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Characterization of Soundscapes in Shallow Water Habitats of the Florida Keys (USA) and Their Influence on the Settlement of Larval Fish and Invertebrates

John R. Butler
Old Dominion University, butlerj.jack@gmail.com

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CHARACTERIZATION OF SOUNDSCAPES IN SHALLOW WATER HABITATS OF THE
FLORIDA KEYS (USA) AND THEIR INFLUENCE ON THE SETTLEMENT OF LARVAL FISH
AND INVERTEBRATES

by

John R. Butler
B.S. December 2009, University of Florida

A Dissertation Submitted to the Faculty of
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Approved by:

Mark J. Butler, IV (Director)

Jenni Stanley (Member)

Holly Gaff (Member)

Ian Bartol (Member)
CHARACTERIZATION OF SOUNDCAPES IN SHALLOW WATER HABITATS OF THE FLORIDA KEYS (USA) AND THEIR INFLUENCE ON THE SETTLEMENT OF LARVAL FISH AND INVERTEBRATES

John R. Butler
Old Dominion University, 2016
Director: Dr. Mark J. Butler, IV

In recent decades, changes in climate and water quality in Florida Bay and the Florida Keys (FL, USA) caused expansive cyanobacteria blooms that in turn precipitated massive sponge die-offs that drastically altered sponge-dominated hard-bottom communities in south-central Florida Bay. This area served as a model system to explore the effect of ecosystem change and habitat restoration on underwater soundscapes and larval recruitment. I had four main objectives: (1) characterize the underwater soundscapes of three near-shore, benthic habitats: mangrove islands, seagrass meadows, and hard-bottom (Chapter 2); (2) quantify larval settlement within healthy, degraded, and restored hard-bottom areas to test whether habitat degradation altered larval settlement (Chapter 3); (3) empirically test the role of sound in promoting larval recruitment to hard-bottom habitat (Chapter 3); and (4) employ the passive sonar equation and distance sampling techniques to evaluate how the loss of large sponges affected the densities and abundances of snapping shrimp (Chapter 4).

I found that near-shore habitats exhibit distinct soundscapes, that habitat degradation alters those soundscapes, and that habitat restoration can reestablish natural soundscapes. Habitat type and time of day significantly affected soundscapes, whereas lunar phase did not. Healthy hard-bottom and mangrove habitats exhibited louder spectra and more snapping shrimp snaps than did degraded hard-bottom or seagrass beds. However, four years after
restoration, the acoustic spectra and numbers of snapping shrimp snaps on restored hard-bottom were similar to those of healthy hard-bottom.

Habitat quality and moon phase both significantly affected larval recruitment. Overall, healthy hard-bottom habitat attracted significantly more larvae than either degraded or restored hard-bottom, particularly during full moon. Playback of healthy hard-bottom soundscapes within degraded hard-bottom areas prompted higher larval settlement, particularly during the full moon.

Estimates of snapping shrimp populations within degraded areas were significantly lower than estimates within healthy areas. Shrimp abundance estimates on healthy hard-bottom sites were one to two orders of magnitude greater than those on degraded sites. These studies demonstrate that tropical coastal habitats differ in soundscape characteristics, that habitat degradation affects soundscapes and the ecological process of larval settlement and recruitment, and that restoration of hard-bottom habitat can aid in returning these functions.
This dissertation is dedicated to my mother, Mary Anne Butler, who always pushed me to be the best that I could be.
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I could not have completed this dissertation without the support of many wonderful people. Firstly, I would like to thank my family. Though they never understood why I moved to Virginia to study in the Florida Keys, they always encouraged me to pursue my passions. Unbeknownst to him at the time, my father, Miller Butler, was the one who instilled in me a love of the ocean that would later lead me to pursue this degree.

I owe my wife Casey more gratitude that she knows. Her support and (sometimes not-so-gentle) encouragement was essential in this work. She taught me how interesting sponges were, answered all of my questions about the lives of invertebrates, and could always be counted on to come “shagging”.

My lab mates, from both ODU and UF, helped immensely as I was designing these experiments and collecting the data. Jason Spadaro showed me how to make and check the larval collectors we call “shags”, even if we only ever spoke in movie quotes; Josh Anderson was always good for a dance off at the DAB; Becky Squibb always had an easier way of doing complicated things; and my other lab mates that helped along the way: Gaya Gnanalingam, Ben Gutzler, and Marla Valentine. Two interns, Avery Bischoff and Jeri Wisman, suffered through the grunt work of checking shags for many months, and for that I owe them many thanks.

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Lastly, I would like to thank my advisor, Mark Butler. Without his support and guidance, I would not be the scientist I am today. Through counting and recounting sponge transplants, remaining flexible on days when nothing goes to plan, and rum-induced scientific discussion, I hope I continue to learn from him.
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Environments unspoiled by humans no longer exist. Direct and indirect anthropogenic disturbances have extensively altered and degraded environments. For instance, logging activities in the Brazilian Amazonian rainforest, one of the world’s most diverse environments, have cleared 300,000 km\(^2\) between 1975 and 1990 (Figure 1 in Nobre et al. 1991), instances of coral bleaching and disease due to climate change have steadily risen over the past few decades (Hughes et al. 2003), and industrial fishing fleets have depleted stocks of once plentiful fishes (Myers & Worm 2003), among many other examples. Human population density is three times higher in coastal areas compared to inland areas (Small & Nicholls 2003), which focuses and exacerbates the effects of human habitation (e.g., pollution and nutrient run-off or coastal development) on estuarine and near-shore environments (Kennish 2002).

The degradation and loss of ecological traits alters ecological processes and how ecosystems function. The literature is rich with discussion of how biodiversity loss degrades ecosystem functioning (Loreau et al. 2001; Duffy 2003; Worm et al. 2006; Cardinale et al. 2012, among a host of others) by altering ecological processes, such as primary production (Tilman et al. 1996; Tilman 1997; Hooper et al. 2005), decomposition (Hector et al. 2000), or trophic interactions (Cardinale et al. 2002; Duffy 2003). Scientific studies in terrestrial (Tilman 1996; Tilman & Downing 1996; Tilman et al. 2006), and aquatic (Steneck et al. 2002; Valdivia & Molis 2009) communities that tested the diversity-stability hypothesis (McNaughton 1977) indicate
that diversity often helps to minimize ecosystem changes in the face of environmental change. Thus, biodiversity lost from ecological communities results in lower resistance and resilience to disturbance (Chapin et al. 2000). Yet, the implications of lost biocomplexity for ecosystem function are still poorly understood, as are the myriad processes in play in natural ecosystems that constitute “ecosystem functions”.

