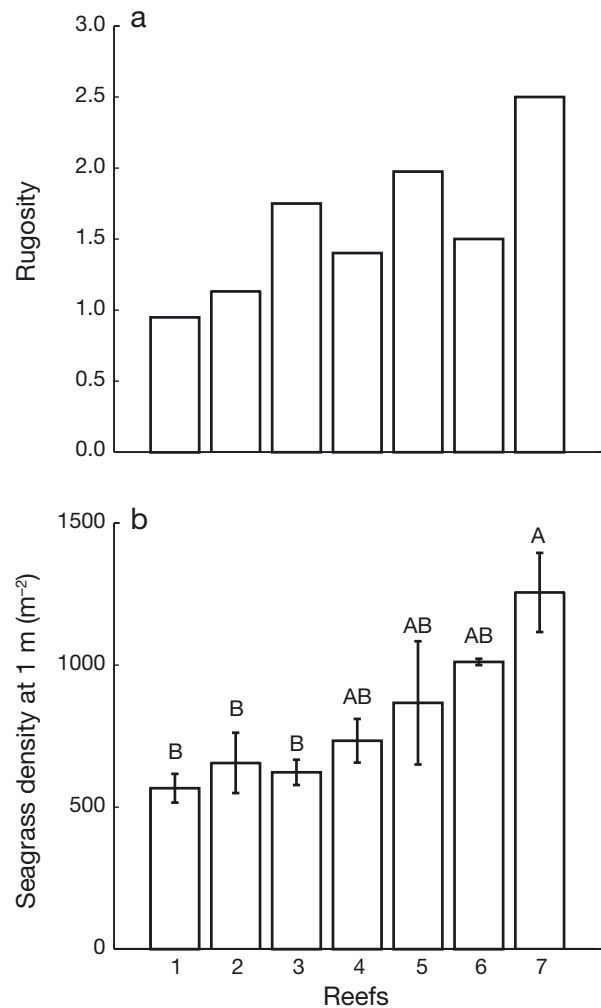


Fig. 7. (a) Rugosity and (b) mean seagrass density at 1 m for each reef. Error bars: SE for seagrass density at 1 m ( $n = 3$ ). A 1-way ANOVA with Tukey-Kramer post hoc tests was used to differentiate reefs based on seagrass density. Letters above each bar: statistical differences between reefs (from 1-way ANOVA and Tukey-Kramer post hoc test); reefs that do not share the same letter are significantly different from each other

Table 2. Mean ( $\pm$ SE) values for fish diversity, evenness, abundance, biomass, and total length for each reef. Values were derived from 7 visual fish surveys between February and June 2016. Surveys were performed on 26 Feb, 1, 3, and 6 March, and 13, 26 and 27 May

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



versely with Shannon diversity indices, with reefs 1 and 3 having higher average fish abundance than reefs 6 and 7 (Tukey-Kramer,  $p < 0.05$ ) (Table 2). Reef 5 had the highest average total biomass and there was no significant difference in average total biomass among all other reefs (Kruskal-Wallis:  $F_{6,28} = 39.56$ ,  $p < 0.001$ ) (Table 2).

