



Soundscapes of natural and artificial temperate reefs: similar temporal patterns but distinct spectral content

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ABSTRACT: Marine soundscapes often differ among habitats; however, relatively little is known about whether soundscapes on naturally occurring habitats differ from soundscapes on human-made structures. To address this knowledge gap, we investigated whether temporal and spectral characteristics of biological sound production differ between natural and artificial offshore reefs. Specifically, we analyzed recordings from 5 week-long hydrophone deployments on 2 natural rocky reefs and 2 artificial reefs on the North Carolina, USA, continental shelf. Analysis of sound pressure levels (SPLs) on hourly and seasonal scales revealed similar temporal patterns between the reef types. These patterns were largely driven by 4 dominant fish vocalizers with seasonal chorusing patterns, including a toadfish *Opsanus* sp. Despite similar temporal patterns within reef types, soundscape spectral content was more similar within than between reef types, especially during the April deployment, which had the most acoustic activity. Our findings suggest that the soundscapes of shipwreck artificial reefs may differ from the soundscapes of natural rocky reefs, possibly due to differing community composition. As sound plays an important role in the navigation and settlement of many marine species, soundscape differences between natural and artificial habitats could affect ecosystem function through species behavior and interactions.

KEY WORDS: Marine soundscape · Artificial reef · Temperate reef · Spectral dissimilarity index · Bioacoustics

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1. INTRODUCTION

The ways in which animals make and perceive sounds play an important role in the ecology of many species. Individuals use sound to communicate and interpret a wide array of social and ecological cues,

including territorial aggression, group cohesion, mate attraction, gamete release synchronization, navigation, and settlement (Suthers et al. 2004, Popper & Hawkins 2019). Among the more than 30 000 extant fishes, over 800 teleost fish species representing 30 families are known to produce species-specific calls

for communication (Rountree et al. 2006). Moreover, all fishes possess the morphological capability to perceive acoustic particle motion, and many species have specialized hearing due to connections between the inner ear and gas-filled sacs, such as swim bladders (Ladich 2014). These connections can facilitate lower hearing thresholds, broader frequency sensitivity, and detection of sound pressure (Popper & Fay 2011).

The collection of biological sounds in combination with geological and anthropogenic sounds across a landscape form the soundscape (Pijanowski et al. 2011). Early research in marine soundscape ecology identified that ambient acoustic levels are elevated in structured habitats compared to adjacent unstructured benthos (Lillis et al. 2014a). Furthermore, different habitat types have been documented to have different soundscape characteristics, even when situated within a few km of one another. For example, the soundscape of sea urchin-dominated reefs in New Zealand contain a greater number of snapping shrimp snaps and increased acoustic activity in an 800–2500 Hz frequency band compared to macroalgae-dominated reefs and beach habitats (Radford et al. 2010). Additionally, Radford et al. (2014) documented distinct temporal and spectral characteristics at adjacent fringing reefs, back reefs, and lagoon sites.

Across numerous taxa and life stages, marine organisms respond to underwater sound. For example, many species of coral reef fish larvae (Tolimieri et al. 2000, 2004, Leis & Lockett 2005) and crab post-larvae (Radford et al. 2007) exhibit a directional swimming response to broadcasted reef sounds, and juvenile and adult coral reef fish use sound to guide nocturnal migrations (Radford et al. 2011a). Similarly, among the planktonic larvae of sessile invertebrates, oyster (Lillis et al. 2013) and coral (Vermeij et al. 2010) settlement increases in response to reef sound. As a result of the broad use of sound as a navigational and settlement cue among marine organisms, differences in broadcasted soundscapes among distinct habitats and habitat types may affect recruitment processes, community structure, and habitat function.

Artificial reefs are frequently introduced to marine environments to increase habitat availability and enhance fishery productivity (Pickering & Whitmarsh 1997). To understand the success of artificial reef deployment for conservation and management goals, comparisons with natural reefs are required (Carr & Hixon 1997). Following colonization by fish, artificial reefs often support different community compositions and greater biomass than natural reefs. This pattern of increased biomass is especially pronounced in planktivorous species, leading to an altered trophic

structure of artificial reef communities compared to natural reef communities (Arena et al. 2007, Simon et al. 2013, Paxton et al. 2017). Differences in community composition between artificial and natural reefs may produce distinct soundscapes on each reef type, especially in terms of biophony. If marine organisms are using sound to navigate their environment and make habitat selections, differences in the soundscapes of natural and artificial reefs could lead to recruitment of different species, thereby affecting the function of artificial reefs. A few studies have explored soundscape characteristics at artificial patch reefs, frequently constructed out of cinder blocks (Ghazali et al. 2013, Lyon et al. 2019); however, to our knowledge, the soundscape characteristics of artificial reefs have not been compared to natural reefs.

In the present analysis, we evaluated whether temperate marine soundscapes differed between natural and artificial reefs. Specifically, we documented the fish vocalizers that exhibited seasonal chorusing behavior as well as described and compared the temporal and spectral soundscape characteristics of 4 temperate reefs offshore of North Carolina—2 natural and 2 artificial. Lastly, we discussed more broadly the potential ecological implications of distinct soundscapes broadcasted on natural and artificial reefs and on individual habitats.

2. MATERIALS AND METHODS

2.1. Study sites

Two natural and 2 artificial reefs in Onslow Bay, NC, USA, were selected for soundscape description and comparison (Fig. 1a). Onslow Bay has a heterogeneous seafloor consisting of sandy benthic substrates and hardbottom formed by rocky reef ledges and pavements, as well as numerous artificial reefs, including historic shipwrecks, intentionally scuttled ships, and other human-made structures (Department of the Navy 2009). The reefs included in this study ranged from 41.5–50.4 km from Beaufort Inlet, and 35.4–42.4 km from the shelf break. The natural reefs included 2 rocky reef ledges: 210 Rock (34° 14.448' N, 76° 35.538' W) and West Rock (34° 19.368' N, 76° 36.396' W), located in 32 and 30 m depths, respectively. The artificial reefs included a 55.8 m US Coast Guard Buoy Tender at 34 m depth, 'Spar' (34° 16.626' N, 76° 38.730' W), and a 133.8 m US Navy Cable Layer at 35 m depth, 'Aeolus' (34° 16.698' N, 76° 38.592' W). Both artificial reefs were intentionally scuttled as part of the North Car-

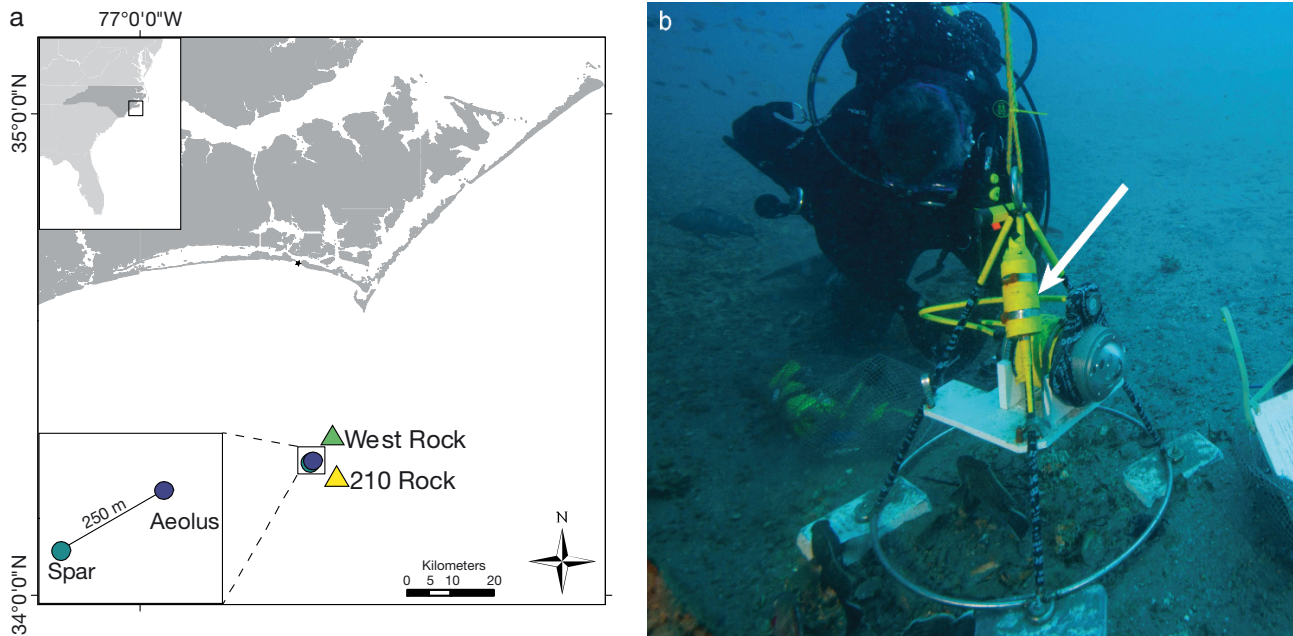


Fig. 1. (a) Study reef sites offshore of Onslow Bay, NC. Triangles: natural reefs; circles: artificial reefs; star: Beaufort Inlet. (b) Hydrophone deployment setup; arrow: position of the SoundTrap. Photo credit: J. McCord, Coastal Studies Institute

olina Division of Marine Fisheries Artificial Reef Program (AR-305; NC DMF 1988). The ‘Spar’ was sunk in June 2004 and is fully intact. The ‘Aeolus’ was sunk in July 1988 and consists of an intact bow and stern with a region of rubble in the middle.