One burgeoning field of research on ecological processes is the study of soundscape production and how sound interacts with the environment – soundscape ecology (Pijanowski et al. 2011a, 2011b). A soundscape refers to all of the sounds that emanate from an environment (Krause 2002; Pijanowski et al. 2011a), and those soundscapes can serve as an ecological resource (Dumyahn & Pijanowski 2011). The sounds within a soundscape can be grouped into three broad categories (Krause 2002). Geophony includes sounds produced by geophysical phenomenon, such as atmospheric motion, rainfall, or earthquakes (Swanson et al. 1988). Biophony includes sounds produced by organisms, whether on land (e.g., amphibians, birds, or insects) or in the sea (e.g., cetaceans, fish, arthropods) (Marler & Slabberkoorn 2004). Lastly, anthrophony includes sounds generated by human sources, such as sirens or road noise on land, or boats, drilling, or active sonar in the ocean (Raimbault & Dubois 2005).

Ecosystems are dynamic, influenced by natural and anthropogenic factors (Christensen et al. 1996; Hobbs & Harris 2001), and so too are soundscapes (Fig. 2 in Pijanowski et al. 2011b), which vary in time and space. For example, Krause et al. (2011) measured the temporal variability of soundscapes within four habitats of Sequoia National Park (old growth forest, oak savannah, dry savannah, and riparian) over the course of a year and found that soundscapes varied not only among sites, but also by time of day (morning, noon, or dusk) and season.
(winter, spring, summer, or fall). A variety of organisms contribute to the soundscape of an area and use the soundscape in different ways. Birds devote considerable energy into songs and calls, particularly during breeding season (Hopp et al. 1998; Marler & Slabberkoorn 2004), and birds tend to call at distinct frequencies and intensities, as well vary the timing of calls to avoid acoustic competition among species (Farina et al. 2011). Sinsch et al. (2012) applied acoustic niche theory (Krause 1987) to the soundscape of a montane wetland in Africa and showed that there was very little acoustic niche overlap in the advertisement calls of the Anuran frog community. Invertebrates also display complex acoustic behaviors. Henry and Wells (2010) applied acoustic niche theory to show that two sibling species of lacewings (Chrysoperla plorabunda and Chrysoperla adamsi) partition the acoustic niche space to avoid mating with the incorrect species.

The study of sound in the sea is as varied as the study of terrestrial soundscapes, and many sources contribute to the din of the ocean. Though the principles of sound in water are the same as those in air, the high density of water compared to air complicates sound transmission. Water’s density makes it an excellent conductor of sound, and sound travels five times faster in water than in air (1500 m/s in water VS 300 m/s in air). Because the speed of sound is proportional to frequency and wavelength, the difference in the speed of sound between water and air means that wavelengths in water are also about five times greater than wavelengths in air. In addition, sound attenuates less over the same distance in water than it does in air, enabling long distance transmission of underwater sounds (Slabbekoorn et al. 2010).

Sound waves propagating through water are composed of a pressure component and a
kinetic (particle motion) component (Rogers & Cox 1988; Montgomery et al. 2006). The kinetic component of sound dominates the acoustic nearfield (within ~ 1-2 wavelengths of a sound source), though it decays rapidly (proportional to the inverse of distance squared). Sound pressure decreases less rapidly (proportional to the inverse of distance), and thus dominates the acoustic farfield (> 1-2 wavelengths from a sound source) (Montgomery et al. 2006).

Some of the earliest measurements of undersea sound were made during World War II in several North American harbors to calibrate acoustic mines and harbor defense sonars (Knudsen et al. 1948; Urick 1983). Cato (1976, 1978) described the wind-dependent noise, traffic noise, and evening biological choruses (geophonic sound sources, anthrophonic sound sources, and biophonic sound sources, respectively) in the tropical waters near Australia. More recent research has focused on describing spatiotemporal patterns of underwater sounds (Radford et al. 2008a, 2008b; Radford et al. 2010; McWilliams & Hawkins 2013), whereas other studies have linked soundscapes to the structural characteristics of underwater habitats (Lammers et al. 2008) as well as the biotic composition of those habitats (Kennedy et al. 2010).

Although the description of spatio-temporal patterns in underwater soundscapes and their components continues, those investigations are complimented by many new studies focusing on how marine organisms use underwater sounds.

Perhaps the most well-known sound producing marine organisms are the Cetaceans. Humpback whales (Megaptera novaeangliae), blue whales (Balaenoptera musculus), and other Mysticetes produce loud (~ 190 dB re: 1 μPa), low frequency (< 1 kHz) calls (Winn & Winn 1978; Oleson et al. 2007; Sirović et al. 2007). In contrast, the Odontocetes, such as Bottlenose dolphin (Tursiops truncatus) and sperm whales ( Physeter macrocephalus), produce high
frequency (> 85 kHz) echolocation clicks (Houser et al. 1999; Madsen et al. 2002). Many taxa of fishes also produce sounds during courtship, spawning, or feeding (Connaughton & Taylor 1996; Gilmore 2002; Mann et al. 2009). Indeed, many of the common names for fish families reflect their vociferous nature (e.g., drums [Sciaenidae] and grunts [Haemulidae]). However, one of the most universal sources of biological sound in temperate and tropical waters are snapping shrimp (Cato 1992; Au & Banks 1998), which produce loud (> 160 dB re: 1 µPa), broad frequency “snaps”.

Marine organisms also passively use the marine soundscape. For example, bottlenose dolphin listen for the sounds produced by soniferous prey species (Gannon et al. 2005), while reminiscent of an auditory “cat and mouse” game, male silver perch (Bairdiella chrysoura) reduce the amplitude of their mating calls when the sounds of hunting Bottlenose dolphin are heard within their spawning area (Luczkovich et al. 2000).

Of broader ecological scope and importance, many studies have shown that the larvae of marine organisms orient toward, navigate by, and alter their behavior in response to sounds associated with suitable settlement habitat (Jeffs et al. 2003; Leis et al. 2003; Leis & Lockett 2005; Lillis et al. 2013, among others). The larvae of marine fishes and invertebrates employ a variety of sensory receptors to detect underwater sounds. Statocyst organs found in a diverse array of marine organisms (e.g., cephalopods [Bettencourt & Guerra 2000], crustaceans [Patton & Gove 1992], and fishes [Bretschneider et al. 2001]) function in the detection of the motional component of underwater sound (Budelmann 1992; Popper et al. 2001). These organs operate as differential density accelerometers; the statolith within the organ (see Figure 1 in Popper et al. 2001 for schematic illustration) has a higher density than the surrounding larva, and
therefore moves less than does the larva when subjected to a sound field. A bundle of mechanosensory cilia is connected to the statolith and sense the discrepancy of motion between the statolith and the surrounding tissue (Montgomery et al. 2006).

The detection of the pressure component of underwater sound is typically thought to be limited to organisms containing an enclosed gas bubble (particularly the swim bladder of most fishes [Popper & Fay 1999]). This bubble acts as a pressure-to-motion transducer (Figure 6 in Montgomery et al. 2006), vibrating with the pressure component of the acoustic field. This vibration radiates within the fish’s body and causes indirect stimulation of the otoliths within the inner ear. However, Montgomery et al. (2006) notes that the lack of a gas inclusion does not necessarily preclude an organism from sensing pressure. For example, hair cells in the dogfish *Scyliorhinus canicula* (Fraser & Schelmerdine 2002) and the crab *Carcinus maenas* (Fraser & MacDonald 1994) respond to hydrostatic pressure changes, and their discoveries suggest that other pressure or acoustic sensors may yet be found.