### 3.2.3. Soundscape variables

Generally, more complex artificial patch reefs had higher median values for all soundscape variables (SPLs, ACI, snap rate); this pattern was stronger for high frequency variables compared to low frequency. In terms of spatial variation in the soundscape, reefs differed significantly based on low frequency SPLs (Kruskal-Wallis,  $\chi^2 = 516.85$ ,  $p < 0.001$ ) with reefs 4, 5, and 7 having the highest crepuscular, low frequency SPLs (0.1 to 1.5 kHz) compared to other reefs (Tukey-Kramer,  $p < 0.05$ ) (Fig. 8a). At all other times, low frequency SPLs varied significantly among reefs (Kruskal-Wallis,  $\chi^2 = 6311.35$ ,  $p < 0.001$ ) with reef 5 having the highest low frequency SPLs (Tukey-Kramer,  $p < 0.05$ ). For crepuscular low frequency ACI, values varied significantly among reefs (Kruskal-Wallis,  $\chi^2 = 615.03$ ,  $p < 0.001$ ) with reef 5 having the highest values followed by reefs 1, 4, and 7 (Tukey-Kramer,  $p < 0.05$ ) (Fig. 8b). Nighttime high frequency (4 to 20 kHz) SPLs varied significantly among reefs (Kruskal-Wallis,  $\chi^2 = 673.68$ ,  $p < 0.001$ ) and were highest for reefs 5, 6, and 7 (Tukey-Kramer,  $p < 0.05$ ) (Fig. 9a). Daytime high frequency SPLs also varied significantly among reefs (Kruskal-Wallis,  $\chi^2 = 823.09$ ,  $p < 0.001$ ) and showed similar spatial patterns between reefs as nighttime high frequency SPLs (Tukey-Kramer,  $p < 0.05$ ). High frequency ACI varied significantly among reefs (Kruskal-Wallis,  $\chi^2 = 602.61$ ,  $p < 0.001$ ) and reefs 4, 5, and 7 had the highest nighttime high frequency ACI (Tukey-Kramer,  $p < 0.05$ ) (Fig. 9b). Nighttime snap rates varied significantly from reef to reef (Kruskal-Wallis,  $\chi^2 = 624.18$ ,  $p < 0.001$ ) and were highest for reefs 5, 6, and 7 (Tukey-Kramer,  $p < 0.05$ ) (Fig. 9c). Daytime snap rates varied significantly among reefs (Kruskal-Wallis,  $\chi^2 = 586.70$ ,  $p < 0.001$ ) being highest for reefs 5, 6, and 7 (Tukey-Kramer,  $p < 0.05$ ).

### 3.3. Relationships between fish community structure and habitat complexity

There was a negative and statistically significant correlation between mean fish abundance per patch

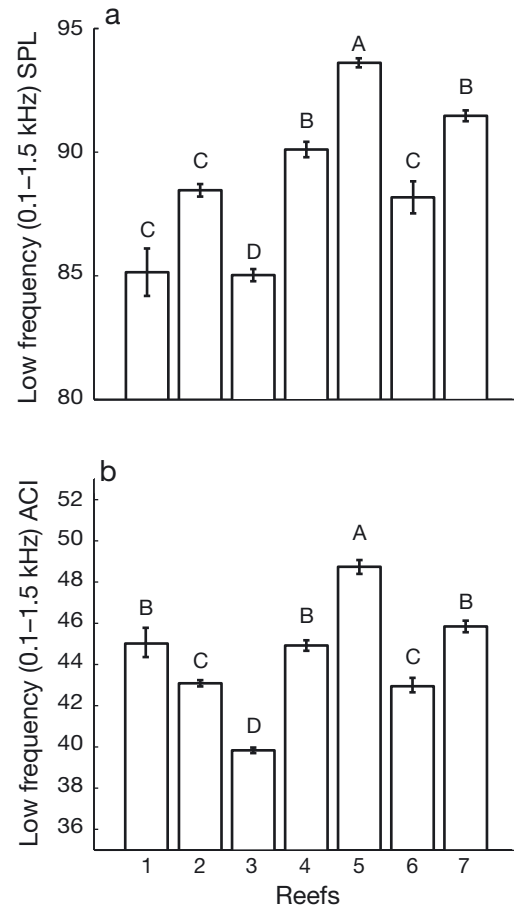


Fig. 8. Median, crepuscular, low frequency (0.1–1.5 kHz) (a) sound pressure levels (SPLs) (dB re 1  $\mu$ Pa) and (b) acoustic complexity (ACI) for each reef. Soundscape metrics at crepuscular hours were chosen because acoustic biological activity was highest for low frequencies at these times. Error bars: uncertainty in the median SPL and ACI estimated from 10 000 bootstrap samples. Differences among reefs 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

reef and seagrass density at 1 m 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 Shannon diversity, evenness, or total biomass and any habitat variables (linear regression, all  $p > 0.110$ ).

