



Underwater soundscapes in near-shore tropical habitats and the effects of environmental degradation and habitat restoration



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ABSTRACT

Most marine habitats have unique soundscapes and, among other potential ecological consequences, the larvae of many fish and invertebrates use habitat-specific sounds to locate appropriate settlement habitat. Anthropogenic stressors have degraded coastal ecosystems worldwide, but the effects of this degradation on the sounds emanating from deteriorated habitats are largely undocumented, as is the effectiveness of habitat restoration in reestablishing natural soundscapes. In this study, we investigated how ambient sound emanating from three near-shore, tropical habitats (subtidal mangrove prop-root habitat, seagrass, and sponge-dominated hard-bottom) in the Florida Keys, Florida (USA) varied with time-of-day and lunar phase. We also examined whether the destruction of sponge communities in hard-bottom habitats struck by cyanobacteria blooms alters the soundscape of that habitat, and if restoration of sponge communities can reestablish natural underwater soundscapes. Soundscapes of each habitat were examined using several acoustic metrics, including spectral analysis and counts of fish calls and snapping shrimp snaps. Mangrove, healthy hard-bottom, and restored hard-bottom habitats had higher soundscape spectra levels than seagrass and degraded hard-bottom whether at noon or dusk during new or full moons. Low-frequency sounds, most likely fish calls in the ~300 Hz frequency range, were most prevalent in mangroves during dusk full moons. There were also higher numbers of snapping shrimp snaps in mangrove, healthy hard-bottom, and restored hard-bottom habitats than in degraded hard-bottom and seagrass beds, especially during the prominent dusk snapping shrimp chorus. Our results demonstrate that near-shore tropical habitats have unique soundscapes that are diminished by habitat degradation, but can be reestablished by habitat restoration, at least in the case of sponge-dominated hard-bottom.

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1. Introduction

Soundscape ecology – the study of sounds that emanate from a landscape – is a growing field whose roots lie in terrestrial ecology (Pijanowski et al., 2011), but now include many studies in marine ecosystems (Harris and Radford, 2014). This field of science merges aspects of psychology, behavior, humanities, and ecology to examine how soundscapes (i.e., all sounds emanating from a specific landscape) vary over space and through time, how anthropogenically generated and naturally generated sounds interact, and how best to monitor and conserve soundscapes for their intrinsic and ecological value (Pijanowski et al., 2011).

Underwater sound and seascape ecology has been studied for decades (Harris and Radford, 2014), with some of the earliest works by Tait (1962) and Cato (1976, 1978) who described biological choruses that peak at dawn and dusk. More recent studies have described the biotic and abiotic components of underwater sounds (Radford et al., 2008a,b; Schärer et al., 2014; Staaterman et al., 2014), how sounds

vary over diel and lunar periods (Radford et al., 2008a,b) and among marine habitats (Radford et al., 2010; Kennedy et al., 2010; McWilliam and Hawkins, 2013), how anthropogenic factors distort natural soundscapes (Watanabe et al., 2002), and how marine animals use underwater sound to navigate to specific habitats (Tolimieri et al., 2000; Montgomery et al., 2006; Stanley et al., 2012; Lillis et al., 2013 and others). Because soundscapes vary temporally and spatially, they carry with them information about the habitat from which they originated, and can do so over long distances exceeding those possible with visual, chemical, or tactile cues (Rogers and Cox, 1988; McCauley and Cato, 2000; Montgomery et al., 2006; Radford et al., 2007).

Many taxa of marine fishes and invertebrates produce sounds (Myrberg, 1981; Ladich, 2004; Versluis et al., 2000; Bouwma and Herrnkind, 2009; Schärer et al., 2014; Staaterman et al., 2014) and possess a wide range of auditory sensory abilities (Rogers and Cox, 1988; Popper and Fay, 2011). Some fish larvae avoid reef noise to avoid the gauntlet of predators stationed near reefs (Simpson et al., 2011), but a number of studies have shown that reef sounds increase the settlement of larval fishes and invertebrates (Tolimieri et al., 2000, 2004; Jeffs et al., 2003; Radford et al., 2007). For example, settlement-stage crab larvae detect and interpret habitat-associated differences in underwater

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sound (Stanley et al., 2012), as do oyster larvae that are attracted to the sound of oyster beds in which they prefer to settle (Lillis et al., 2014).

As more studies link the ecological processes of larval recruitment and soundscape production, it will become increasingly important to monitor and conserve coastal soundscapes. Unfortunately, habitat degradation, whether by anthropogenic influences or natural disturbance, disproportionately affects near-shore environments (Vitousek et al., 1997; Limburg, 1999; Watanabe et al., 2002; Lotze and Milewski, 2004), where the nursery habitats of many marine organisms occur. Marine habitat restoration and restoration ecology are becoming indispensable tools not only to repair damaged environments, but also to test ecological theories (Peterson and Lipcius, 2003; Halpern et al., 2007). Yet, how habitat degradation diminishes underwater soundscapes, and whether habitat restoration aids in soundscape recovery remains largely untested.

The goals of the present study were threefold. First, we sought to compare soundscapes among three shallow, near-shore benthic habitats of the Florida Keys (mangrove, seagrass, hard-bottom) during new and full moons in the summer through the use of several acoustical metrics. We also examined how degradation affects the soundscapes of a specific habitat: sponge-dominated, shallow hard-bottom. Finally, we determined whether the restoration of hard-bottom sponge communities, previously destroyed by harmful algal blooms, also results in the return of natural soundscapes.