2.2. Acoustic data collection

Underwater sound was recorded concurrently on each site during up to 5 approximately week-long deployments between November 2015 and August 2016 (Table S1 in the Supplement at www.int-res.com/articles/suppl/m649p035_supp/). Both natural reefs and the ‘Spar’ were sampled during all 5 deployments. We intended to sample 2 artificial reefs during all deployments; however, strong current and sediment movement at an initially selected artificial reef site impeded data collection. As a result, the ‘Aeolus’ was selected as a contingency site during the third through the fifth deployments.

Continuous recordings were made using calibrated, omni-directional hydrophones (SoundTrap 202 STD; Ocean Instruments) mounted 0.5 m above the seafloor on a weighted, metal conical frame which was placed approximately 5 m from the habitat structure (Fig. 1b). The positions of the hydrophones and frames were fixed across all deployments.

Sound pressure was recorded continuously at a rate of 96 kHz, with instruments producing a flat

(± 3 dB) frequency response between 0.020 and 43.0 kHz. To reduce computational challenges associated with continuous recordings and facilitate rapid visual screening of acoustic activity via spectrogram, the audio was initially subsampled to 2 min recordings every 15 min for the duration of the deployments. These subsamples mimic the typical duty cycle employed in many marine soundscape ecology studies (e.g. Bohnenstiehl et al. 2018). All acoustic processing was conducted in MATLAB (MathWorks 2019) using purpose-written code (R2019a). Each file was demeaned, and response corrected to μPa using the hydrophone-specific calibration value.

Time-series and spectral analysis of the 2 min subsamples identified sporadic, anomalously large amplitude impulsive signals that drastically altered the sound pressure level (SPL) time-series and power spectra (Fig. 2, Fig. S1). These impulsive signals may be produced when a swimming animal collides with the instrument frame or hydrophone (i.e. fish bumps; e.g. Buskirk et al. 1981, Bowman & Wilcock 2014). To remove the effect of the impulsive signals and reduce the intrusion of anthropogenic noise, each 2 min recording was further subsampled by extracting the 8 quietest 5 s duration, non-overlapping time windows within the file. This resulted in a summary of 40 s of recorded audio every 15 min. To accomplish this subsampling, a fast Fourier transform (FFT) was applied to the full 2 min file,

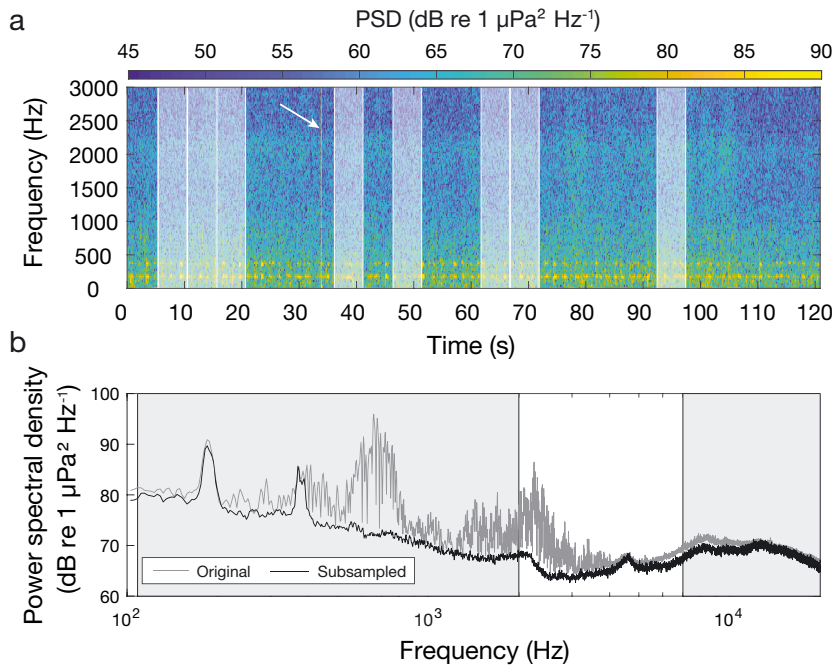


Fig. 2. Demonstration of the effect of a 'fish bump' on the average power spectral density (PSD) of a 2 min audio file. (a) Spectrogram of a representative file recorded on 210 Rock in April 2016. Arrow: an impulsive signal, likely the result of an animal collision with the hydrophone. White shaded columns: the 8 quietest, 5 s subsamples extracted to remove the effect of the fish bump. (b) PSD demonstrating that the subsampling methodology preserves the toadfish peaks while removing the noise due to the fish bump. Gray shaded areas: frequencies summarized in each frequency band

with the number of sample points (NFFT) equal to 2^{15} points, 0% overlap, and Hanning window). Next, the average RMS bandwidth power of every 5 s, non-overlapping time window within the 2 min file was summarized and sorted from quietest to loudest. The average acoustic spectra for each file were then calculated by summarizing only the 8 quietest 5 s windows (Fig. 2, see the Supplement for further explanation). Across a deployment, this acoustic summary resulted in a matrix where each column represented the mean spectra of a recording and each row contained the power at a given frequency (frequency resolution, $\Delta f = 2.92$ Hz). Band-limited SPLs were then calculated by integrating the acoustic power over the appropriate rows in this matrix. All SPL values are RMS and reported in units of dB referenced to 1 μPa .

2.3. Statistical analyses

2.3.1. Fish chorusing

Spectrograms and acoustic spectra of individual recordings were visually inspected to identify domi-

nant fish vocalizations and chorusing as well as rapidly screen for anthropogenic noise. The source of frequently observed sounds (biological, anthropological, or unknown) and the species identity of biological vocalizers were confirmed by both aural and visual inspection of the recording when possible. Observed vocalizations were compared to described fish calls in bioacoustic catalogues (Fish & Mowbray 1970) and the peer-reviewed literature in attempt to identify the species (Lobel et al. 2010, Staaterman et al. 2014, Mooney et al. 2016). Representative calls and daily calling pattern of each type of dominant fish vocalization were documented via spectrogram with an appropriate time and frequency resolution for each call type. Average acoustic features of each call type were summarized using purpose-written code by extracting call samples from all sites and deployments when calls were observed.

2.3.2. Temporal patterns

To evaluate acoustic activity in an ecologically relevant manner, data were separated into a low- and high-frequency band. The low-frequency band, from 0.1–2.0 kHz, was selected to isolate sounds from fishes and minimize ambient noise from geologic origins, such as rain or wind at the surface (Urlick 1983, Hildebrand 2009). The high-frequency band, 7–20 kHz, was selected to isolate invertebrate sounds, predominantly snapping shrimp (Everest et al. 1948). The gap between selected frequency bands intentionally excludes intermediate frequencies, which contain overlaps between fish and invertebrate sounds.

Temporal variation in SPL was examined on daily and seasonal scales. As week-long recordings were made at up to 5 time points over the course of 10 mo, we refer to each deployment by the month in which it occurred and among-deployment variation as seasonal variation. To evaluate differences in observed SPLs among the reef types, sites, and deployments, we conducted a 2-way ANOVA for each frequency band. To identify which sites and deployments were contributing to significant differences, we conducted pairwise comparisons using Tukey's HSD tests. Due

to observed diurnal patterns in SPLs and their relation to the photoperiod, we isolated the recordings between sunset and astronomical twilight (henceforth called dusk) when daily SPLs peaked across all sites and deployments, for comparison. To account for temporal autocorrelation among the acoustic files, dusk SPLs were averaged for each day within a deployment. As a result, the number of replicates included for each site and deployment combination was equal to the number of days in a deployment.