### 3.4. Relationships between habitat complexity, fish community structure, and acoustic variables

Some marine soundscape studies have suggested that SPLs and ACI may be positively correlated with

habitat complexity and fish biodiversity (e.g. Bertucci et al. 2016, Harris et al. 2016). In contrast to expectations, neither median low frequency (0.1 to 1.5 kHz) SPLs recorded during crepuscular periods, nor ACI were correlated with any habitat complexity or fish community variables (linear regression, all  $p > 0.072$ ) (Fig. 10). There were, however, significant correlations between habitat complexity and high frequency (4 to 20 kHz) soundscape variables. For example, at high frequencies, median nighttime SPLs were positively correlated with reef rugosity ( $r = 0.86 \pm 0.14$ ,  $p = 0.015$ ) (Fig. 11a). Median nighttime high frequency SPLs were not correlated with average Shannon diversity, evenness, or biomass (linear regression, all  $p > 0.145$ ). Nighttime high frequency ACI values were not correlated with any of the habitat complexity or fish community variables (linear regression, all  $p > 0.068$ ) (Fig. 10). Median nighttime snap rates were positively correlated with rugosity ( $r = 0.79 \pm 0.26$ ,  $p = 0.013$ ) (Fig. 11b). Nighttime invertebrate snap rate was not significantly correlated with average fish diversity, evenness, abundance, or biomass (linear regression, all  $p > 0.064$ ).

#### 4. DISCUSSION

This study investigated spatiotemporal variation in artificial patch reef soundscapes and the potential relationships with selected habitat characteristics and the associated fish community. 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? In this study, there are 2 general answers: (1) no, the low frequency sounds that might be produced by fish did not correlate with the fish community or the rugosity and seagrass density of artificial patch reefs, and (2) yes, invertebrate snaps (likely associated with snapping shrimp) were positively correlated with structural rugosity. SPLs in the low frequency band (0.1 to 1.5 kHz), indicative of reef fish vocalizations, peaked twice per day at 3 of the most complex sites around sunrise and sunset; however, the relationships between habitat and low frequency SPLs and ACI were not significant. SPLs in the high frequency band (4 to 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 community structure. High frequency SPLs and snap rates were significantly correlated