2. Materials and methods

2.1. Site selection

Our study was carried out in Florida Bay, and the near-shore waters of the Florida Keys, Florida (USA) where the coastal environment is a patchwork of seagrass beds, mangrove islands, and hard-bottom habitat that provide shelter and foraging grounds for a variety of juvenile fish and crustaceans. Turtlegrass (*Thalassia testudinum*) dominates the seagrass beds and banks (Hall et al., 1999), and Red Mangrove trees (*Rhizophora mangle*) line the seaward edge of mangrove islands (Ley et al., 1999), their submerged prop roots providing substrate and shelter for sessile and motile animals. Sponges, octocorals, ahermatypic stony corals, and macroalgae characterize hard-bottom, but large sponges, like the loggerhead sponge *Spheciospongia vesparium* and vase sponge *Ircinia campana*, are the dominant vertical structural features of these communities (Chiappone and Sullivan, 1994; Butler et al., 1995; Bertelsen et al., 2009).

Unfortunately, hard-bottom communities within the central and lower portions of Florida Bay have suffered massive sponge die-offs (Butler et al., 1995; Stevely et al., 2011), leaving barrens denuded of sponges. This habitat destruction has inspired hard-bottom sponge community restoration efforts, wherein sponges have been transplanted from unaffected hard-bottom areas onto 25 m × 25 m experimental restoration sites (n = 24 sites; ~700 sponge transplants of up to seven species per site) within the degraded area (M. Butler, unpubl. data). Thus, the degradation of sponge communities and their subsequent restoration on experimental sites afforded us the opportunity to compare soundscapes in unaffected “healthy”, degraded, and restored hard-bottom.

Sites for sound recordings were selected haphazardly within four habitat types (seagrass, mangrove edge, hard-bottom affected by sponge die-offs, and hard-bottom unaffected by sponge die-off), using the South Florida Benthic Habitats ArcGIS shapefile (FWC-FWRI); habitat designations were visually confirmed by divers. Recordings were also made at existing hard-bottom restoration sites, thus constituting a fifth habitat type at which we recorded sound. We sought to maintain a balanced sampling design with equal replication of each habitat type, however, due to equipment failure and inclement weather conditions, the actual number of replicates within each habitat type, moon phase, and time of day combinations was unequal: healthy hard-bottom and

mangrove, N = 8; degraded hard-bottom, N = 7; seagrass, N = 4; and restored hard-bottom, N = 3. Fig. 1 shows a map of the study area and acoustic recording sites.

2.2. Acoustic recordings

From mid-May to mid-August in 2012 and 2013, habitat recordings were made using submersible hydrophone systems. Each system included a manufacturer-calibrated Aquarian Audio H2a omnidirectional hydrophone (Aquarian Audio Products: sensitivity – 180 dB re: 1 V/μPa [± 4 dB 20 Hz–4 kHz]; flat frequency response 10 Hz–100 kHz), connected to a Roland Edirol R-05 solid-state WAV recorder (Roland Corporation, Japan; 48 kHz; 16 bit) housed within a waterproof housing. The system (hydrophone and recorder) was calibrated using pure sine wave signals from a signal generator, measured in line with an oscilloscope. Recordings were analyzed using MATLAB software (MathWorks Inc.) with code specifically written for the calibration of hydrophone systems. The set-up was weighted to be negatively buoyant and placed at the site with the hydrophone elevated ~0.5 m off the substrate.

Recording systems were deployed for 24-hour periods up to two days prior to or two days following a new or full moon. Continuous recordings were made at each site, and a fifteen-minute clip was pulled from the recording at solar noon and sunset time periods (<http://www.timeanddate.com/astronomy/usa/key-west>). Habitats were only recorded during calm conditions (i.e., no breaking surface waves with wind speed < 15 kts [<http://www.ndbc.noaa.gov>]) to reduce the influence of weather-driven sound generation; only recording clips without obvious anthropogenic noise (e.g., from boats) were analyzed. All habitat types were represented within each recording period (i.e., each five-day period around a moon phase) to allow for direct comparison of soundscapes among habitat types.

2.3. Acoustic and statistical analyses

Digital recordings were analyzed using MATLAB 2014b software (MathWorks, Inc.) and R (R Foundation for Statistical Computing). Sound clips were analyzed in the manner of Radford et al. (2010), wherein five 10-second subsamples were extracted from each 15-minute sound clip. For each 10-second subsample, a threshold level was set on the raw data and any transient (<0.2 s) spike above this threshold was counted as a snapping shrimp (Alpheidae) snap. Mean number of snaps for each sound clip was compared using a split-split plot ANOVA (whole plot = habitat type, sub-plot = moon phase, sub-sub-plot = time of day, block = site), and the data were rank transformed because they did not meet the ANOVA assumptions of normality and homoscedasticity. Tukey's HSD test was used to determine homogenous subsets within significant factors, and interaction plots were used to examine significant interaction terms.

For each 15-minute sound clip, the acoustic complexity index was also calculated (Pieretti et al., 2011), which uses power spectra to calculate the variability in acoustic energy within a soundscape. Overall acoustic complexity was calculated for each recording (Window type: Blackman, FFT size: 1024), and the ACI scores were analyzed using a split-split plot ANOVA (whole plot = habitat type, sub-plot = moon phase, sub-sub-plot = time of day, block = site). The data were inverse-transformed to meet ANOVA assumptions, and interaction plots were used to examine significant interaction terms. In addition, sound clips were low-pass filtered below 1000 Hz to remove snapping shrimp influence, and ACI scores were recalculated for the sound clips. However, the results from this analysis were the same as the results using the overall ACI scores, so only those results are presented below. Because the ANOVAs for both snapping shrimp snaps and sound spectra used data from the same sound clips and are thus not truly independent, we maintained experiment-wise error by adjusting our critical p-values for determining significance to the 0.025 level or lower.