For each frequency band, we evaluated the differences between reef types and among sites separately for a total of 4 ANOVAs (low frequency by reef type, low frequency by site, high frequency by reef type, high frequency by site). We first investigated differences in dusk SPL aggregated by reef type. The full model for each frequency band included dusk SPL as the response variable and reef type, deployment, and an interaction between reef type and deployment as predictor variables. The site-level model also included site, deployment, and an interaction between site and deployment as predictor variables for each frequency band. For all models (reef-type level and site level, for high- and low-frequency bands) removal of the interaction term significantly worsened the fit of the model, and inspection of normal Q - Q plots demonstrated that the assumptions of normality were met; therefore, we proceeded with the full model and Gaussian distributions for both frequency bands. All statistical analysis was conducted using the programming software R v.3.6.0 (R Core Team 2019).

2.3.3. Spectral content

To evaluate dissimilarity in soundscape spectral content at each site, we used distance-based redundancy analysis (dbRDA)—a multivariate method that uses pairwise ecological distances to map variables in reduced dimensional space allowing visual assessment of patterns in the data. The dbRDA was conducted on each deployment individually, resulting in 5 ordinations. The distance between pairwise samples was calculated using the spectral dissimilarity index developed by Sueur et al. (2008). The spectral dissimilarity is calculated as:

$$D_f = \frac{1}{2} \sum_{f=1}^N |S_1(f) - S_2(f)|, \text{ with } D_f \in [0,1] \quad (1)$$

where D_f represents the dissimilarity between 2 samples on a scale from 0–1, f represents the frequency bins over which the index is evaluated, and $S_1(f)$ and $S_2(f)$ represent the probability mass functions of the 2

spectra being compared. In our study, $S_n(f)$ and D_f were evaluated over the low-frequency band (0.1–2.0 kHz) using the mean hourly spectra recorded during nighttime hours. Only nighttime recordings were included because this was an observed period of increased biological activity and reduced anthropogenic noise.

To identify what acoustic activity was driving sample separation, the proportion of total acoustic power within select frequency bands was calculated for each sample. These frequency bands were determined by viewing the spectra and identifying common peak frequencies (e.g. 0.1–0.3, 0.3–0.5, 0.5–0.8, and 0.8–2 kHz). The formula for each dbRDA was the spectral dissimilarity distance matrix constrained by the proportion of acoustic power contained within these smaller frequency bands. As such, the frequency bands driving sample separation are indicated by the loading vectors, and the eigenvalues of each ordination dimension represent the amount of variability explained by the loading constraints.

To evaluate whether spectral content varied by reef type, a multivariate ANOSIM was conducted on the spectral dissimilarity matrix from each deployment. ANOSIM is a nonparametric test that evaluates the null hypothesis that there are no differences in dissimilarity within and between groups. To evaluate this hypothesis, ANOSIM ranks all pairwise dissimilarities from a distance matrix, summarizes the mean ranks between and within groups, calculates a test statistic, and evaluates significance via Monte Carlo permutations ($n = 1000$). The test statistic, R , is expected to be 0 under the null hypothesis and 1 when all pairs between groups are more dissimilar than pairs within groups (Clarke 1993). All multivariate analyses were conducted using the ‘vegan’ package in R (Oksanen et al. 2019).

3. RESULTS

3.1. Fish chorusing

The dominant fish vocalizers that exhibited seasonal chorusing patterns consisted of toadfish *Opsanus* sp. boatwhistles, and 3 unidentified vocalizers described as a knock, creak, and growl (Fig. 3). Though the unidentified calls were compared to similar calls reported in various fish call databases, there were no matches close enough to confidently report a species identity. To facilitate future identification, temporal and spectral features of each call type were summarized (Table 1). Additionally, examples of each call type and chorus are included in the Supplement (Audio Files S1–S7).

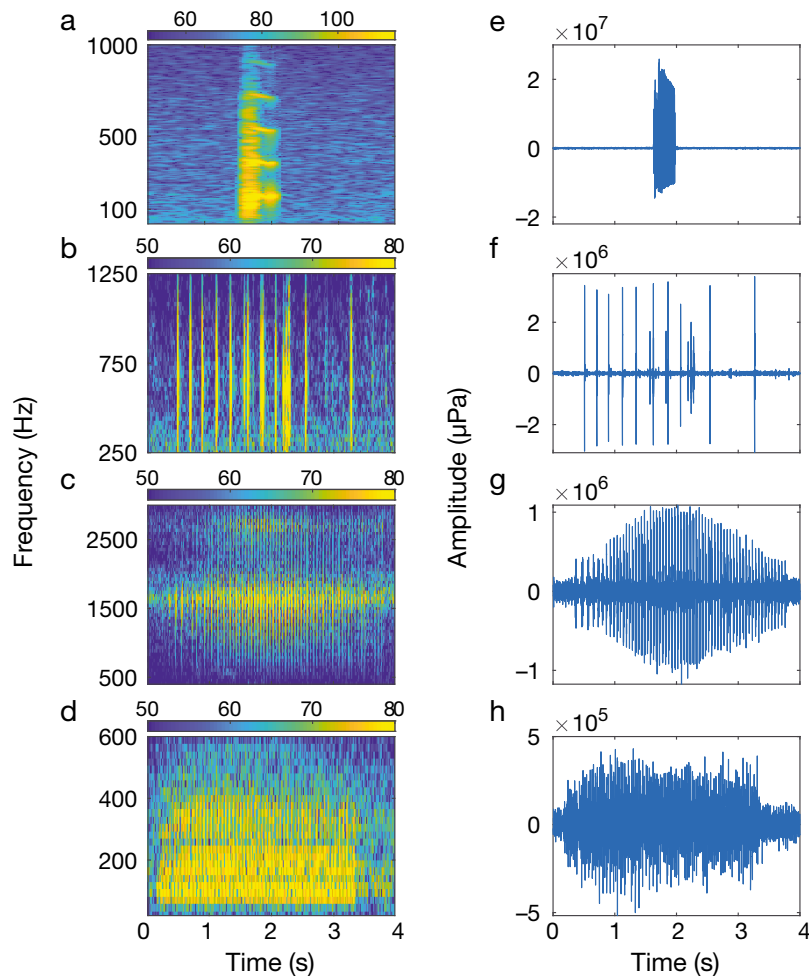


Fig. 3. (a–d) Spectrograms and (e–h) waveforms of dominant fish calls observed. Note variations in y-axes scales. Color bar: power spectral density (dB re 1 $\mu\text{Pa}^2 \text{Hz}^{-1}$) (a,e) Toadfish boatwhistle (spectrogram n-point fast Fourier transform [NFFT] = 2^{15} , 90% overlap); (b,f) unidentified knocks (spectrogram NFFT = 2^{12} , 90% overlap); (c,g) unidentified creak (spectrogram NFFT = 2^{11} , 90% overlap); (d,h) unidentified growl (spectrogram NFFT = 2^{12} , 90% overlap)

Fish choruses were observed in November, April, and June, and all chorusing species were observed on both natural and artificial reefs. Toadfish chorusing was observed in April and June but was most abundant in April. During April, toadfish calls were observed on all sites at all times throughout the day, with the onset of chorusing usually observed at 20:00 h EDT and lasting until 06:00 h (Fig. 4a). The daily patterns in SPL in the low-frequency band in April can be attributed largely to this calling behavior of toadfish across all sites (Fig. 5). Toadfish choruses also were observed on all sites except West Rock in June, with chorus onset around 21:00 h lasting until 05:00 h.

The unidentified knock was an impulsive sound frequently in sets of multiple knocks (Fig. 3b). Choruses of the knocks were observed on all sites during April, while occasional knocks were observed in all deployments. During April, the daily pattern consisted of a rapid onset of a dusk chorus at 20:00 h that was maintained for approximately 1 h with occasional knocks continuing for up to 4 h (Fig. 4a).