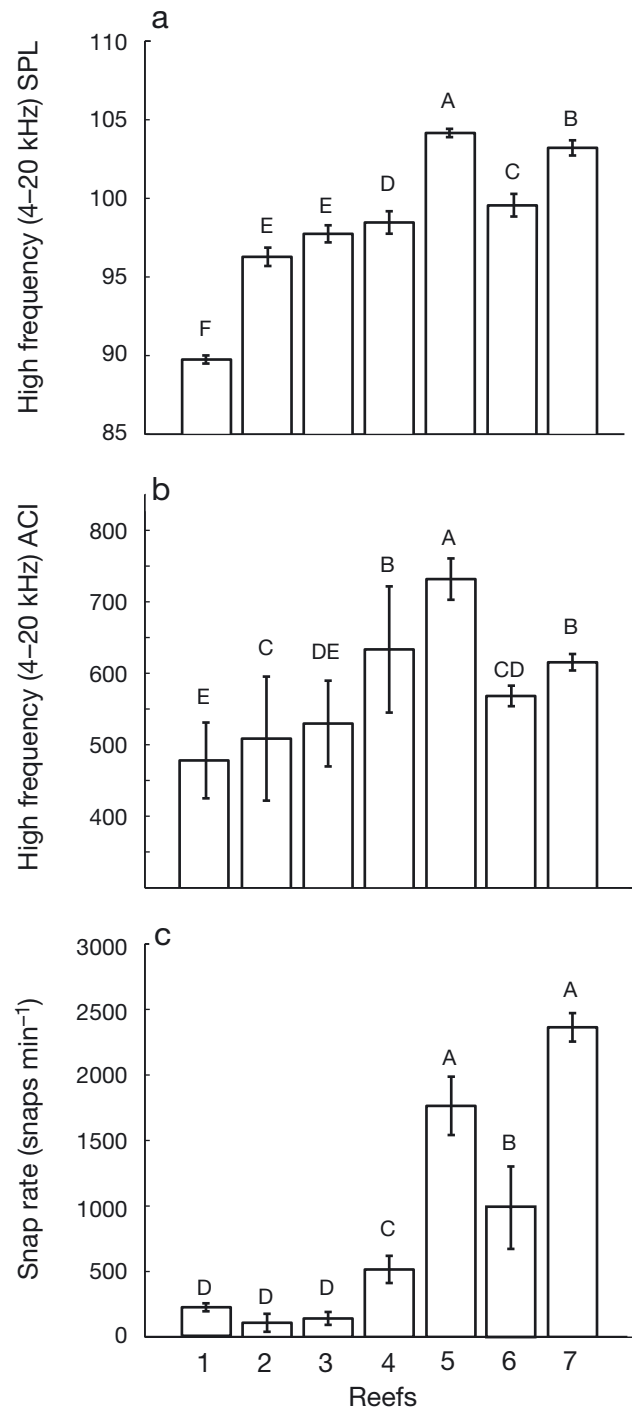


Fig. 9. Median nighttime, high frequency (4–20 kHz) (a) sound pressure levels (SPLs) (dB re 1  $\mu$ Pa) (b) acoustic complexity (ACI), and (c) snap rate for each reef. Soundscape metrics at nighttime were chosen because acoustic biological activity was highest for high frequencies at these times. Error bars: uncertainty in the median SPL, ACI, and snap rate estimated from 10 000 bootstrap samples. Differences among reefs 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