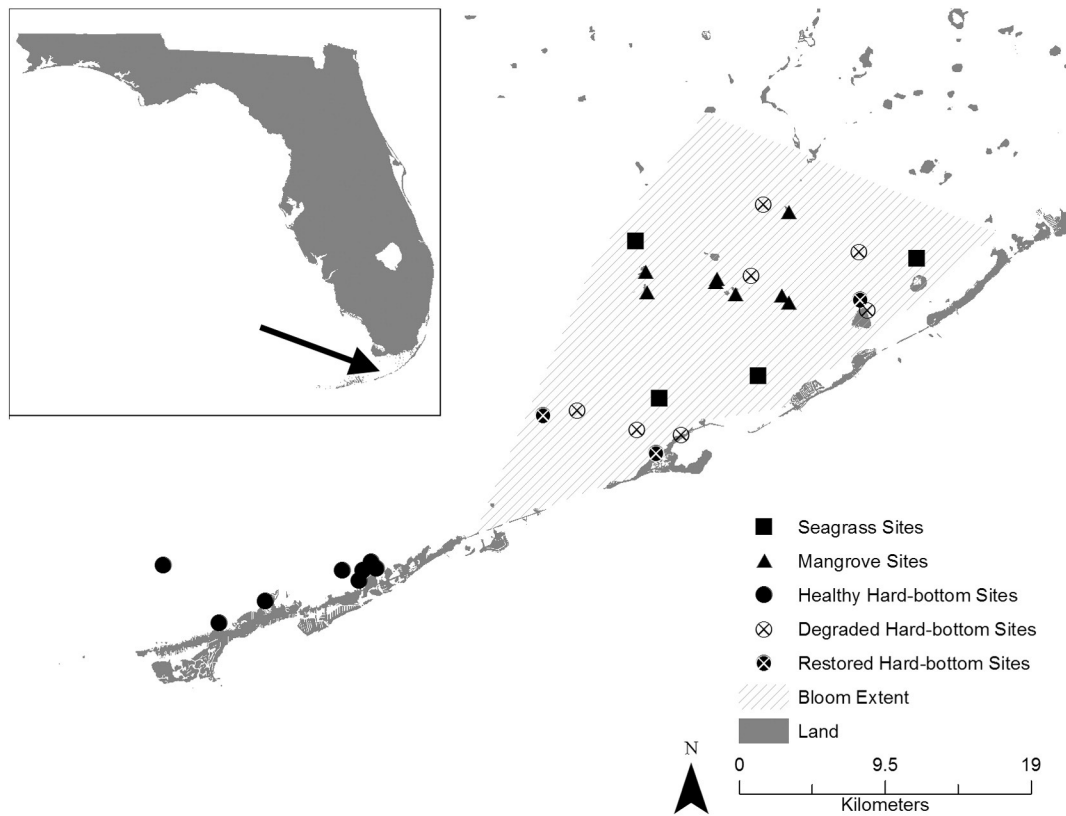


Fig. 1. Map of the study area, including the extent of the hard-bottom area degraded by cyanobacteria blooms. Acoustic recording sites are designated by different symbol shapes: seagrass — square; mangrove — triangle; hard-bottom — circle. Within hard-bottom habitat, site type is designated by different circles: healthy hard-bottom — solid circle; degraded hard-bottom — open circle with X; restored hard-bottom — closed circle with X.

In addition, composite power spectra were generated to show trends in the soundscapes of each habitat type at different moon phases and times of day. Composite spectra were calculated by generating spectra (Window type: Blackman, FFT size: 1024) for individual sites within each habitat type at given moon phases and times, and all spectra for a specific habitat type, moon phase, and time combination were root-mean-square averaged to yield the composite spectra. For example, eight healthy hard-bottom sites were recorded at noon during the full moon. Power spectra for each site were generated, and these spectra were root-mean-square averaged to generate a single spectrum that represents the healthy hard-bottom soundscape at noon during the full moon. In addition, representative 10-second subsamples for each habitat type, moon phase, and time of day combination were chosen, and spectrograms were generated to show general characteristics of each (Window type: Blackman, FFT size: 1024).

3. Results

3.1. Composite habitat spectra and representative spectrograms

Inspection of the composite spectra (Fig. 2) showed that regardless of moon phase, the dusk composite spectra for healthy hard-bottom, restored hard-bottom, and mangrove were louder (i.e., the spectra levels were greater) within the 1–4 kHz band than their corresponding noon spectra. The degraded hard-bottom and seagrass composite spectra varied little between noon and dusk, and were generally lower than those of the other three habitats. All spectra showed a broad peak around 2 kHz–3 kHz, which is likely due to Alpheid shrimp noise, though this peak is less pronounced in the degraded hard-bottom and seagrass spectra where snapping shrimp abundance was probably lower.