Regardless of sensory modality, the larvae of a host of marine organisms are using underwater sound to as an orientation and navigation cue. A number of studies have indicated that the larvae of many marine organisms are attracted to underwater sound emanating from coastal environments (Stobutzki & Bellwood 1998; Jeffs et al. 2003; Simpson et al. 2004; Leis & Lockett 2005; Vermeij et al. 2010). Furthermore, there is evidence that larvae of some fish and crustacean species are using specific components of the underwater soundscape to locate suitable settlement habitat (Simpson et al. 2008; Stanley et al. 2012).

However, like their terrestrial counterparts, underwater soundscapes do not escape anthropogenic influence. Low frequency (10 – 50 Hz) ambient sea noise closely related to noise
generated by shipping vessel traffic has increased 10-12 dB in the last half century (Ross 1993; McDonald et al. 2006), concomitant with a doubling of the number of commercial shipping vessels and a quadrupling of vessel gross tonnage (McDonald et al. 2006). In addition to increased noise from shipping traffic, the construction and operation of offshore wind farms can produce noises up to 220 dB re 1 µPa over frequencies from 100-10000 Hz (Fig. 10 in Thomsen et al. 2006), while blasts from seismic air-guns used for oil and gas exploration can have peak source levels of 250 dB re 1 µPa from 20-150 Hz (Engas et al. 1996). And this growing cacophony of anthropogenic underwater sounds has ecological consequences. Noise generation by whale-watching vessels alters the diving and swimming behavior of belugas (Delphinapterus leucas) and causes killer whales (Orcinus orca) to increase the amplitude of their calls (Lesage et al. 1999; Holt et al. 2009). Noise from coastal construction adversely affects Bottlenose dolphin hearing and communication (David 2006), and pile driving during the construction of offshore wind farms has the potential to mask communication and alter the behavior of harbor porpoises (Phocoena phocoena) and harbor seals (Phoca vitulina) (Thomsen et al. 2006). Studies have shown that boat noise alters the behavior of fishes (Slabbekoorn et al. 2010 and Popper et al. 2014 for reviews). Furthermore, there is growing evidence that anthropogenic underwater sounds pervade wilderness and protected areas (Hooker et al. 1999; Agardy et al. 2011) and alter the behavior of wildlife (Codarin et al. 2009; Picciulin et al. 2010).

Although the shallow waters of Florida Bay are classified as “wilderness habitat” by the US National Park Service, those habitats and the adjacent near-shore waters of the Florida Keys, have been drastically altered in recent decades by anthropogenically-driven changes in water quality, habitat structure, and underwater soundscapes - this is the ecosystem in which I
conducted my dissertation research. Florida Bay is a shallow, sub-tropical estuary lying between the southern tip of mainland Florida and the Florida Keys archipelago. The environment is a mosaic of seagrass meadows, mangrove islands, and hard-bottom habitats recognized for its productivity and importance as a nursery and foraging ground for a variety of marine organisms (Butler et al. 1995; Briceno & Boyer 2010). Hard-bottom habitat, characterized by limestone bedrock covered by a thin veneer of sand and macroalgae, constitutes roughly one third (~ 67,000 ha) of the near-shore environment of the Florida Keys and Florida Bay. Sponges dominate the animal biomass of hard-bottom communities where octocorals and ahermatypic stony corals also occur (Herrnkind & Butler 1994; Bertelsen et al. 2009). In 1991, 2007, and 2013 blooms of cyanobacteria engulfed large portions of Florida Bay and persisted for many months (Butler et al. 1995; Phlips et al. 1999; Blakey et al. 2015), killing nearly all of the sponges that once dominated hard-bottom areas in the region (Butler et al. 1995; Stevely et al. 2011; M. Butler, unpubl. data). The large-scale decimation of sponges in this ecosystem resulted in a series of dramatic changes in the Florida Bay - Florida Keys ecosystem, including alterations in: water quality, nitrogen cycling, nursery habitat structure, and underwater soundscapes. Currently, hard-bottom restoration efforts are underway (M. Butler, Old Dominion University) to examine whether sponge community restoration is feasible and if it aids the return of ecosystem functions to the degraded areas.

Within this context, I set out to examine how hard-bottom degradation and its subsequent restoration at experimental sites affects the ecosystem processes of soundscape production and larval recruitment. Firstly (Chapter 2), I characterized the underwater soundscapes of near-shore benthic habitats of Florida Bay and the Florida Keys: seagrass beds,
submerged mangrove prop roots, and hard-bottom. Additionally, I examined whether the soundscapes of hard-bottom sites degraded by sponge die-offs differed from hard-bottom sites unaffected by die-offs, and whether the soundscapes of hard-bottom areas undergoing active restoration were more similar to the soundscapes of degraded areas or to the soundscapes of healthy areas.

Secondly (Chapter 3), I examined whether degradation of hard-bottom habitat altered larval fish and invertebrate settlement among areas of healthy hard-bottom, degraded hard-bottom, and restored hard-bottom. Furthermore, I tested whether the incoming settlement-stage larvae use underwater sounds as a navigation cue by broadcasting the soundscapes of healthy hard-bottom within degraded hard-bottom areas and comparing larval settlement at playback sites versus silent control sites.

Lastly (Chapter 4), I evaluated how the loss of sponges on hard-bottom areas might affect populations of snapping shrimp, cryptic organisms producing conspicuous “snaps” that dominate hard-bottom soundscapes. To accomplish this, I employed remote acoustic monitoring techniques and distance sampling theory to estimate snapping shrimp population density and abundance within healthy and degraded hard-bottom areas.
CHAPTER 2

UNDERWATER SOUNDCAPES IN NEAR-SHORE TROPICAL HABITATS AND THE EFFECTS OF ENVIRONMENTAL DEGRADATION AND HABITAT RESTORATION

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. 2011a), but now include many studies in marine ecosystems (Fay 2009; Harris et al. 2015). 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. 2011a,b; Dumyahn & Pijanowski 2011).

Underwater sound and seascape ecology has been studied for decades (Harris et al. 2015), 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; Wilkens et al. 2012; Sharer 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 & 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 & Cox 1988; McCauley & Cato 2000; Montgomery et al. 2006; Radford et al. 2007).