The unidentified creak was observed on the ‘Spar’ and West Rock in November from approximately 19:00–06:00 h, with periods of most intense chorusing during crepuscular periods (Fig. 4b). This call consisted of multi-

Table 1. Acoustic features of fish calls that exhibited seasonal chorusing. Sample calls and pulses were extracted from each site, and deployment chorusing was observed. The distribution of toadfish fundamental frequency was bimodal; as such, the mean \pm SD of each mode is reported. The multiple values of bandwidth and peak frequency for the creak and growl describe each pulse in a pulse set. –: features that were not applicable to certain call types

	Toadfish	Knock	Creak	Growl
Duration (ms)	508.3 \pm 106.4	7.7 \pm 6.3	2281.1 \pm 488.5	3350.1 \pm 229.5
Fundamental frequency (Hz)	147.9 \pm 13.7	–	–	–
No. of harmonics	2 (1–4)	–	–	–
Bandwidth (Hz)	–	553.4 \pm 138.1	326.8 \pm 100.6 420.2 \pm 137.7	146.5 \pm 24.7 367.8 \pm 96.0
Peak frequency (Hz)	–	653.4 \pm 153.2	1669.4 \pm 101.7 2728.7 \pm 156.1	100.8 \pm 22.9 160.9 \pm 57.3
No. of pulses in set	–	6.7 \pm 4.0	56.3 \pm 11.8	111.0 \pm 7.8
Pulses s^{-1}	–	7.8 \pm 8.9	24.8 \pm 1.4	33.2 \pm 1.1
No. of calls summarized	161	399 pulses, 10 sets	646 pulse sets, 75 pulse trains	94 pulse sets, 23 growl trains

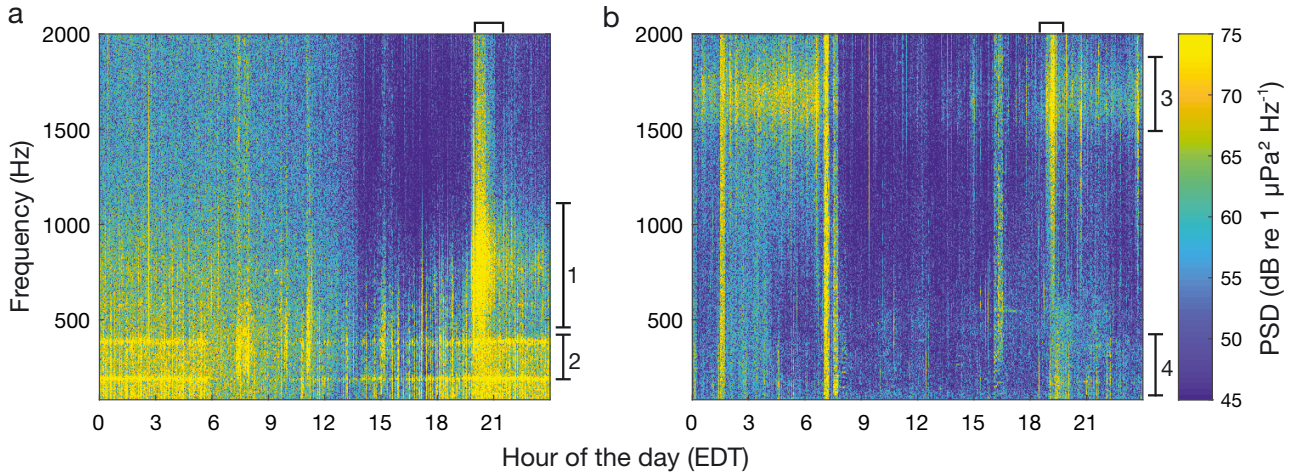


Fig. 4. Daily patterns of fish chorusing events during April and November. Each figure is a stacked spectrogram of all 2 min subsamples from a single day with representative fish chorusing events (NFFT = 2^{15}). The bracket on top of each panel identifies dusk, and the numbered brackets on the right side identify the frequency bands of interest for each vocalizer (1: knock; 2: toadfish; 3: creak; 4: growl). (a) Knock and toadfish choruses recorded during April on 210 Rock. Toadfish vocalizations were present throughout the day but peak during dusk, while the unidentified knock chorus was only present at dusk. (b) Creak and growl choruses recorded during November on West Rock. The creak chorus peaked during crepuscular periods while the growl chorus was only present at dusk. PSD: power spectral density

ple pulse sets in a pulse train. Each pulse set consisted of 3 pulses alternating in frequency (Fig. 3c). The first and third pulses had a peak frequency of 1669.4 ± 101.7 Hz on average while the second pulse peaked at 2728.7 ± 156.1 Hz. Each pulse varied in duration, lasting 1.7 ± 0.8 and 2.1 ± 1.0 ms, respectively. The first and second pulse were separated by 5.0 ± 1.6 ms and the second and third were separated by 4.9 ± 1.5 ms.

Choruses of the unidentified growl, a low-frequency sound with a 90–500 Hz bandwidth, were also observed on all sites in November and January (Fig. 3d). The chorus had a rapid onset at 19:00 h and lasted for 1 h, with occasional growls observed until 07:00 h (Fig. 4b). Similar to the creaking sound, the growl consisted of multiple pulse sets in a pulse train. Each pulse set contained 2 pulses alternating in frequency with 26.5 ± 11.8 ms between the center of each pulse.

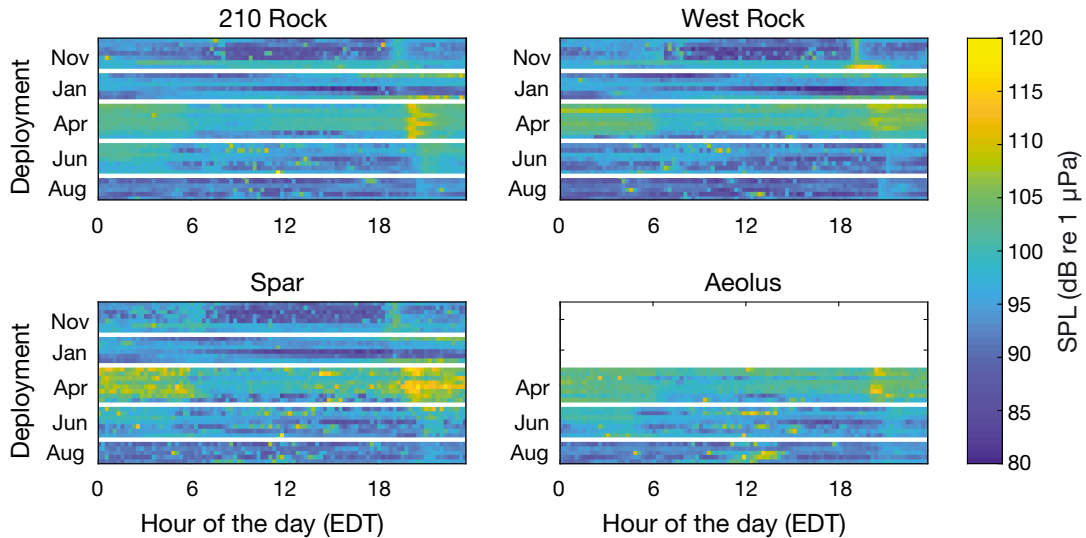


Fig. 5. Daily patterns in acoustic activity in the low-frequency band. Peak sound pressure levels (SPLs) were observed at dusk on all sites and deployments, and were especially pronounced during November, April, and June when fish chorusing was observed. Each pixel represents the average SPL within one 40 s subsample, and each row of pixels is the SPL variation over a single 24 h period. White rows separate the deployments. All recordings within each deployment were concurrent on each reef

The first pulse had an average duration of 40.1 ± 11.7 ms and peak frequency of 100.8 ± 22.9 Hz, while the second pulse was 19.5 ± 4.9 ms long with a 160.9 ± 57.3 Hz peak frequency.

3.2. Temporal patterns

In general, the temporal patterns of biological sound production were similar across all reefs. Within the low-frequency band (0.1–2 kHz), dominated by fish sounds, daily patterns across all sites consisted of increased SPLs at dusk and generally greater SPLs at night than during the day (Fig. 5). Seasonally, the intensity of the dusk peak varied, corresponding with the presence of fish chorusing. During November, there was also a peak in acoustic activity on the ‘Spar’ and West Rock at dawn that can be attributed to chorusing by the unidentified creaking species.

Within the low-frequency band, dusk SPL did not differ between natural and artificial reefs (ANOVA, $F_{\text{reef type}(1,113)} = 2.63$, $p = 0.108$). All sites broadly exhibited similar seasonal trends; however, dusk SPL significantly differed among sites (ANOVA, $F_{\text{site}(3,105)} = 3.37$, $p < 0.021$), deployment (ANOVA, $F_{\text{deployment}(4,105)} = 63.56$, $p < 0.001$), and an interaction between site and deployment (ANOVA, $F_{\text{site} \times \text{deployment}(10,105)} = 2.00$, $p = 0.040$). Post hoc Tukey’s HSD tests revealed that differences in dusk SPLs were driven largely by sea-

sonal variation, as there were no significant differences among sites within a deployment (Fig. 6). Overall, dusk SPLs decreased significantly from November–January, increased drastically to a maximum in April, then decreased to a minimum in August (Fig. 7). The April deployment, which coincided with the most abundant fish chorusing, was significantly louder than all others. Lastly, SPLs between the sites across the entire sampling period only significantly differed between 2 sites, with the ‘Spar’ supporting greater levels than West Rock (Tukey’ HSD, $p = 0.015$).