The dusk, full moon composite spectra showed the greatest variability among habitats. Healthy hard-bottom, restored hard-bottom, and

mangrove habitats had more low frequency (<1 kHz) noise when compared to seagrass and degraded hard-bottom, and the mangrove spectrum was markedly higher than any of the other spectra throughout frequencies less than 1 kHz. The healthy hard-bottom and restored hard-bottom spectra were of similar shape within all four moon phase/time-of-day combinations and were louder in the higher frequencies (>10 kHz) than the degraded hard-bottom, mangrove, or seagrass habitats. The healthy hard-bottom habitat spectra, however, exhibited a greater mean spectrum level during noon (47.91 ± 9.72 ; mean \pm s.e.) and dusk (47.97 ± 9.7) than did the restored hard-bottom habitat (38.33 ± 16.05 & 40.75 ± 16.05 , respectively).

Examination of representative spectrograms (Fig. 3) showed similar trends as the composite spectra. Throughout the four moon phase/time-of-day combinations, spectrograms of the healthy hard-bottom soundscape and restored hard-bottom soundscape looked similar, both exhibiting more snaps than the degraded hard-bottom soundscape. The spectrograms of the degraded hard-bottom soundscape where sponges are now absent looked similar to the spectrograms of the seagrass soundscapes; both are relatively quiet habitats, where the silence is occasionally punctuated by transient snaps by shrimps. The spectrograms of the mangrove soundscape are less noisy than either healthy hard-bottom or restored hard-bottom, although high energy, broadband snaps and low frequency fish calls are not uncommon (Fig. 4). The energy of the fish calls was highest around 300 Hz, with subharmonics around 600 Hz, 900 Hz, and 1200 Hz adding additional low frequency energy to the soundscape.

3.2. Number of snaps and acoustic complexity

Habitat type ($F_{4,25} = 41.54$, $p < 0.001$) and time-of-day ($F_{1,531} = 130.24$, $p < 0.001$) significantly affected the number of snaps per 10 s, as did their interaction ($F_{4,531} = 12.51$, $p < 0.001$). Moon phase and

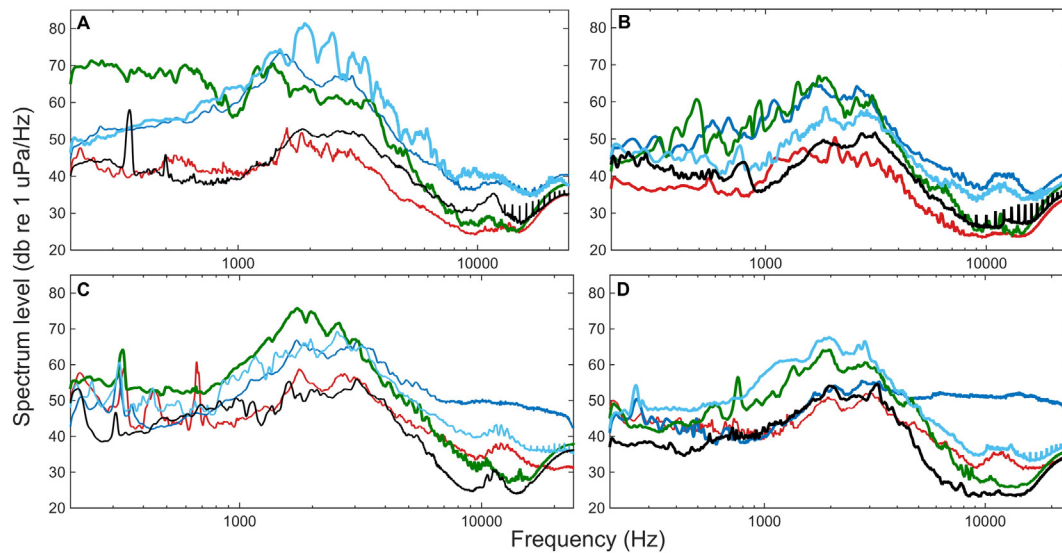


Fig. 2. Composite soundscapes for each habitat type (colored lines: affected hard-bottom – red; unaffected hard-bottom – dark blue; restored hard-bottom – light blue; mangrove – green; seagrass – black) during each moon phase and time-of-day. Full moon dusk (A), full moon noon (B), new moon dusk (C), and new moon noon (D).

the three-way interaction of habitat type by moon phase by time-of-day were marginally non-significant ($F_{1,24} = 5.21$, $p = 0.032$ and $F_{4,531} = 2.70$, $p = 0.03$, respectively). The plot of the habitat type by time interaction (Fig. 5) indicates that the number of snaps per 10 s during noon and dusk in mangrove habitats does not follow the same trend as the other habitats; that is, the number of snaps within mangroves at noon is higher than expected. Recordings made at dusk in all habitats had more snaps per 10-s (444.54 ± 19.47 ; mean \pm s.e.) than did noon recordings (266.59 ± 12.93 ; mean \pm s.e.).

Tukey's post-hoc test on habitat type (Table 1) revealed three homogenous subsets. Mangrove habitats produced the highest number of snapping shrimp snaps, significantly higher than other habitat types except healthy hard-bottom. Healthy hard-bottom and restored hard-bottom exhibited significantly more snaps than did either degraded hard-bottom or seagrass habitat. Time-of-day ($F_{1,50} = 59.72$, $p < 0.001$) was the only factor to significantly affect the acoustic complexity indices of the underwater soundscapes. Dusk soundscapes (396.82 ± 6.47 ; mean \pm s.e.) were more acoustically complex than noon soundscapes (376.11 ± 5.69 ; mean \pm s.e.). Fig. 6 exhibits the variability of the ACI scores. Fig. 6A shows the difference between noon and dusk time periods, broken down by moon phase, and Fig. 6B shows how the various habitats differed with moon phase and time of day.