Many taxa of marine fishes and invertebrates produce sounds (Myrberg 1981; Ladich 1997; Versluis et al. 2000; Bouwma & Herrnkind 2009; Sharer et al. 2014; Staaterman et al. 2014) and possess a wide range of auditory sensory abilities (Rogers & Cox 1988; Lovell et al. 2005; Mooney et al. 2010; Popper & 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 habitat-specific sounds increase the settlement of larval fishes and invertebrates (Tolimieri et al. 2000, 2004; Leis et al. 2002; Jeffs et al. 2003; Simpson et al. 2005; Radford et al. 2007). For example, settlement-stage crab larvae detect and interpret habitat-associated differences in underwater 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 & 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, I 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. I also examined how degradation affects the soundscapes of a specific habitat:
sponge-dominated, shallow hard-bottom. Finally, I determined whether the restoration of
hard-bottom sponge communities, previously destroyed by harmful algal blooms, also results in
the return of natural soundscapes.

MATERIALS AND METHODS

Site Selection

My 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
macrolagae 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 & 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 25m x 25m 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 me the opportunity to compare unaffected “healthy”, degraded, and restored hard-bottom soundscapes.

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) and visually confirmed by divers. Recordings were also made at existing hard-bottom restoration sites, thus constituting a fifth habitat type. I 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: unaffected hard-bottom and mangrove, N = 8; affected hard-bottom, N = 7; seagrass, N = 4; restored hard-bottom, N = 3 (Fig. 1).
Figure 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.
**Acoustic recordings**

From mid-May to mid-August in 2012 and 2013, habitat recordings were made using submersible hydrophone systems. A manufacturer-calibrated Aquarian Audio H2a omnidirectional hydrophone (Aquarian Audio Products: sensitivity -180dB re: 1V/µPa +/- 4dB 20Hz-4KHz]; 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 ~ 0.5m 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.

**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, the number of snapping shrimp (Alphaeidae) snaps was counted. 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. A 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. 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. 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. Because the ANOVAs for both snapping shrimp snaps and sound spectra used data from the same sound clips and are thus not truly independent, I maintained experiment-wise error by adjusting our critical p-values for determining significance to the 0.025 level or lower.

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 for 10 second sound clips from recordings of
individual sites within a habitat type at given moon phases and times (Window type: Blackman, FFT size: 1024), and all spectra for a specific habitat type, moon phase, and time were root-mean-square averaged to yield the composite spectra. 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).

RESULTS

Composite habitat spectra and representative spectrograms

Inspection of the composite spectra (Fig. 1) showed that regardless of moon phase, the dusk composite spectra for unaffected hard-bottom, restored hard-bottom, and mangrove were louder (i.e., the spectra levels, expressed in dB re 1 µPa, were greater) than their corresponding noon spectra. The affected 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 adding energy to these frequencies (Au & Banks 1998), though this peak is less pronounced in the affected hard-bottom and seagrass spectra where snapping shrimp abundance was probably lower.

The dusk, full moon composite spectra showed the greatest variability among habitats. Unaffected hard-bottom, restored hard-bottom, and mangrove habitats had more low frequency (<1 kHz) noise when compared to seagrass and affected hard-bottom, and the mangrove spectrum was 8 – 25 dB re 1 µPa louder than any of the other spectra throughout
frequencies less than 1 kHz. The unaffected hard-bottom and restored hard-bottom spectra were of similar shape within all four moon phase/time-of-day combinations and were 6 – 9 dB re 1 µPa louder in the higher frequencies (>10 kHz) than the affected hard-bottom, mangrove, or seagrass habitats. The unaffected hard-bottom habitat spectra, however, exhibited a greater mean spectrum level (100 – 24,000 Hz) during noon (47.91 ± 9.72 dB re 1 µPa /Hz; mean ± s.e.) and dusk (47.97 ± 9.7 dB re 1 µPa /Hz) at both moon phases than did the restored hard-bottom habitat (38.33 ± 16.05 & 40.75 ± 16.05 dB re 1 µPa /Hz, respectively).

Examination of representative spectrograms (Fig. 2) showed similar trends as the composite spectra. Throughout the four moon phase/time-of-day combinations, spectrograms of the unaffected hard-bottom soundscape and restored hard-bottom soundscape looked similar, both exhibiting more snaps than the affected hard-bottom soundscape. The spectrograms of the affected 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 unaffected hard-bottom or restored hard-bottom, although high energy (>80 dB re 1 µPa), broadband snaps and low frequency fish calls are not uncommon (Fig. 3). The energy of the fish calls was highest within the fundamental frequency - around 300 Hz, with subharmonics around 600 Hz, 900 Hz, and 1200 Hz adding additional low frequency energy to the soundscape.
Figure 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).
Figure 3. Representative healthy hard-bottom spectrogram at dusk during a full moon (colorbar units: dB re 1 µPa).
Figure 4. Representative degraded hard-bottom spectrogram at dusk during a full moon (colorbar units: dB re 1 µPa).
Figure 5. Representative restored hard-bottom spectrogram at dusk during a full moon (colorbar units: dB re 1 µPa).
Figure 6. Representative mangrove spectrogram at dusk during a full moon (colorbar units: dB re 1 µPa).
Figure 7. Representative seagrass spectrogram at dusk during a full moon (colorbar units: dB re 1 µPa).
Figure 8. Spectrogram of a snapping shrimp snap (A) and a toadfish call (B).
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 seconds, as did their interaction ($F_{4,531} = 12.51, p << 0.001$). Moon phase and 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. 4) indicates that the number of snaps per 10 seconds 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-seconds (444.54 ± 19.47; mean ± s.e.) than did noon recordings (266.59 ± 12.93; mean ± s.e.).

The 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 ± s.e.) were more acoustically complex than noon soundscapes (376.11 ± 5.69; mean ± s.e.).
Figure 9. Profile plot of the habitat type by time interaction effects on the number of snapping shrimp snaps/10 secs. Affected hard-bottom (AHB), seagrass (SG), unaffected hard-bottom (UHB), mangrove (M), and restored hard-bottom (RHB) are along the x-axis; noon (dashed) and dusk (solid) are separate lines. Error bars are standard error of the mean.
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 ten seconds. Results of a Tukey’s HSD test of all pairwise treatment means is shown below the ANOVA table; treatment group means sharing an underline are not significantly different at the $P(\alpha) = 0.05$ level.

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1 Error term: Site(Habitat)
2 Error term: Moon*Site(Habitat)

Results of Tukey’s HSD

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DISCUSSION

My results demonstrate that tropical near-shore 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 ~300Hz (see below), 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, offers 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 reestablishing a natural soundscape in hard-bottom habitats previously subject to sponge die-offs.

The acoustic characteristics of near-shore 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. (2013) 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 and the response of fish and invertebrate larvae to those sounds (Tolimieri et al. 2000; Simpson et al. 2004, 2006, 2011; McCauly and Cato 2000; Montgomery 2006; Radford et al. 2007; Stanley et al. 2009; Kennedy 2010; Stanley et al. 2012; McWilliam and Hawkins 2013 and others). With the exception of the current study, I am unaware of any published descriptions of the soundscapes of near-shore tropical habitats, the most prominent and ecologically important being: seagrass, hard-bottom, and the submerged prop root edges of mangrove islands.