Within the invertebrate-dominated high-frequency band (7–20 kHz), crepuscular peaks in SPLs and elevated SPLs at night were observed in all sites and seasons (Fig. 8). Investigation of dusk SPLs identified significant differences between the reef types, with artificial reefs supporting louder high-frequency soundscapes (ANOVA, $F_{\text{reef type}(1,113)} = 99.55$, $p < 0.001$). SPLs also varied by deployment (ANOVA, $F_{\text{deployment}(4,113)} = 19.89$, $p < 0.001$) and an interaction between reef type and deployment (ANOVA, $F_{\text{reef type} \times \text{deployment}(4,113)} = 8.73$, $p < 0.001$). Tukey’s HSD test revealed that artificial reef SPLs were significantly higher than natural reefs in November ($p < 0.001$), January ($p < 0.001$), and April ($p < 0.001$), but not in June ($p = 0.587$) or August ($p = 0.998$; Fig. 9).

Comparisons of dusk SPLs at the site level revealed significant differences among sites (ANOVA, $F_{\text{site}(3,105)} = 342.85$, $p < 0.001$), deployments (ANOVA,

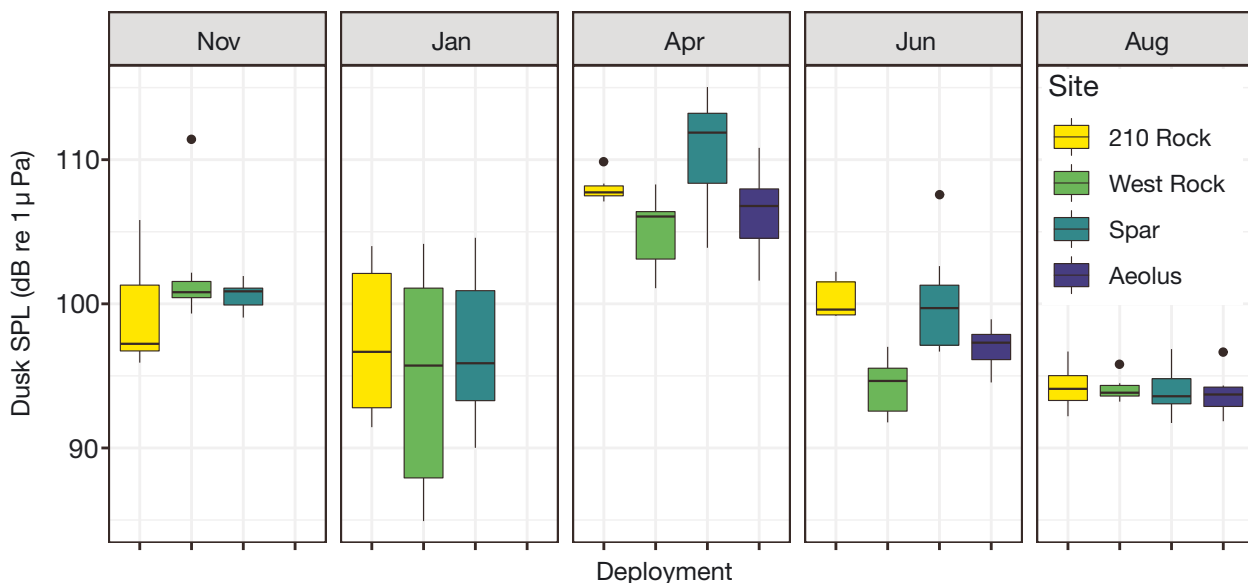


Fig. 6. Boxplots of average sound pressure levels (SPLs) at dusk within the low-frequency band (0.1–2 kHz) highlight that variations in SPL are driven by seasonal variability rather than differences among sites. Black bar: median; lower and upper box edges: first and third quartiles; whiskers: extend to either the most extreme value or to 1.5 times the interquartile range; black dots: outliers

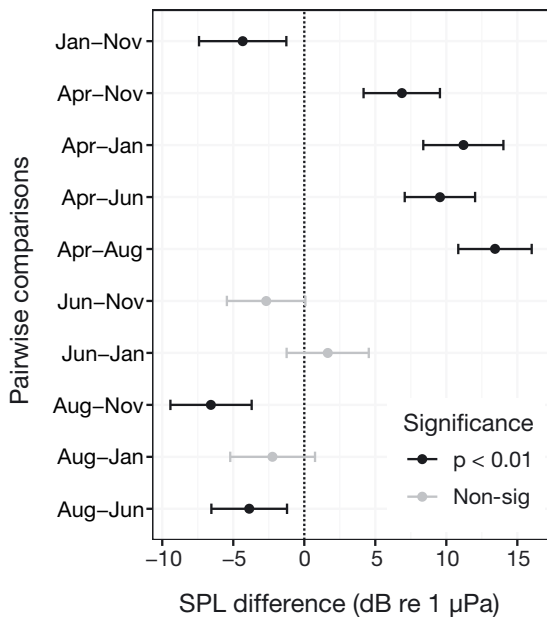


Fig. 7. Tukey's HSD 95% CIs of pairwise comparisons between deployments for low-frequency (0.1–2 kHz) dusk sound pressure levels (SPLs), demonstrating that dusk SPLs during April were significantly higher than all other deployments and drove the variability among deployments

$F_{\text{deployment}(4, 105)} = 124.17, p < 0.001$), and their interaction ($F_{\text{site} \times \text{deployment}(10, 105)} = 13.45, p < 0.001$). Pairwise comparisons among the deployments revealed that seasonal variation was mostly driven by reduced

SPLs during January (Fig. 10a), while variation among the sites was driven by increased SPLs on the 'Spar' and reduced SPLs at West Rock (Fig. 10b). Pairwise comparisons among sites within deployment revealed many significant differences. Notably, dusk SPLs were always higher on the 'Spar' than the 'Aeolus' (Tukey's HSD, Apr $p < 0.001$; Jun $p < 0.001$; Aug $p < 0.001$) and tended to be higher on 210 Rock than West Rock (Tukey's HSD, Jan $p < 0.001$; Apr $p < 0.001$; Aug $p < 0.001$).

3.3. Spectral content

During seasons with increased SPLs and fish chorusing events, specifically April and June, the spectral content of each reef's soundscape became more distinct. This is shown by tighter grouping of samples within sites and greater separation between sites (Fig. 11). Moreover, as each sample represents 1 h, temporal trends in spectral activity can be observed over the course of the night. Pairwise D_f values for each ordination ranged from 0.1–0.8, suggesting that there were substantial differences between some pairwise spectral probability mass functions.

Evaluating low-frequency spectral differences using dbRDA allowed the ordinations to be described in terms of the acoustic activity driving the differences between sites. The smaller frequency bands used to constrain each ordination generally

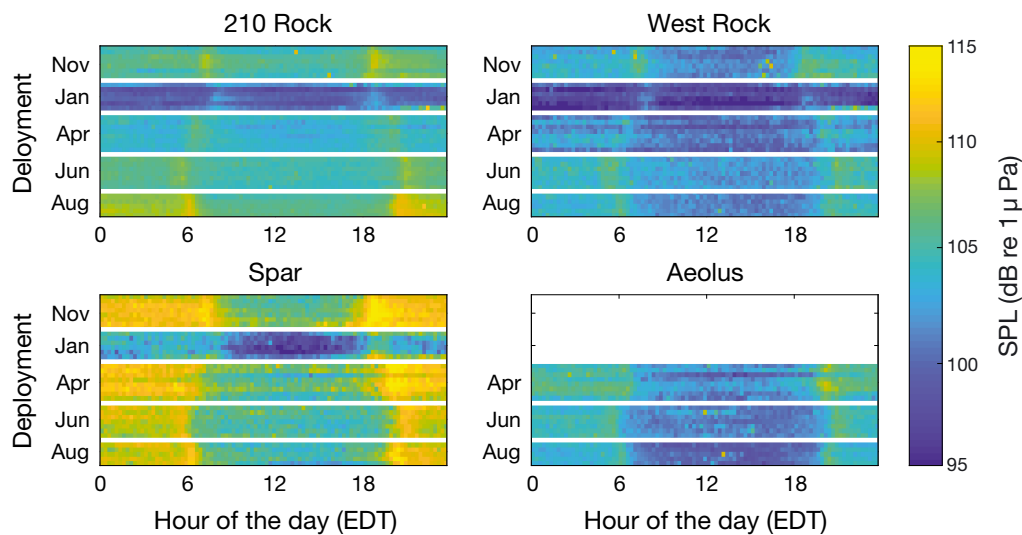


Fig. 8. Diurnal patterns in acoustic activity within the high-frequency band (7–20 kHz). Crepuscular peaks in sound pressure levels (SPLs), attributed to snapping shrimp, are persistent across seasons and track the seasonal photoperiod. All sites exhibited the minimum SPLs in January. Each pixel represents the average SPL within one 40 s subsample, and each row of pixels is the SPL variation over a single 24 h period. White rows separate deployments. All recordings within each deployment were concurrent on each reef