4. Discussion

Our results demonstrate that tropical nearshore habitats in the Florida Keys, indicative of similar marine habitats throughout the Caribbean, have unique acoustic signatures that vary with time-of-day and lunar phase, and often over small spatial scales (sometimes less than a kilometer) among adjacent but dissimilar habitats. Mangrove, healthy hard-bottom, and restored hard-bottom habitats had higher soundscape spectra levels than seagrass and degraded hard-bottom whether at noon or dusk during new or full moons. Low-frequency sounds, most likely toadfish calls at ~ 300 Hz, were most prevalent in mangroves during dusk full moons. There were also more snapping shrimp snaps measured in mangrove, healthy hard-bottom, and restored hard-bottom habitats than in degraded hard-bottom and seagrass beds, especially at dusk. Such differences among habitats, time-of-day, and lunar phase when coupled with the distance and consistency with which sound propagates underwater, offer a predictable navigational cue for organisms seeking those habitats. Environmental damage can significantly alter the soundscape of marine habitats, as demonstrated by the acoustic differences between hard-bottom sites that had or had not been exposed to sponge-killing cyanobacteria blooms. Equally striking, however, was the effectiveness of restoring sponge communities on

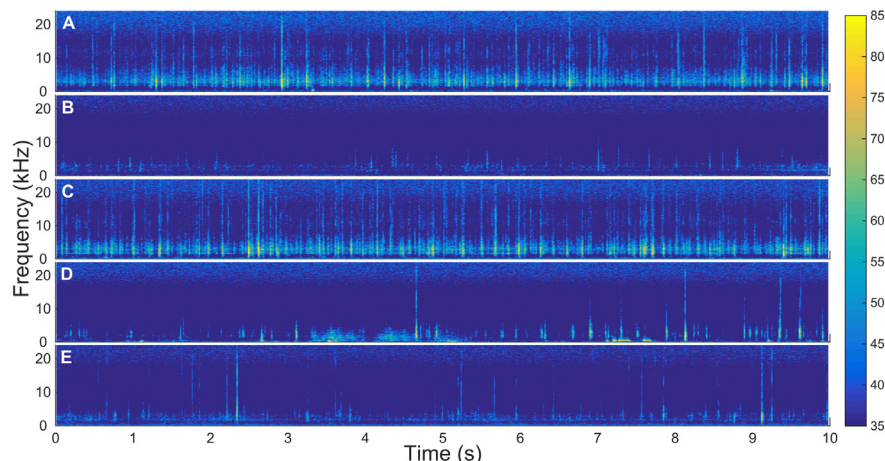


Fig. 3. Representative spectrograms for five habitats at dusk during a full moon (colorbar units: dB re 1 μ Pa): (A) unaffected hard-bottom, (B) affected hard-bottom, (C) restored hard-bottom, (D) mangrove, and (E) seagrass. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

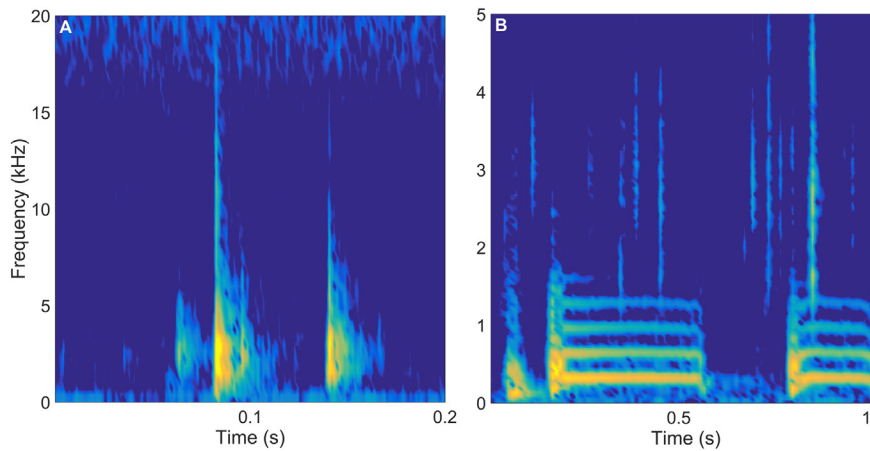


Fig. 4. Spectrogram of a snapping shrimp snap (A) and a toadfish call (B).

reestablishing a natural soundscape in hard-bottom habitats previously subject to sponge die-offs.

4.1. The acoustic characteristics of nearshore tropical habitats

Underwater sounds have been recorded and described in a variety of habitats. For example, Radford et al. (2010) characterized differences in sound in subtidal habitats (macroalgal-dominated reef, sea urchin-dominated reef, sandy beach) along a wave-swept coast in New Zealand. Many of the noises they recorded were generated by waves and tidal currents, but others were of biological origin such as the prominent mid-frequency (800 to 2500 Hz) rasp of sea urchins grazing at night on algae-covered rocks. More recently, Lillis et al. (2014) recorded sounds in coastal North Carolina (USA) where the acoustic signatures of oyster reefs had consistently higher levels of sound in the 1.5–20 kHz range compared to nearby soft bottom habitats. Many recordings have been made of tropical coral reefs (Tait, 1962; Cato, 1976, 1978; McCauley and Cato, 2000; Kennedy et al., 2010, among others) and the response of fish and invertebrate larvae to those sounds (Tolimieri et al., 2000; Simpson et al., 2004, 2008, 2011; Montgomery et al., 2006 for a review). With the exception of coral reefs, we are unaware of any published descriptions of the soundscapes of nearshore tropical habitats, the most prominent and ecologically important being: seagrass, hard-bottom, and the submerged prop root edges of mangrove islands.