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 & Fine 2002a). Male toadfish in the genus Opsanus produce their characteristic “boatwhistle-like” sound 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 & Fine
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 my recordings were the pulsed, broadband (~2 – 5 kHz) pops and 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 (Au & Banks 1998), within the frequency range detectible for marine fish and invertebrate larvae (Tolimieri et al. 2000; Jeffs et al. 2005). The number of snaps produced by snapping shrimp varied widely at each of the habitats I 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 an affected 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 (Albers 1965; Urick 1984; Knowlton and Mouton 1963; Readhead 1996; Au & 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 measureable 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 trophic structure (Behringer and Butler 2006), and diminished capacity for water column filtration (Peterson et al. 2006). I 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 potential 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, Cato (1978) recorded reef noise detectable above surface wind noise up to 25 km offshore in Australian waters. Over the past few decades, there has been increasing interest in the role sound may play in the orientation of pelagic larval fishes, decapods, and mollusks to coastal nurseries. Though it has been traditionally thought that only fish larvae with enclosed gas bladders can detect and localize the far-field pressure component of sound (Popper & Fay 1999; Webb & Smith 2000; Montgomery et al. 2006), sensory setae in adult organisms lacking gas bladders may also allow them to detect hydrostatic pressure changes (e.g., in the dogfish Scyliorhinus canicula [Fraser & Shelmerdine 2002], in the crab Carcinus maenas [Fraser & Macdonald 1994]). Philips & Macmillan (1987) suggested that the
rows of pinnate sensory setae on the antennae of the puerulus-stage lobster *Panulirus cygnus*
are far-field vibratory receptors, possibly allowing the puerulus to orient to vibrations
generated along the coast. Furthermore, laboratory- and field-based assays have shown
behavioral responses to sound cues in larval fishes and invertebrates (Tolimieri et al. 2000,
2002, 2004; Jeffs et al. 2003; Radford et al. 2007; Stanley et al. 2012). Tolimieri et al. (2000,
2002, 2004), Jeffs et al. (2003) and Simpson et al. (2004, 2005) were among the first to playback
underwater sounds and demonstrate that sound guides reef fish larvae and larval decapods.
Stanley et al. (2009) found that the megalopae of five crab species altered their swimming
behavior and metamorphosed more quickly when exposed to experimentally replayed ambient
reef noise in a laboratory setting. More recently, research by Lillis et al (2013) showed that
oyster larvae are attracted to sounds present on temperate oyster reefs. I have also played
back sounds recorded on healthy, unaffected hard-bottom habitats at hard-bottom sites now
devoid of sponges due to cyanobacteria blooms and measured fish and larval recruitment onto
artificial collectors (Chapter 3). Similar to studies in other habitats, I found that the magnitude
and diversity of larval recruits is higher on sites where we played back the sounds of healthy,
intact hard-bottom communities.

*Quantitative discrimination of soundscapes among habitats*

Humans can easily distinguish by ear subtle differences 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. I 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. 5A). Figure 5B shows the ACI scores for each habitat type during the full and new moons at noon and dusk. Though the differences in ACI scores among habitats were not significant, the plot shows the same general trend as the composite soundscapes and number of snaps. Recordings of seagrass sites and degraded hard-bottom 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 recordings to which I applied this index are dominated by the broadband, loud snaps of snapping shrimps that add energy to a range of frequencies. Though 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. To my knowledge, this is the only study to create composite spectra for separate habitats. The composite spectra provide a simpler way to view habitat spectra and estimate trends within and among soundscapes, 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. 2D) indicates that fish calls within these frequencies (Fig. 3) are likely adding that energy.
Figure 10. (A) Dusk exhibited a higher ACI score than noon, though there was no difference between full moon (black) and new moon (grey) phases. (B) ACI scores for each habitat type (AHB – affected hard-bottom; SG – seagrass; UHB – unaffected 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.
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 & 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 Spheciospongia 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 et al. 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 acoustic 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 and Arvedlund & 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 & 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, Mark Butler's laboratory at Old Dominion University 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 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. My 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. I 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. This study demonstrates that restoration via transplantation of foundational species, in this 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. The purposeful destruction of habitats so as to experimentally rebuild them ecological piece by ecological piece just to understand ecosystem function is unconscionable. However, restoration of habitats already degraded by natural or
anthropogenic factors provides a way to gain insights to the interplay of ecological processes and ecosystem functions. Yet, restoration without the benefit of carefully planned research and monitoring are opportunities lost.
CHAPTER 3

THE EFFECTS OF NEAR-SHORE TROPICAL HARD-BOTTOM HABITAT DEGRADATION AND RESTORATION ON LARVAL FISH AND INVERTEBRATE RECRUITMENT AND THE ROLE OF UNDERWATER SOUNDCAPES

INTRODUCTION

The planktonic larvae and post-larvae of marine animals use a variety of cues from the surrounding environment to locate suitable settlement habitat, including: coastal or conspecific odors, salinity, temperature, pressure, flow, light, physical structure, magnetism, and sound.

The literature regarding larval settlement cues abounds, beginning with early studies of phototaxis (Kawaguti 1941; Thorson 1964; Ritz 1972) that sparked subsequent investigations on a variety of species. From that research we now have a much clearer understanding of light’s influence on the behavior and settlement of larvae from a diverse set of species, including corals (Kawaguti 1941; Lewis 1974; Morse et al. 1988; Mundy & Babcock 1998), barnacles (Crisp & Ritz 1973; Forward & Costlow Jr 1974; Lang et al. 1979), sponges (Warburton 1966; Bergquist et al. 1970; Moldonado & Young 1996; Leys & Degnan 2001), crabs (Forward et al. 1989; Sulkin & van Heukelem 1982), and lobsters (Ritz 1972; Butler et al. 2011) among others.

Others have shown that marine larvae respond to chemical cues (chemotaxis), mainly substances that are indicative of suitable settlement habitat (Morse & Morse 1984; Weiner et al. 1989; Butler & Herrnkind 1991; Goldstein & Butler 2009) or compounds associated with conspecifics or food (Burke 1986; Pawlik 1992). For example, Zimmer-Faust & Tamburri (1994)
and Harder et al. (2002) showed that larvae of the oyster *Crassostrea virginica* and of the polychaete *Hydroides elegans*, respectively, settled rapidly in response to chemicals released into the water column by biofilms indicative of appropriate settlement habitat (Harder et al. 2002).

Often, marine larvae use multiple cues simultaneously or sequentially to locate suitable nursery areas. For example, American blue crab (*Callinectes sapidus*) megalopa use subtle changes in salinity, temperature, pressure, and organic chemical cues to move to upstream nursery zones within estuaries, a behavior called “selective tidal stream transport” (Forward et al. 1989; Olmi 1994; Forward et al. 2001). Similarly, gradients in salinity, pressure, and chemicals released from red algae guide post-larval spiny lobsters (*Panulirus argus*) to coastal nurseries from up to 20 km offshore (Goldstein & Butler 2009). Lecchini et al. (2005) determined that visual, olfactory, and even auditory (i.e., “sound”) cues influence the settlement of the coral reef fish *Chromis viridis*.