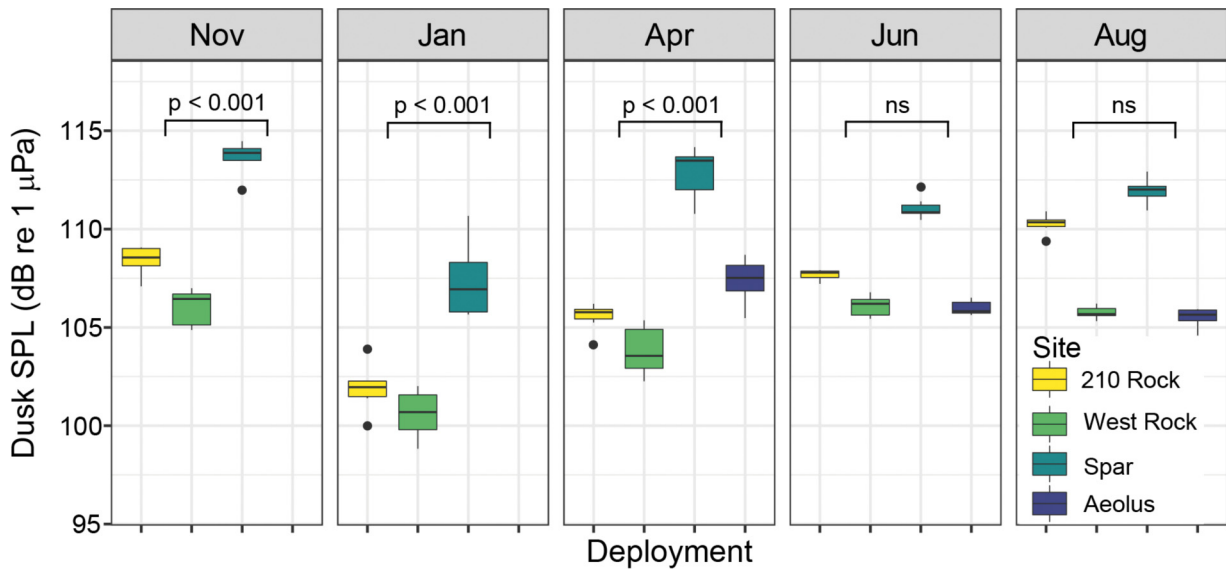


Fig. 9. Average daily sound pressure level (SPLs) at dusk in the high-frequency band (7–20 kHz). During the first 3 deployments, dusk SPLs were significantly higher on artificial reefs than natural reefs, while variation among sites was driven by increased SPLs on the ‘Spar’. The p-values are the result of Tukey’s HSD test of pairwise comparisons between the reef types. Boxplot parameters as in Fig. 6

represented a unique dominant fish caller in the average spectra. Activity in the 100–300 Hz range was usually attributed to miscellaneous low-frequency sounds and in some deployments a toadfish peak. The 300–500 Hz band was indicative of toadfish, the 500–800 Hz band of the unidentified knock, and the 800–2000 Hz band of the unidentified creaking call.

Comparison of spectral dissimilarities between natural and artificial reefs revealed that spectral content

significantly varied by reef type in all deployments except November (ANOSIM, $R = 0.06$, $p = 0.19$). The separation between reef types was greatest during April (ANOSIM, $R = 0.64$, $p = 0.001$), with artificial reef position driven by activity in the 300–500 Hz band while natural reefs were driven by 100–300 Hz activity. Separation between reef types was also significant in January (ANOSIM, $R = 0.39$, $p = 0.001$), June (ANOSIM, $R = 0.40$, $p = 0.001$), and August (ANOSIM, $R = 0.38$, $p = 0.001$).

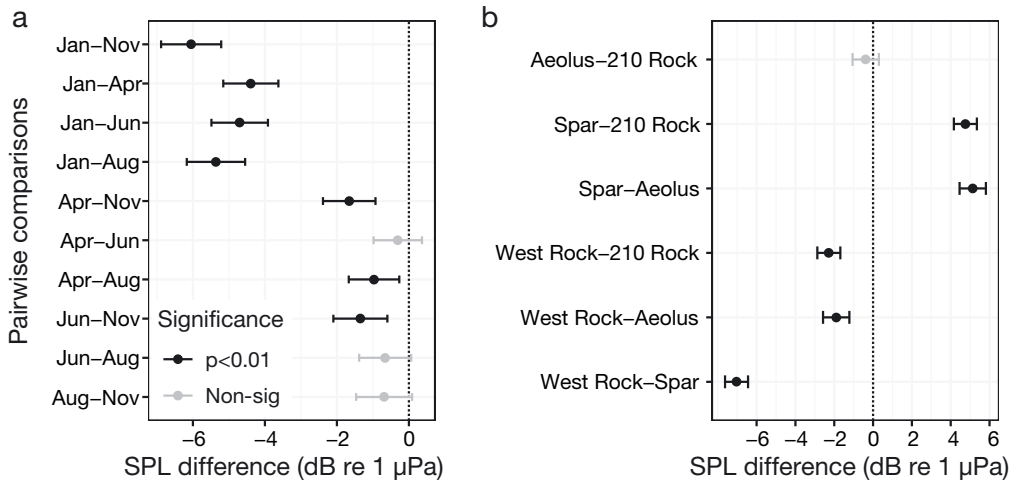


Fig. 10. Tukey’s HSD 95% CI of pairwise comparisons between (a) deployments and (b) sites for the high-frequency (7–20kHz) dusk sound pressure levels (SPLs). Results demonstrate seasonal variation is driven by reduced SPLs during January, while variation among the sites is driven by elevated SPLs on the ‘Spar’ and reduced SPLs on West Rock. Moreover, within reef type the ‘Spar’ and 210 Rock are louder than the ‘Aeolus’ and West Rock, respectively

Analysis of November showed that activity within the 100–300 Hz band was driving the separation of 210 Rock from the other sites, while the overlap in ‘Spar’ and West Rock samples was driven by activity in the 800–2000 Hz band (Fig. 11a). This 800–2000 Hz activity, on both a natural and artificial reef, aligns with the timing of the unidentified creaking chorus and explains the lack of significant difference between the reef types during November (Fig. 11b). Overall, the loading vectors explained 93.8% of the variation among the samples, with 58.3% captured on axis 1 and 35.5% captured on axis 2.

In January 2016, the average spectra of each site contain a unique peak that drove its loading (Fig. 11d). The ‘Spar’ and West Rock samples were each tightly clumped, suggesting minimal spectral change throughout the night, with ‘Spar’ being driven by the 300–500 Hz band and West Rock, the 800–2000 Hz band. The majority of 210 Rock samples plotted between the ‘Spar’ and West Rock; however, an increase in activity in the 500–800 Hz band from 2–6 h after sunset drove some separation of the samples (Fig. 11c,d). Overall, the loading vectors explained 86.0% of the variation among the samples, with 60.0% captured on axis 1 and 26.0% captured on axis 2.

Within April, each site showed distinct spectral separation from the other sites, although a consistent temporal trend was observed among all sites (Fig. 11e). This temporal trend was driven by an increase in activity in the 500–800 Hz band attributed to the knocking chorus, ranging from 1–4 h after sunset, with the duration of the increase varying across sites (Fig. 11f). Overall, the loading vectors explained 84.7% of the variation among the samples in April, with 48.4% of the variation captured on axis 1 and 36.3% captured on axis 2.

Within June, natural reef samples each ordinated closely within site, with the loadings of 210 Rock driven by activity in the 100–300 Hz band and West Rock driven by the 500–800 and 800–2000 Hz bands (Fig. 11g). Although within-site grouping was apparent for the artificial reefs, their samples broadly ordinated similarly with their loadings driven by minimal activity in the 300–500, 500–800, and 800–2000 Hz bands (Fig. 11g,h). Overall, the loading vectors explained 91.2% of the variation among the samples in June, with 58.1% of the variation captured on axis 1 and 33.1% captured on axis 2.

In August, the samples within each site clumped tightly together with minimal separation among the sites (Fig. 11i). The loadings of West Rock were driven by a broad peak between 1500 and 1750 Hz and aligned strongly with the 800–2000 Hz vector

(Fig. 11i,j). Among the other 3 sites, the average spectra showed that there were few to no distinct spectral peaks associated with a specific caller (Fig. 11j). Overall, the loading vectors explained 87.6% of the variation among the samples in August, with 75.2 and 12.4% of the variation captured on axis 1 and 2, respectively.