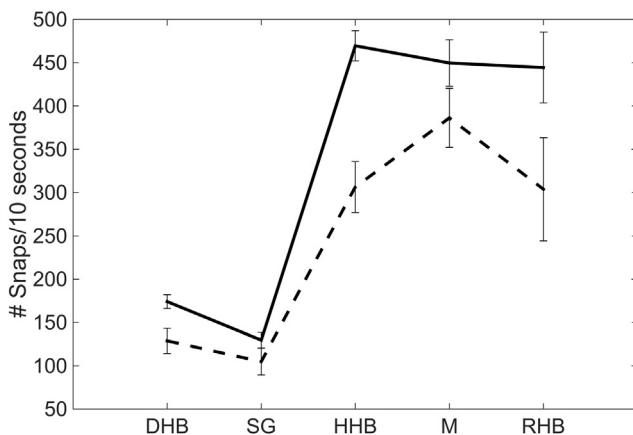


Fig. 5. Profile plot of the habitat type by time interaction effects on the number of snapping shrimp snaps/10 s. Degraded hard-bottom (DHB), seagrass (SG), healthy hard-bottom (HHB), mangrove (M), and restored hard-bottom (RHB) are along the x-axis; noon (dashed) and dusk (solid) are plotted as separate lines. Error bars are standard error of the mean.

Low frequency fish calls were conspicuous sounds within the soundscapes of these near-shore environments. Having a fundamental frequency of around 300 Hz, these calls are likely the calls of the Gulf toadfish, *Opsanus beta* (Thorson and Fine, 2002a). Male toadfish in the genus *Opsanus* produce their characteristic boatwhistle through the use of a sonic muscle (Skoglund, 1961). This muscle is attached to the fish's swim bladder – essentially a resonating gas bubble (Bergeijk, 1964; Harris, 1964) – and vibrates in a one to one relationship with the call's fundamental frequency (i.e., the muscle vibrates at 300 Hz for a 300 Hz call) (Skoglund, 1961; Fine et al., 2001). Nesting males produce the tonal boatwhistles to attract mates (Winn, 1972) and to compete with other males (Winn, 1967, 1972; Thorson and Fine, 2002b). Toadfish call rate varies seasonally due to changes in water temperature (Breder, 1968; Fine, 1978), and daily with a peak around sunset (Breder, 1968).

However, the most prominent and easily discerned sound in our recordings were the pulsed, high frequency (~2–5 kHz) pops or clicks produced when snapping shrimps rapidly close their chelae during agonistic or defensive interactions. This closure creates a cavitation bubble that when it collapses, generates a sound as loud as 183–189 dB re: 1-μPa at 1-m, well within the frequency range detectible for marine fish (Leis et al., 2002) and possibly invertebrate larvae (Stanley et al., 2011, 2012). The number of snaps produced by snapping shrimp varied widely at each of the habitats we studied. The maximum number of snaps counted in a single ten second interval (1729 snaps) occurred at a restored hard-bottom site during dusk on a new moon, and the minimum (0 snaps) was recorded at a degraded hard-bottom site during the same time of day and moon phase.

Snapping shrimps are a ubiquitous source of biological sound in tropical and temperate waters around the world (Au and Banks, 1998). This diverse group of crustaceans includes many free-living species, but many species are associated with sponges including some species that are obligate dwellers of sponges and are the only known eusocial marine animals (Duffy, 1992). Large sponges that harbor snapping shrimps are particularly abundant and important components of tropical hard-bottom communities and coral reefs in south Florida and other areas of the Caribbean. Given the association between many snapping shrimp species and sponges, it is not surprising that the decimation of sponge communities in hard-bottom areas subject to blooms of cyanobacteria significantly dampens the noise level in affected habitats, particularly in the 2–5 kHz frequency range.

The destruction of the diverse sponge community on hard-bottom habitats in the Florida Keys impacted by infrequent but intense blooms of cyanobacteria has had measurable ecological consequences including: the loss of nursery habitat structure for fish and crustaceans (Butler et al., 1995; Herrnkind et al., 1997), possible changes in benthic

Table 1

Split-split plot ANOVA results testing the effects of habitat type, moon phase, and time of day on the number of snapping shrimp snaps per 10 s. Results of Tukey's HSD test of all pairwise treatment means are shown below the ANOVA table; treatment group means sharing an underline are not significantly different at the $p(\alpha) = 0.05$ level.

Factor	Sum of squares	DF	F	p
Habitat type	9,774,453	4	41.54	<0.0001
Error ^a	1,455,855	25		
Moon phase	109,286	1	5.22	0.032
Habitat × Moon	154,000	4	1.383	0.154
Error ^b	502,804	25		
Time of day	1,039,305	1	130.24	<0.0001
Moon × Time	15,828	1	1.984	0.16
Habitat × Time	399,380	4	12.51	<0.0001
Habitat × Moon × Time	86,212	4	2.70	0.030
Error	4,237,383	531		

^aError term: Site(Habitat)

^bError term: Moon*Site(Habitat)

Results of Tukey's Test:

Habitat Type:	Seagrass	Degraded HB	Restored HB	Healthy HB	Mangrove
Mean #Snaps:	93.4	119.7	468.6	474.0	532.0

trophic structure (Behringer and Butler, 2006), and diminished capacity for water column filtration (Peterson et al., 2006). We found that underwater soundscape spectra on hard-bottom sites affected by sponge die-offs also differed, having fewer fish calls and shrimp snaps. The most obvious ecological ramification of this alteration in underwater acoustics is the loss of navigational cues for settling larvae and perhaps motile adult taxa.