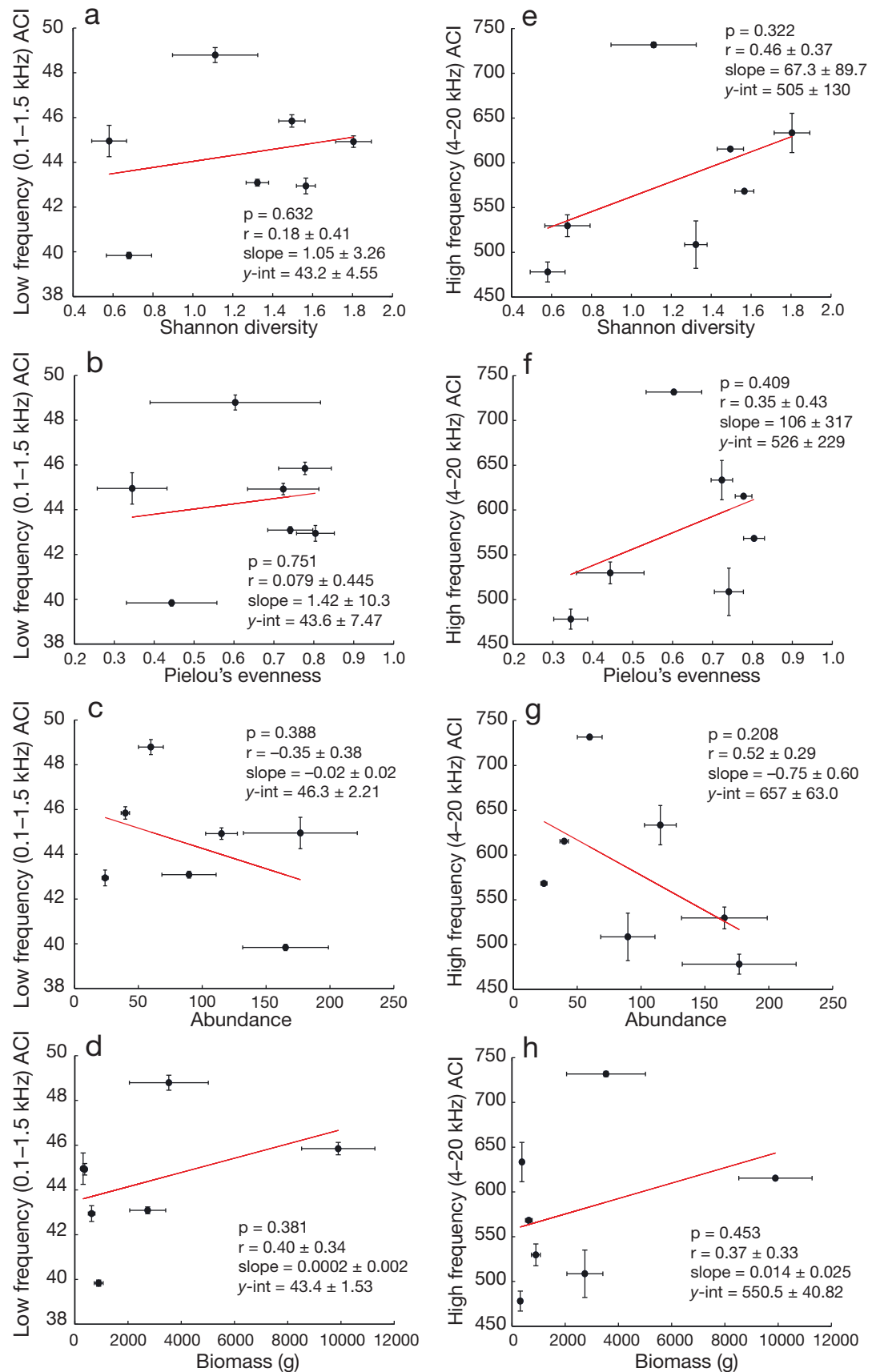


Fig. 10. Relationship between (a–d) median crepuscular low frequency (0.1–1.5 kHz) acoustic complexity (ACI) and (e–h) median nighttime high frequency (4–20 kHz) ACI, and fish diversity, evenness, abundance, and biomass. Vertical error bars: uncertainty in the median ACI estimated from 10 000 bootstrap samples. Horizontal error bars: SE 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

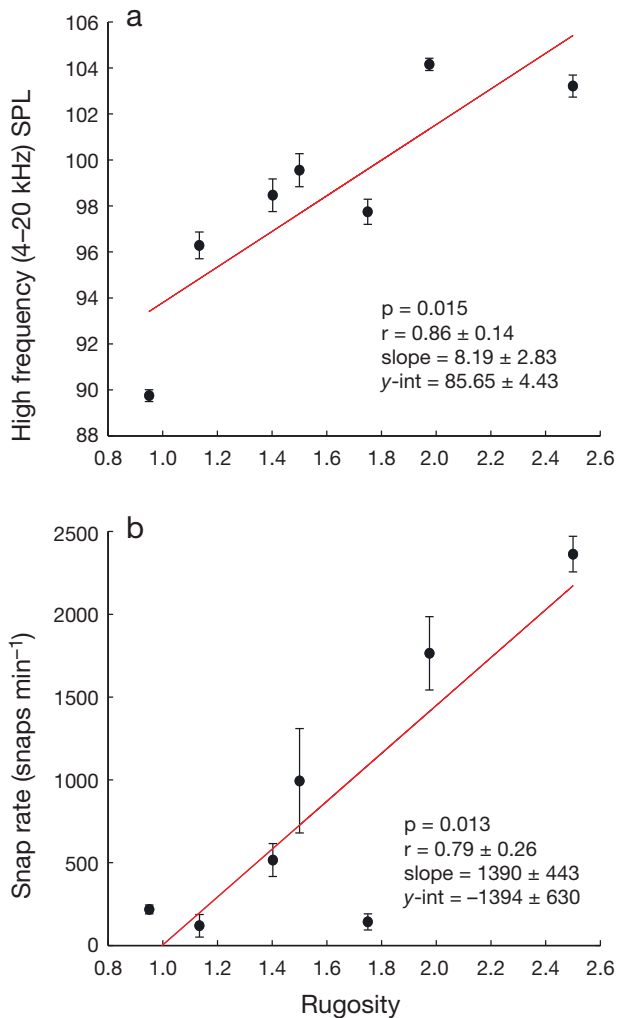


Fig. 11. Relationship between (a) median nighttime high frequency (4–20 kHz) sound pressure level (SPL) (dB re 1  $\mu\text{Pa}$ ) and (b) invertebrate snap rate with rugosity for each reef. Error bars: uncertainty in the median SPL and snap rate estimated from 10 000 bootstrap samples. Statistical analysis was performed using linear regression models, with uncertainty in correlation coefficient, slope, and intercept determined by bootstrap procedure

with structural rugosity. Low frequency SPLs showed no relationships with habitat complexity or fish community structure. Acoustic complexity values were not related to fish community structure or habitat complexity for either low or high frequencies.