4. DISCUSSION

Our research demonstrates that soundscape characterization is a novel approach towards testing whether artificial reefs mimic natural reefs. We documented the soundscapes of 4 temperate reefs—2 natural and 2 artificial—during 5 sampling periods across a 10 mo period. Although the broad temporal patterns were consistent across all reefs regardless of reef type, these patterns were driven largely by the timing of dominant sound sources. Further analyses of finer details available in the spectral content revealed distinct soundscapes on each site, with spectral differences generally greater between natural and artificial reefs than within reef types. This separation between natural and artificial reefs was especially pronounced during time periods with increased acoustic activity and higher SPLs. These spectral differences may be the result of differing community compositions and trophic structures on natural and artificial reefs. Moreover, consistent soundscape differences across reef types could affect artificial reef function through species behavior and interactions in response to sound.

4.1. Comparisons between reef types

While the general pattern of crepuscular peaks in SPLs aligning with the seasonal photoperiod was similar between the reef types, high-frequency dusk SPLs were significantly higher on artificial reefs than natural reefs during 3 out of 5 deployments. More complex habitat structures, such as those of healthy sponge-dominated reefs, are known to host higher densities of snapping shrimp and are associated with higher observed snap rates and high-frequency SPLs (Butler et al. 2016). One possible explanation for elevated SPLs on artificial reefs is that the higher vertical relief and resulting habitat complexity of shipwrecks (Paxton et al. 2017) could support higher densities of snapping shrimp than the comparatively diffuse habitat structure of a natural rocky reef ledge.

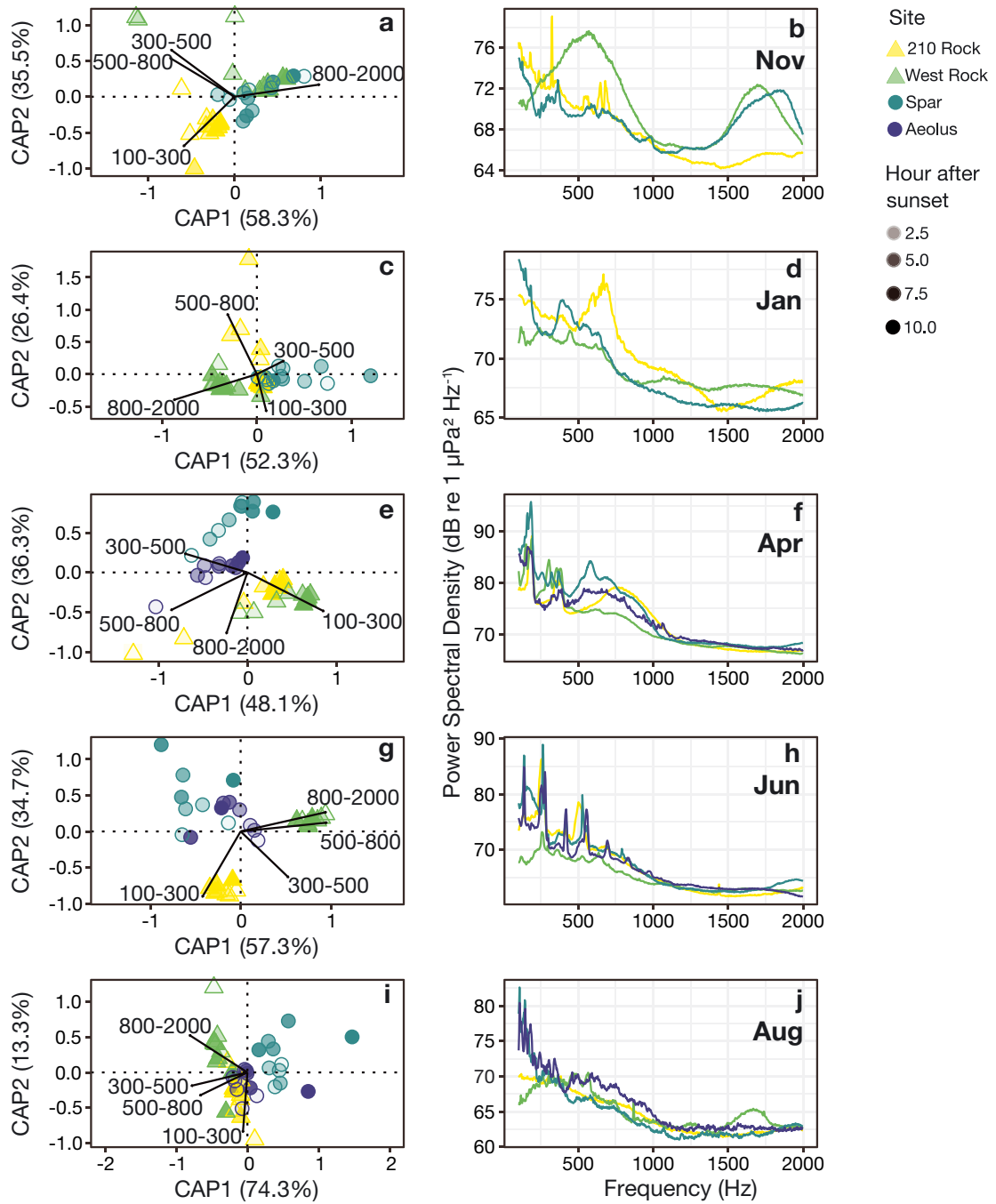


Fig. 11. Multivariate analyses of the spectral dissimilarity index; during deployments with increased acoustic activity in the low-frequency band (0.1–2 kHz) there is distinct separation of the spectral content at each reef, with increased separation between reef types. This difference between natural and artificial reefs was especially pronounced during April. As each reef type contains the same dominant vocalizers, differences between natural and artificial reefs are likely the result of less dominant vocalizations and miscellaneous acoustic activity. Left column: distance-based redundancy analysis ordinations of the spectral dissimilarity index for each deployment; right column: average spectra for each site within each deployment (note change in power spectral density scale)

Many marine soundscape studies have evaluated differences among sites or habitat types; however, few have employed multivariate analyses such as

dbRDA. The strong consistency between the observed average spectra and separation of samples according to the ordination loading sug-

gests that this method is appropriate and informative for evaluating differences in soundscape spectral composition. Across most deployments, the samples grouped most similarly within their site and were separated from samples of other sites, demonstrating that each site exhibited a unique spectral composition. This is notable especially for the 2 artificial reefs which are situated only 250 m from one another.

The April deployment, which consisted of the highest SPLs and most abundant low-frequency acoustic activity, provided the most interesting result. During April, the night soundscape of all sites contained choruses of toadfish and unidentified knocks. Despite the presence of the same chorusing species on each reef, there was still substantial spectral separation of the sites. The soundscapes also were separated by reef type, with the artificial reefs exhibiting similar spectral content in the 300–500 Hz band and the natural reefs in the 100–300 Hz band.

Within our study system in Onslow Bay, NC, comparative surveys of natural and artificial reefs have found that artificial reefs, and specifically ships, support greater fish biomass than natural reefs, whereas other metrics such as species richness are similar between reef types (Paxton et al. 2017, 2019). Moreover, differences in community composition by reef type are driven by greater abundances of large piscivores and water-column planktivores, such as jacks and scad, respectively, on artificial reefs, leading to an altered trophic structure (Paxton et al. 2017). Given the presence of the same dominant vocalizers across all reefs, the spectral separation between reef types is likely a result of differences in the proportion of the total soundscape that the dominant vocalizers occupy, as well as differences in miscellaneous acoustic activity, including less dominant calls and sounds associated with feeding, that are not currently attributable to a certain vocalizer or behavior. As artificial and natural reefs frequently support communities that differ in trophic structure (Arena et al. 2007, Simon et al. 2013, Paxton et al. 2017), it is plausible that there would be differences in sounds associated with feeding on natural and artificial reefs. It would be valuable to explore whether these non-vocalization sounds can be attributed to specific sources or behaviors, possibly through the use of combined visual surveys and multi-hydrophone localization arrays.

The differences in spectral composition documented on the temperate hardbottom reefs included in this study may have important ecological implications. Multiple studies have shown that different habitats, and specifically different reef types, broad-

cast distinct soundscapes (Radford et al. 2010, 2014, Lillis et al. 2014a). We provide initial evidence that shipwreck reefs may broadcast soundscape distinct from natural reefs as well. Given the ability of fishes to localize a sound source (Sand & Bleckmann 2008, Hawkins & Popper 2018) and marine organisms' attraction to habitat-associated soundscapes, soundscape differences between habitats may play a role in facilitating recruitment to reef habitats and could perpetuate differences among reef types or benthic habitats more broadly. Models of sound propagation away from reefs suggest that habitat-associated sounds, and specifically chorusing events, can be detected on the order of kilometers away from a reef. (Radford et al. 2011b, Lillis et al. 2014b). We propose that if a migrating individual encountered competing acoustic cues from adjacent habitats and the soundscape of one reef has a dominant signal in a preferred frequency band, such as one associated with conspecifics, the individual may be more likely to settle at that reef. As different species of fishes have unique auditory sensitivities, these behavioral patterns could ultimately support distinct communities on separate reefs. Future research on whether marine animals are able to perceive small differences in acoustic signals and whether they are attracted to acoustic activity in specific frequency ranges would facilitate a better understanding of whether the spectral differences we observed across multiple reefs have a meaningful ecological effect.