Underwater sound is unique as a navigational cue. Sound propagates long distances in water and, unlike chemical or thermal cues that travel on currents, sound travels in all directions. For example, high amplitude sounds in the range of 1200–1600 Hz have an attenuation rate of about 0.1 dB km, and thus would be detectable at least 10 km away (Jeffs et al., 2005). Over the past decade, there has been increasing interest in the role sound may play in the orientation of pelagic larval fishes, decapods, and molluscs to coastal nurseries. Tolimieri et al. (2000, 2004), Jeffs et al. (2003) and Simpson et al. (2004, 2005) were among the first to play-back underwater sounds and demonstrate that sound guides reef fish larvae and larval decapods. More recently, research by Lillis et al. (2013) showed that oyster larvae are attracted to sounds present on temperate oyster reefs. We have also played back sounds recorded on healthy hard-bottom habitats at degraded hard-bottom sites now devoid of sponges and measured fish and larval recruitment onto artificial collectors (J. Butler and M. Butler, unpubl. data). Similar to studies in other habitats, we found that the magnitude and diversity of larval

recruits are higher on sites where we played back the sounds of healthy, intact hard-bottom communities.

4.2. Quantitative discrimination of soundscapes among habitats

Humans can easily distinguish subtle differences in sound among habitats amidst a maelstrom of complex sounds. Yet, the quantitative comparison of acoustic signatures is not straightforward. The acoustic complexity index (Pieretti et al., 2011) was developed to quantify the variability of the acoustic intensities within a soundscape. The algorithm uses a step-down process to calculate an overall ACI score for a recording; the first step is to create a matrix of intensities divided into frequency bins and temporal steps, and to calculate the absolute difference in intensity between two adjacent values within the same frequency bin.

We employed this index hypothesizing that because of the transient nature and high intensity of snapping shrimp snaps, the absolute difference between one cell containing a snap and one cell not containing a snap would be great. Thus habitats dominated by snapping shrimp snaps will have high variability between adjacent frequency bins and will lead to high ACI scores. For example, the difference in the number of snaps between noon and dusk appears to drive the large difference in the complexity indices between these two time periods (Fig. 6A). Fig. 6B shows the ACI scores for each habitat type during the full and new moons at noon and dusk. Though the differences in ACI scores

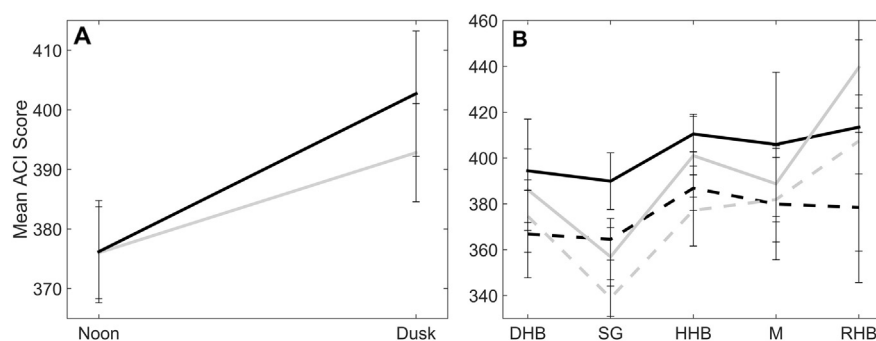


Fig. 6. (A) Dusk exhibited a higher ACI score than noon, though there was no difference between full moon (black) and new moon (gray) phases. (B) ACI scores for each habitat type (DHB — degraded hard-bottom; SG — seagrass; HHB — healthy hard-bottom; M — mangrove; RHB — restored hard-bottom). Black lines indicate full moon, gray lines indicate new moon; solid lines indicate dusk, dashed lines indicate noon. Error bars are standard error of the mean.

among habitats were not significant, the plot shows the same general trend as the composite soundscapes and number of snaps. Recordings of degraded hard-bottom sites and seagrass sites exhibit lower ACI scores than healthy hard-bottom, restored hard-bottom, or mangrove habitats. In addition, full moon recordings tended to exhibit higher ACI scores than their new moon counterparts.

The acoustic complexity index was developed to quantify the complexity of biophony in terrestrial environments. Bird songs add much of the complexity to terrestrial soundscapes, and can vary widely in frequency and amplitude. The recordings to which we applied this index are dominated by the broadband, loud snaps of snapping shrimps that add energy to a range of frequencies. Though sound from one habitat type might exhibit more snaps than another, they are not adding to the “complexity” of the soundscape because these snaps add energy across many frequencies. Fish calls, however, are tonal and add acoustic energy to just a few frequencies; thus, the acoustic complexity index might still be a viable means of quantifying differences in marine environments where fish vocalizations from many different species of fishes are prominent (e.g., coral reefs).