#### 4.1. Caveats

The artificial patch reefs used in this study were originally used to conduct experimental manipulations of nutrient additions on coral patch reefs and adjacent seagrass growth dynamics (Allgeier et al.

2013, 2018, Layman et al. 2013, 2016). We recognize that the habitat characteristics and associated fish communities of the artificial patch reefs used in the present study may not have been the same as natural reefs; however, their use did allow us to manipulate habitat complexity and test if the soundscape reflected these differences in habitat complexity. Additionally, the fish vocalizations recorded in the present study could not be identified because they did not match any of the fish vocalizations found via online databases such as DOSITS (<https://dosits.org/>) and FishBase ([www.fishbase.de/](http://www.fishbase.de/)), which limited the behavioral context of the sounds that were recorded.

#### 4.2. Temporal soundscape characteristics

For each artificial patch reef, high frequency (4 to 20 kHz) SPLs 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 SPLs, associated with the acoustic activity of snapping shrimp, which may display daytime, nighttime, or crepuscular preferences (Lammers et al. 2006, 2008, Staaterman et al. 2014, Kaplan et al. 2015, Lillis & Mooney 2018). Long-term monitoring of high frequency snapping shrimp sounds in more temperate waters indicate seasonal shifts in the diurnal pattern of snapping activity, with a higher rate of activity occurring at night during summer months compared to winter months (Radford et al. 2008, Bohnenstiehl et al. 2016, Ricci et al. 2016). Since snapping shrimp are represented by hundreds of species with diverse life histories and social dynamics (Anker et al. 2006), the diversity of diurnal patterns reported in the literature may reflect potential species-specific responses to biotic and abiotic factors (Lillis et al. 2017).

As reported in other studies (e.g. Bohnenstiehl et al. 2016, Ricci et al. 2016, Lillis & Mooney 2018), 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 and declined with increasing snap rate (Fig. 6b). Similarly, several papers have identified changes in ACI based on the broadband signals associated with snapping shrimp (e.g. Kaplan et al. 2015, Butler et al. 2016). At reef 7, ACI varied approximately 40% in response to changes in invertebrate snap rate (Fig. 6b). In this study, the percentile change in ACI from a soundscape dominated by only one soniferous species in high frequencies is greater



than the percentile change in ACI in other studies (~16.7%) that have attributed 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. Other studies have indicated that ACI may vary temporally based on fish call rate, not necessarily fish call diversity (Desjonquères et al. 2015, Buscaino et al. 2016, Staaterman et al. 2017, Bohnenstiehl et al. 2018).

Low frequency (0.1 to 1.5 kHz) SPLs showed crepuscular or diurnal patterns for 3 artificial patch reefs (4, 5, and 7) with relatively high complexity. Seasonal patterns in low frequency SPLs and ACI, such as relationships with lunar phase or temperature, were not observed at these artificial patch reefs. For several coral reef habitats, low frequency SPLs were elevated during the new moon when many soniferous marine organisms are most acoustically active (McCauley & Cato 2000, McCauley 2012, Staaterman et al. 2014). In the US Virgin Islands, low frequency SPLs were found to be higher around times of dusk and dawn compared to other times (Kaplan et al. 2015).

#### 4.3. Spatial soundscape characteristics

Recently, studies have found potential relationships between habitat health and/or composition and underwater soundscapes. In sponge-dominated hard-bottom habitats in the Florida Keys, snapping shrimp snaps were considerably higher in healthy areas compared to degraded ones (Butler et al. 2017). In the US Virgin Islands, the soundscapes of 3 reefs with varying coral and macroalgal cover were correlated significantly with coral cover, whereas high frequency SPLs 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 & Bell 1992). This study adds further evidence that high frequency SPLs or invertebrate snap rates have the potential to indicate benthic composition, quality, and complexity (Lillis et al. 2014, Bohnenstiehl et al. 2016, Butler et al. 2016, 2017).