Indeed, underwater sound is used by the pelagic larvae of many fishes (Pomacentridae, Tripterygiidae and Clupeidae), decapods (e.g., crabs and lobsters), bivalves (e.g., mussels and oysters), and corals to orient toward coastal settlement habitats, especially coral reefs (Tolimieri et al. 2000; Kingsford et al. 2002; Leis et al. 2002; Jeffs et al. 2005; Vermeij et al. 2010; Lillis et al. 2013). Unlike chemical cues that are distributed by currents or visual cues limited by light’s high attenuation in water, underwater sound has the potential to carry biologically relevant information long distances irrespective of water movement or depth.

Geophony (sounds generated by geophysical phenomena) and biophony (sounds of biological origin) comprise the natural soundscape of a habitat (Pijanowski et al. 2011). Marine
soundscapes, all the sounds originating from a given area or habitat, have been studied for decades. Geophonic sources of underwater sound include rainfall, earthquakes, and wind-driven surface agitation (Hildebrand 2009), and many studies have shown a significant relationship between ambient underwater noise and wind speed (Knudsen et al. 1948; Wenz 1962; Kreman 1984). Biophonic sources of underwater noise also have a long history of study, beginning with research by Tait (1962) and Cato (1978) who described crepuscular choruses dominated by snapping shrimp and urchins in the waters off New Zealand and Australia. More recent studies have investigated how sounds vary temporally within habitats, especially between day and night and among lunar cycles (Radford et al. 2008a, 2008b; Staaterman et al. 2014), and spatially among habitats (Kennedy et al. 2010; McWilliam & Hawkins 2013; Radford et al. 2010, 2014). This temporal and spatial specificity of habitat-associated soundscapes provides marine larvae with information about the habitats from which the sounds originated - a navigational cue.

Early studies in New Zealand and Australia determined that noise generated along coastal reefs, a possible navigation cue for larvae searching for settlement habitat, could be directionally detected up to 10 km offshore (Tait 1962), and that detectable reef noise would be louder than wind-generated surface noise up to 25 km offshore (Cato 1978). More recent studies have empirically tested the role of sound in larval recruitment by experimentally broadcasting reef noise at off-reef sites. Those experimental investigations have revealed that some larval fish and decapods do indeed respond underwater sounds (Jeffs et al. 2003; Simpson et al. 2005; Tolimieri et al. 2000, 2004). More recent studies by Stanley et al. (2009, 2011) found that ambient underwater reef sound altered the swimming behavior, reduced the
time to metamorphosis, and induced settlement in five temperate and tropical brachyuran crab species. Others have documented that some reef fish and invertebrate larvae use different components of reef noise to find appropriate settlement sites, thus indicating their ability to discern habitat-associated differences in soundscapes. For instance, Stanley et al. (2012) recorded soundscapes of habitats with distinct acoustic spectra, replayed those recordings in laboratory tanks containing Brachyuran crab megalopae, and showed that the time to metamorphosis of megalopae was reduced when presented with acoustic recordings of their preferred settlement habitat. Simpson et al. (2008) measured the response of a variety of settlement stage reef fish to the filtered components of reef noise (either 570 – 2000 Hz or below 570 Hz) and found that the larvae preferred the 570 – 2000 Hz frequency component of reef noise.

Unfortunately, marine ecosystems worldwide are degraded by anthropogenic stressors (Jackson et al. 2001; Pew Oceans Commission 2003; Halpern et al. 2008), including acoustic interference. Coastal ecosystems are particularly vulnerable to degradation (Vitousek et al. 1997; Limburg 1999; Lotze & Milewski 2004), which reduces their ecological functioning and interrupts ecological processes (Solan et al. 2004; Worm et al. 2006; Diaz & Rosenberg 2008). Some studies have examined the effect of habitat degradation on ecological functions such as productivity (Short & Wyllie-Echevarria 1996) or the provisioning of shelter from predation (Turner et al. 1999), but few have examined how habitat degradation affects soundscape generation.

In Chapter 2, I described how the loss of structure-forming sponges in near-shore hard-bottom habitats diminished soundscapes in degraded areas, and demonstrated that habitat
restoration via sponge outplanting aided the recovery of a natural soundscape. Because sound plays a role as a navigational cue to many larvae seeking appropriate nursery habitats, habitat degradation may also interrupt the processes of larval recruitment and settlement via its effect on the acoustic properties of the habitat. However, if habitat restoration can return a natural soundscape, then it has the potential to ameliorate the effect of soundscape deterioration on larval recruitment.

The goals of this study were two-fold. Firstly, I aimed to quantify the settlement of larval and post-larval fish and invertebrates within areas affected and unaffected by habitat degradation, as well as areas undergoing restoration, and to test if recruitment differs among these areas. My second goal was to empirically test the role of sound in larval recruitment by determining if broadcasting the sound of unaffected habitat within degraded areas prompts higher larval settlement.

MATERIALS AND METHODS

These studies were carried out in Florida Bay and near-shore waters of the Florida Keys (USA), which are a mosaic of seagrass meadows, mangrove-fringed islands, and sponge-dominated hard-bottom. Over the course of the past two decades, these areas have seen substantial ecological changes. Expansive, recurring cyanobacteria blooms have engulfed large swaths of the habitats of Florida Bay and have precipitated large-scale sponge die-offs within ~500 km² of the central and southern portions of the bay (Butler et al. 1995; Philips et al. 1999). Sponges dominate the animal biomass of hard-bottom, filter the water column above these communities, and provide habitat and shelter for motile organisms (Chiappone & Sullivan 1994;
Butler et al. 1995; Peterson et al. 2006). Thus, the near complete loss of these crucial inhabitants of hard-bottom has changed the ecological character of the environment. In an effort to combat the loss of ecological functions, a study to test the feasibility of restoring sponge communities by outplanting sponges taken from areas unaffected by the cyanobacteria blooms into areas affected by the sponge die-offs is underway (M. Butler, Old Dominion University). My study takes advantage of that restoration study by utilizing some of the sites established in that project.

Quantifying settlement of larval fishes and invertebrates

To test the effect of habitat degradation and subsequent habitat restoration on the settlement of larval fishes and invertebrates, nine sites were selected in different hard-bottom areas: three sites in “healthy” hard-bottom outside the extent of the cyanobacteria blooms to serve as positive controls, three sites within hard-bottom areas degraded by the blooms to serve as negative controls, and three sites where sponge outplantings had been placed as part the restoration feasibility study. At each site, three larval collectors were deployed. These collectors were made of frayed rope woven into a mesh backing 50 cm wide by 100 cm long and mimic the physical structure of bottom vegetation sought by many types of settling fish and macroinvertebrate larvae, including the Caribbean spiny lobster *Panulirus argus* (Fig. 6). The collectors were tethered to concrete blocks and suspended in the water column by buoys attached to the top of the collectors.