4.2. Comparisons among sites

We documented strong diurnal patterns in biological acoustic activity, with tight ties to the photoperiod. Within the fish-dominated, low-frequency band, these patterns were similar to those documented in other marine soundscape studies, with SPLs quietest during the day, loudest at dusk, and remaining elevated through the night. While there were no significant differences between the reef types, the diurnal pattern was generally consistent across all sites and seasons with the level of the dusk peak varying seasonally accordant with the amount of fish chorusing observed. Across all sites, the daily pattern was least apparent during January and August, coinciding with the deployment with the quietest dusk SPLs. During these deployments, few distinct fish calls were observed and there was no presence of fish chorusing. Alternatively, the diurnal patterns in acoustic activity were most apparent in April and can largely be attributed to frequent call-

ing and chorusing by toadfish *Opsanus* sp. and the dusk chorus of the unidentified knock.

Investigation of low-frequency spectral content identified distinct soundscapes on all reefs, with separation among the sites most pronounced during April and June. As previously summarized, the April soundscape consisted of choruses of toadfish and the unidentified knock. The onset of the knock chorus, with a peak frequency around 650 Hz, occurred immediately after sunset and continued most intensely for 1 h, with occasional knocks observed until approximately 4 h after sunset. This pattern is clearly visible in the corresponding ordination, with a temporal shift away from activity in the 500–800 Hz band as the night progressed. This common temporal pattern among the dominant vocalizer yet maintained spectral separation among the sites and reef types most clearly summarizes the finding of similar temporal patterns but distinct spectral content on temperate reefs.

Within the invertebrate-dominated, high-frequency band, acoustic levels were consistently lowest during the day, peaked at dawn and dusk, and were elevated at night. Similar to the low-frequency band, the strength of this daily pattern exhibited strong seasonal variation, with the quietest SPLs observed across all sites sampled in January. Snapping shrimp acoustic activity in shallow-water estuarine systems varies with abiotic variables, such as temperature (Bohnenstiehl et al. 2016). The coldest temperatures in Onslow Bay, NC, are generally around January, which may explain the decrease in acoustic activity during that deployment (Whitfield et al. 2014). Additionally, comparisons among sites revealed that dusk SPLs were always higher on the 'Spar' and 210 Rock than the 'Aeolus' and West Rock, respectively. This relationship between sites was also mirrored in the low-frequency band during multiple deployments.

It is interesting to consider whether there are site-level traits that could explain the consistent pattern of higher SPLs on specific reefs within a reef type. Research in a variety of other marine systems has identified correlations between habitat and community metrics, such as density, abundance, species diversity, and coral cover, and increased SPLs in specific frequency bands (Kennedy et al. 2010, Freeman & Freeman 2016, Staatterman et al. 2017). A few possible mechanisms to explain the elevated SPLs on the 'Spar' and 210 Rock are differences in community composition, abundance, or trophic structure that relate to differences in habitat traits such as complexity, vertical relief, size of the reef, or proximity to

other reefs. Additionally, reef location and context, such as proximity to the shelf break, prevailing current speed and direction, or level of anthropogenic noise disturbance, could affect the community composition and associated soundscape.

Overall, this consistent pattern in relative SPLs among sites in addition to the documented spectral differences among the soundscapes of each reef warrants further exploration of the relationship between habitat and community traits and the soundscape of temperate natural and artificial reefs. As there are known differences in habitat metrics and community composition on each reef we sampled, our findings provide further support that marine soundscapes may be indicative of habitat and community metrics and could be a valuable remote sensing tool to index fish communities. To gain a deeper understanding of whether the documented soundscape differences are correlated with specific habitat or community features, further exploration (with a larger sample size) of soundscape characteristics paired with habitat and community traits across multiple reefs within each reef type are needed.

4.3. Fish chorusing

Animal vocalizations serve numerous social and ecological roles, and fish vocalizations are frequently associated with reproductive or agonistic behaviors. For example, fish chorusing, or periods of frequent to constant calling, are almost always associated with reproductive behaviors and spawning (Bass & Rice 2010). The acoustic signature of spawning activity makes passive acoustic monitoring and soundscape description a useful method for studying the spatial and temporal variability of marine population dynamics, as well as evaluating habitat utilization. Because our sampling events were spread across multiple seasons throughout the year, we were able to capture some of the temporal variability potentially related to spawning activity on or near the habitats studied. For a thorough understanding of temporal dynamics, long-term recordings with minimal gaps are required.

The sonic behaviors of toadfish are among the most well-studied for any fish species. Toadfish make their characteristic boatwhistle call, associated with mating and nest defense, by rapid contraction of muscles lining the swim bladder (Fine & Lenhardt 1983). The oyster toadfish, *O. tau*, is the only documented toadfish in the inshore waters of North Carolina and is known to make seasonal migrations from offshore wintering

locations to inshore and estuarine habitats for spawning in spring (Schwartz 1974). The late spring onset of toadfish chorusing we observed on temperate offshore reefs matches seasonal chorusing onset documented in a Chesapeake Bay oyster reef system, as well as on offshore reefs in Georgia and Florida (Ricci et al. 2017, Rice et al. 2017). It is unclear whether the toadfish calls we documented are from a resident offshore population that foregoes seasonal migrations inshore, or if they are a species other than *O. tau*, such as the leopard toadfish *O. pardus*, which inhabits deeper rocky reefs year-round in the Gulf of Mexico, or an analogous undescribed *Opsanus* species.

In attempt to identify the specific source of the unidentified choruses, the call features were compared to documented vocalizers in other soundscape studies and soniferous fish collections in the Western North Atlantic. The observed knock vocalization is similar in pulse duration and frequency range to known pomacentrid calls, such as the dusky and bicolor damselfish (*Stegastes adusus* and *S. partitus*), both of which are present on the studied reefs (Spanier 1979). However, pomacentrids are generally more acoustically active during the day, while the knock chorus was observed at dusk (Lobel et al. 2010). In laboratory recordings, tomtate *Haemulon aurolineatum*, which are abundant on the studied reefs and have a spring spawning season, have also been documented making a similar impulsive vocalization. However, tomtate vocalizations have a longer pulse duration (40–130 ms) and more of a grunt quality than a knock.

The unidentified creak was compared to vocalizations of the striped cusk eel *Ophidion marginatum*, but inspection of the frequency spectrum revealed the cusk eel pulse is centered on only one frequency (Mooney et al. 2016), while the creak pulses alternated between 2 frequencies. For the unidentified growl, gray snapper *Lutjanus griseus* adult and larvae make a similar low-frequency growl (Staaterman et al. 2014), though to our knowledge there has not been documentation of gray snapper choruses in field or laboratory settings. As a result, visual confirmation of the growl source is required to confidently assign a species identity. While it would be ideal to identify each vocalizer to species, or even family, to enhance understanding of the ecological role of marine soundscapes and their interaction with individuals, it is still possible to explore these interactions without specific identification. Moreover, documentation of the unidentified vocalizations in the literature is critical to facilitating future identification.

4.4. Caveats

In the current study, we did not evaluate how the soundscapes varied in response to abiotic factors, such as lunar phase, temperature, wind, or sea state. As the sites included in this study are geographically close to one another and range in depth from 30–37 m, it is unlikely that wind is a substantial contributor to the soundscape differences documented. Future research investigating how these abiotic factors affect the soundscape of temperate reefs would help to infer whether differences in acoustic levels are site-level differences that can be attributed to ecological differences among the habitats. Additionally, it is important to note that the distance between the sound source and the hydrophone will affect observed SPL, and due to the unique geometries of each reef we were unable to fully standardize the position of the hydrophone relative to the extent, quantity, or characteristics of each reef habitat.

Lastly, we acknowledge that the sample size of the present study limits our ability to more broadly generalize how the soundscapes of artificial reefs relate to that of natural reefs. However, the consistent spectral differences we observed between reef types, as well as among all sites warrants further exploration. To date, research on how marine soundscapes vary across habitat and community traits has resulted in promising, but equivocal results. Artificial reefs vary greatly and measurably in area, vertical relief, and heterogeneity, with documented differences in the communities they support. With appropriately designed studies, artificial reefs could be a useful system to better understand the mechanistic relationships between soundscape variation and habitat and community traits.

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