Neither high nor low frequency ACI were correlated with reef fish diversity, evenness, abundance, or biomass. Both terrestrial and marine soundscape ecology studies strive to link traditional methods of measuring biodiversity and organism abundance with acoustic metrics such as ACI, which evaluate the spectral and temporal variation in animal vocalizations (Sueur et al. 2008, 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 (Pieretti et al. 2011, Gasc et al. 2013, Sueur et al. 2014), recent attempts to correlate biodiversity with acoustic characteristics in the marine realm have yielded mixed results. In both tropical and temperate marine ecosystems, elevated SPLs and acoustic complexity in low frequency bands have been significantly correlated with relatively high fish diversity and abundance (Kennedy et al. 2010, Kaplan et al. 2015, Nedelec et al. 2015, Harris et al. 2016), although our results do not support the same findings in back-reef habitats that serve as nursery areas.

#### 4.4. Study implications

ACI and SPLs may prove ineffective for evaluating fish biodiversity or presence in back-reef nursery habitats predominantly inhabited by juvenile and sub-adult stages. For example, although vocalizations from juvenile fish species have been documented in the past (Lanzing 1974, Fine et al. 1997, Loesser et al. 1997, Staaterman et al. 2014), this study did not show increased ACI or SPLs in low frequencies with a higher abundance or diversity of adult and juvenile organisms. Sound production as a result of spawning is unlikely in back-reef habitats such as the Bight of Old Robinson, as many of the fish inhabiting these areas are not sexually mature. It may also be adaptive to remain somewhat silent as a sub-adult or 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). Conversely, vocalizations from juvenile and sub-adult fish may simply be too quiet to be detected when employing the acoustic soundscape measures used in this study. Though low frequency (100 to 800 Hz) fish vocalizations were recorded in this study at some of the more complex sites, these vocalizations were infrequent and did not

consist of loud chorusing events characteristic of soundscapes from many coastal habitats. Further research into sound production by juvenile and sub-adult organisms may be needed to better understand the acoustic ecology of nursery habitats.

Though there is strong evidence that larval, juvenile, and adult reef fish rely on reef noise for settlement and locating habitats (Simpson et al. 2005, 2007, Radford et al. 2011, Lillis et al. 2013), the results from the present study suggest that for back-reef areas, the low frequency soundscape is relatively quiet. Another study in the Caribbean that recorded the soundscapes of coral reefs found that low frequency (0.1 to 1 kHz) SPLs range from ~90 to 105 dB re 1  $\mu$ Pa (Kaplan et al. 2015), whereas in this study, low frequency (0.1 to 1.5 kHz) SPLs ranged from ~80 to 94 dB re 1  $\mu$ Pa. 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 soundscapes of patch reef habitats themselves have not previously been recorded (Radford et al. 2011). Though it is likely that juvenile and adult fish locate deeper, offshore coral reefs using a myriad of different cues, including acoustics, it is still unclear if fish differentiate between patch reefs of varying complexity using sound.

Our results show that data derived from hydrophones may potentially indicate structural rugosity 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 & Bell 1992), monitoring invertebrate snaps using acoustics may prove effective in predicting habitat complexity. While this approach will not replace bathymetric sonar, photogrammetry, and LIDAR methods that generate quantitative 3-dimensional models of the seabed, it may prove useful in characterizing the habitats of extremely shallow water environments that cannot be surveyed by boats or in areas where diver surveys would be hazardous. Future studies attempting to link sounds and habitat complexity should be aware of potential seasonality in high frequency sound production

(Bohnenstiehl et al. 2016, Ricci et al. 2017), requiring simultaneous acoustic monitoring of sites with similar abiotic conditions to facilitate robust relative comparisons.

**Acknowledgements.** We thank Richard Appaldo and Enie Hensel for assistance in the field. Funding for this project was provided by NSF (OCE-1234688) to D.B.E. and D.R.B., by NC Division of Marine Fisheries (2017-H-063) to D.B.E., and by the NC State University, Center for Marine Sciences and Technology.

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*Submitted: March 19, 2018; Accepted: November 18, 2018  
Proofs received from author(s): January 8, 2019*