The collectors were deployed in May 2013 and remained in the water for the duration of the study, until September 2013. After every new moon (n = 3) and full moon (n = 3), the
collectors were unclipped from their tether blocks and placed into a mesh bag with 1 mm² holes, into which the collectors were shaken to remove any settled larvae from the collector. The collected larvae were preserved in 70% ethanol and later identified to the lowest taxonomic level possible (at least to genus) using a dissecting microscope.

Larval community assemblage data were Hellinger-transformed (Rao 1995; Legendre & Gallagher 2001) and analyzed via a non-parametric (permuted) multivariate analysis of variance (npMANOVA); moon phase (new or full) and habitat health (healthy, degraded, or restored) were fixed factors, and the random factor of site was nested within habitat health. The Hellinger transform has been suggested as a useful transformation in the analysis of community composition data by making the data more suitable for analysis by ordination techniques (e.g., principal components analysis or multidimensional scaling) (Legendre & Gallagher 2001). The analysis was run using the Fathom toolbox (Jones 2015) for MATLAB (Mathworks, Inc.) and any significant differences for fixed factors were analyzed using a pair-wise npMANOVA.

Data were visually represented using 3-dimensional non-metric multidimensional scaling (3D-nMDS). As the name implies, this ordination technique is non-metric; that is, the MDS algorithm relies on the rank order of samples, not the underlying dissimilarities, to create a map of relative distances between samples in a set number of dimensions (in this case, three) that preserves the ranks among the samples. The algorithm is iterative. To start, samples are randomly distributed throughout the ordination space, and each subsequent iteration moves similar samples closer together and dissimilar samples further apart to reduce the stress of the scaling, a measure of goodness of fit, until a minimum stress value is reached (see Legendre & Legendre 1998, Clarke & Warwick 2001, and Gotelli & Ellison 2013 for reviews and
applications). However, unlike metric ordination techniques such as principal components analysis that preserve the distance between samples, the axes of the nMDS plot represent only a coordinate system in ordination space onto which the samples are plotted, and not the components that drive sample differences (Pos et al. 2014).

Figure 11. Larval collector tethered to a concrete-filled block and suspended in the water column via a buoy on the surface.
Testing if sound playback prompts higher larval settlement

The “blank canvas” of barren hard-bottom created by the sponge die-offs afforded me the opportunity to empirically test whether settlement-stage larvae of fishes and invertebrates use sound to locate appropriate settlement habitat. These hard-bottom barrens are devoid of sponges, thus removing potential cues that larvae might use to find a settlement site, including the underwater soundscape of healthy hard-bottom. A sound playback device, consisting of a Lubell Labs 916C underwater loudspeaker (frequency response 200 Hz – 20 kHz, 180 dB re 1 µPa output @ 1 kHz) connected to a waterproof barrel that housed a solid-state WAV player, an amplifier to drive the speaker, and an AGM battery to power the speaker/amplifier combination, was used to broadcast healthy hard-bottom soundscapes (i.e., soundscapes recorded on hard-bottom areas that were outside the extent of the cyanobacteria blooms) within hard-bottom die-off areas. Eight healthy hard-bottom soundscape recordings were used for playback, one for each trial, to avoid pseudoreplication. These healthy hard-bottom recordings were made using the calibrated hydrophone system described in Chapter 2 on sites outside of the extent of the sponge die-off in areas where sponges still dominate the animal biomass of hard-bottom communities.

Four locations within the sponge die-off area were selected, and two sites at each location were established 1 km apart (Fig. 7). At the sound playback treatment site, the sound playback device was deployed in the evening of each night of the trial and recovered the next morning, and at the silent control site a structural mimic of the sound playback device was deployed. On both the sound playback site and silent control site, two larval collectors as described in the previous section were deployed on the first day of the trial and were retrieved
the final day of the trial. The collectors were placed in opposing directions ~ 10 m from either the playback device or the structural mimic. One trial consisted of five nights: two nights prior to a moon phase of interest, either new moon (n=4) or full moon (n=4), the night of the moon phase, and two nights post moon phase, thus totaling five nights. When retrieved, the larval collectors were placed into a mesh bag (1 mm² holes) and shaken to remove any settled larvae and post-larvae from the collector. Larval collections were preserved in 70% ethanol and later identified to the lowest feasible taxonomic level (at least to genus) using a dissecting microscope. Larval community assemblage data were Hellinger-transformed (Legendre & Gallagher 2001) and analyzed via a two-way analysis of similarity (moon phase – new or full; treatment – sound playback or no sound control), and data were inspected to discern the pattern between treatments when significant differences existed for a factor. Data were again visually represented using 3D-nMDS.
Figure 12. Map showing the four experimental soundscape broadcast locations. Left inset shows the distance between two sites within a location.
RESULTS

Quantifying settlement of larval fishes and invertebrates

Of the 10,391 recruits of 43 different species collected, crustaceans (40% of catch; 4213 individuals of seven species) and mollusks (44% of catch; 4547 individuals of 16 species) dominated the catch of larvae on artificial collectors on my study sites. Table 2 summarizes the collections by moon phase (new or full) and habitat quality (healthy, degraded, or restored).

Table 2. Summary of larval collections in healthy, degraded, and restored hard-bottom areas during new and full moons

<table>
<thead>
<tr>
<th>Source</th>
<th>Healthy</th>
<th>Degraded</th>
<th>Restored</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>1841 individuals</td>
<td>719 individuals</td>
<td>941 individuals</td>
<td>3501 individuals</td>
</tr>
<tr>
<td></td>
<td>29 species</td>
<td>24 species</td>
<td>25 species</td>
<td>36 species</td>
</tr>
<tr>
<td>Full Moon</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>2238 individuals</td>
<td>2559 individuals</td>
<td>2093 individuals</td>
<td>6890 individuals</td>
</tr>
<tr>
<td></td>
<td>30 species</td>
<td>32 species</td>
<td>30 species</td>
<td>39 species</td>
</tr>
<tr>
<td>New Moon</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>4079 individuals</td>
<td>3278 individuals</td>
<td>3034 individuals</td>
<td>10391 individuals</td>
</tr>
<tr>
<td></td>
<td>34 species</td>
<td>34 species</td>
<td>32 species</td>
<td>43 species</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Table 3. Permutational MANOVA results testing the effects of habitat quality, moon phase, and site on larval community assemblage.