The spectrogram is also an invaluable tool in soundscape ecology to visualize and analyze sound clips (Pijanowski et al., 2011); however, creating and analyzing spectrograms for multiple recordings at many sites within a certain habitat type at various moon phases and times of day would be cumbersome. Thus, we created composite spectra for separate habitats. The composite spectra provide a simpler way to view habitat spectra and estimate trends within and among the soundscapes of these habitats, and spectrograms can be used to display why some habitats exhibit more or less intensity within certain frequencies. For example, the composite habitat spectrum for mangrove habitat at dusk during a full moon shows a high level of low frequency noise. Examination of the spectrogram (Fig. 3D) indicates that fish calls within these frequencies (Fig. 4) are likely adding that energy.

4.3. Effects of habitat degradation and restoration on marine soundscapes

Anthropogenic influences (e.g., coastal construction, non-point source pollution, farming run-off) alter and degrade coastal environments and fundamentally alter their functioning (Kennish, 2002; Vasconcelos et al., 2007), so understanding how coastal habitat degradation affects ecosystem processes is important. Some studies have examined the effect of habitat degradation on ecological functions (e.g., productivity; Short and Wyllie-Echeverria, 1996), yet few, if any, studies have examined its influence on the marine soundscape.

Over the past two decades, the hard-bottom communities of Florida Bay have experienced large sponge die-off events (Butler et al., 1995; Stevely et al., 2011), eradicating nearly all sponges, including the structurally dominant loggerhead sponge *S. vesparium*, from large portions of the central and lower bay. These sponges performed many ecosystem services, one of which was to provide habitat within their internal canals for small snapping shrimps, including the only known eusocial marine animals (Duffy, 1992). The widespread loss of shelter for snapping shrimps has likely led to a loss of shrimp populations within sponge die-off areas, and thus the loss of the biological cacophony produced by the shrimp. This is evident by comparing recordings of hard-bottom communities within the sponge die-off area to recordings of hard-bottom outside the die-off area (see Table 1 for means). In addition to providing habitat for infaunal snapping shrimp, the three-dimensional structure created by a community of large sponges in hard-bottom areas also provides shelter for other soniferous animals such as spiny lobster and fish. Therefore, it is not surprising that the composite spectra of hard-bottom areas affected by sponge die-offs are quieter over nearly all frequencies than sponge-rich hard-bottom areas unaffected by sponge die-offs.

It is clear that a loss of sponges of such magnitude has affected ecosystem services such as shelter for fishes and macroinvertebrates (Butler et al., 1995; Herrnkind et al., 1997) and filtration of bacterioplankton (Peterson et al., 2006); however, the deterioration of

soundscapes might exacerbate the loss of other functions, such as larval recruitment and settlement. Though the process of larval recruitment and settlement is well studied (see Kingsford et al., 2002; Arvedlund and Kavanagh, 2009 for reviews), the role of underwater sound in recruitment and settlement, especially at the small spatial scales at which larvae make settlement decisions (e.g., tens to hundreds of meters), is nascent (Montgomery et al., 2006). Because sound propagates well in water and can carry relevant biological information to larvae (Rogers and Cox, 1988; Radford et al., 2010), its loss from degraded habitats could have deleterious effects on larval supply to those areas, with possible consequences for biodiversity and fisheries.

Habitat restoration and the science of restoration ecology aim to ameliorate the plight of anthropogenically degraded coastal habitats. The reestablishment of foundational species returns habitat to the ecosystem, but the interactions among species and with their ecosystem matters more (Bruno and Bertness, 2001). Indeed, research across a range of terrestrial and aquatic ecosystems demonstrates that “positive ecological interactions” among species (e.g., facilitation) are as important as negative ones, such as competition and predation (Halpern et al., 2007). Therefore, restoration efforts should target the reestablishment of functionally significant species that are the strong interactors in their ecosystems (Peterson and Lipcius, 2003).

In 2010, we initiated the restoration of sponge communities in Florida Bay, in which sponges outside of the die-off area were cloned and transplanted onto monitoring sites scattered throughout the die-off area. This restoration effort afforded us a unique opportunity to better understand whether the restoration of sponge biomass and diversity on experimental sites also reestablished ecosystem functions, such as soundscapes, to degraded habitats. This study demonstrates that within three years of restoration, the soundscapes radiating from the restoration sites resembled those from hard-bottom unaffected by the sponge die-offs. The number of snaps produced by snapping shrimp on restoration sites was indistinguishable from those on sites that had not experienced the sponge die-off, and spectrograms of recordings of restoration sites and sponge-rich areas appeared similar. We know of only one other study (Lillis et al., 2014) in which the soundscape of a restored habitat (in that case, oyster reefs) was compared to that of “healthy” baseline habitats. The oyster reef soundscapes measured by Lillis et al. (2014) were made on sites where restoration had begun nearly two decades earlier in 1996, and included area closures, limestone marl substrate additions, and clam and oyster shell supplementation. Our study demonstrates that restoration via transplantation of foundational species, in our case — sponges, can rapidly recover a degraded soundscape.

As anthropogenic influences threaten the ecological integrity of the world's coastal habitats, restoration ecology and soundscape ecology can be useful tools to help guide the repair of damaged ecosystems and, in the process, aid in our understanding of ecological phenomena and processes. Underwater soundscapes are one such phenomenon whose role in ecosystem function is still poorly understood. Purposeful destruction of habitats so as to experimentally rebuild them ecological piece by piece just to understand ecosystem function is unconscionable. But restoration of already degraded habitats without the benefit of carefully planned research and monitoring are opportunities lost.

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