<table>
<thead>
<tr>
<th>Source</th>
<th>DF</th>
<th>SS</th>
<th>MS</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Habitat Quality</td>
<td>2</td>
<td>1.1516</td>
<td>0.5758</td>
<td>2.955</td>
<td>0.030</td>
</tr>
<tr>
<td>Moon Phase</td>
<td>1</td>
<td>0.7767</td>
<td>0.7767</td>
<td>9.199</td>
<td>0.001</td>
</tr>
<tr>
<td>Site</td>
<td>6</td>
<td>1.1689</td>
<td>0.1948</td>
<td>2.3074</td>
<td>0.036</td>
</tr>
<tr>
<td>Habitat Quality x Moon Phase</td>
<td>2</td>
<td>0.2913</td>
<td>0.1456</td>
<td>1.7248</td>
<td>0.146</td>
</tr>
<tr>
<td>Residual</td>
<td>70</td>
<td>24.485</td>
<td>0.3498</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
The results of the npMANOVA (Table 3) indicated that both habitat quality and moon phase significantly affect the assemblage of larvae that recruited to hard-bottom sites. The *a posteriori* pair-wise npMANOVA indicated that larval assemblages recruited to healthy areas differed from those recruited to degraded or restored habitat (F = 2.955; df = 2, 70; p = 0.030). This is particularly evident during full moon when collections of larvae in healthy hard-bottom habitat were double those of degraded or restored habitats. In addition, larvae were more abundant during new moon than full moon (F = 9.199; df = 1, 70; p = 0.001; Table 3). There were also significant differences in larval settlement among sites within a treatment, as indicated by the significance of that effect in the npMANOVA (F = 2.3074; df = 6, 70; p = 0.036; Table 3).

Overall, more recruits settled in hard-bottom habitat unaffected by sponge die-offs than either degraded hard-bottom or restored hard-bottom habitats. Examination of the larval assemblages shows that the largest recruitment differences occurred in thirteen species: seven mollusks, three crustaceans, two fishes, and one echinoderm (Table 4). The 3-dimensional non-metric multidimensional scaling plot (Fig. 8) illustrates how habitat quality and moon phase affected larval recruitment (stress; 0.081, $r^2 = 91.75$). Restored hard-bottom (blue) and degraded hard-bottom (red) grouped together away from healthy hard-bottom (green). In addition, new moon collections (dark color shades) and full moon collections (light color shades) grouped separately for each habitat type. These groupings corroborate the results of the npMANOVA.
Table 4. Summary of the thirteen species with the largest differences among habitats.

<table>
<thead>
<tr>
<th>Genus</th>
<th>Healthy</th>
<th>Degraded</th>
<th>Restored</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Mollusca</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Aplysia</em></td>
<td>5</td>
<td>82</td>
<td>81</td>
</tr>
<tr>
<td><em>Bulla</em></td>
<td>517</td>
<td>85</td>
<td>162</td>
</tr>
<tr>
<td><em>Cerithium</em></td>
<td>517</td>
<td>85</td>
<td>162</td>
</tr>
<tr>
<td><em>Columbella</em></td>
<td>229</td>
<td>83</td>
<td>76</td>
</tr>
<tr>
<td><em>Lima</em></td>
<td>218</td>
<td>157</td>
<td>207</td>
</tr>
<tr>
<td><em>Spondylus</em></td>
<td>77</td>
<td>525</td>
<td>152</td>
</tr>
<tr>
<td><em>Tegula</em></td>
<td>53</td>
<td>10</td>
<td>11</td>
</tr>
<tr>
<td><strong>Crustacea</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Palaemonetes</em></td>
<td>1507</td>
<td>575</td>
<td>550</td>
</tr>
<tr>
<td><em>Panulirus</em></td>
<td>83</td>
<td>257</td>
<td>221</td>
</tr>
<tr>
<td><em>Stenorhynchus</em></td>
<td>23</td>
<td>522</td>
<td>358</td>
</tr>
<tr>
<td><strong>Echinodermata</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Holothuria</em></td>
<td>26</td>
<td>220</td>
<td>138</td>
</tr>
<tr>
<td><strong>Fish (Syngnathidae &amp; Belniidae)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Paraclinus</em></td>
<td>177</td>
<td>62</td>
<td>149</td>
</tr>
<tr>
<td><em>Syngnathus</em></td>
<td>58</td>
<td>19</td>
<td>11</td>
</tr>
</tbody>
</table>
Figure 13. Three-dimensional non-metric multidimensional scaling plot showing groupings of healthy, restored, and degraded hard-bottom sites during full moon (FM) and new moon (NM). Healthy hard-bottom is displayed in green, restored hard-bottom is displayed in blue, and degraded hard-bottom is displayed in red. Moon phase is displayed as shadings of the various colors: light shades indicate full moon, dark shades indicate new moon.
Testing if sound playback prompts higher larval settlement

The larvae of 22 species, 2625 organisms total, recruited onto artificial collectors on the experimental sites over the eight trials. Seven species of mollusks accounted for roughly 76% (2005 individuals) of the collections; a bivalve clam species (likely *Lima* sp.) accounted for 73% (1929 individuals) of the entire collection. The largest difference between the sound playback treatment and silent treatment occurred during the full moon phase, where 510 organisms recruited to the sound treatment, whereas 386 organisms recruited to the silent treatment. This difference was driven by the *Lima* sp. clam – 401 individuals recruited to the sound treatment, and 280 individuals recruited to the silent treatment. The difference between moon phases followed the same trend as the previous experiment above, wherein larvae were more abundant during the new moon phase than the full moon phase. Table 5 summarizes the larval collections by moon phase (new and full) and sound treatment level (sound playback and silent control).

Table 5. Summary of larval collections at sound playback and silent control sites during new and full moon.

<table>
<thead>
<tr>
<th></th>
<th>Sound Playback</th>
<th>Silent Control</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Full Moon</td>
<td>510 individuals</td>
<td>386 individuals</td>
<td>896</td>
</tr>
<tr>
<td></td>
<td>10 species</td>
<td>13 species</td>
<td>13 species</td>
</tr>
<tr>
<td>New Moon</td>
<td>852 individuals</td>
<td>877 individuals</td>
<td>1729</td>
</tr>
<tr>
<td></td>
<td>13 species</td>
<td>14 species</td>
<td>19 species</td>
</tr>
<tr>
<td>Total</td>
<td>1362 individuals</td>
<td>1263</td>
<td>2625</td>
</tr>
<tr>
<td></td>
<td>15 species</td>
<td>19 species</td>
<td>22 species</td>
</tr>
</tbody>
</table>
The results of the two-way analysis of similarity indicate that both sound playback ($R = 0.64$, $p = 0.008$, 1000 permutations) and moon phase ($R = 0.69$, $p = 0.03$, 1000 permutations) significantly affected the larval assemblages that recruited onto artificial collectors at the degraded hard-bottom sites. Figure 9 shows the grouping of treatment combinations in 3D-nMDS plots (stress: 0.038, $r^2 = 96.59$).
Figure 14. Three-dimensional non-metric multidimensional scaling plot showing the relationships among the lunar and sound-playback treatment groups. Sound playback groups are shown in blue, whereas no playback control groups are shown in red. Moon phase is indicated by shading; lighter shades represent full moon, darker shades represent new moon.
DISCUSSION

As human use of ocean resources continues to degrade marine environments, understanding how habitat degradation affects ecosystem processes may lead to more effective conservation, and restoration efforts that salvage damaged ecological function as well as taxonomic structure. In this study, I examined how habitat degradation affects larval recruitment, and whether larvae use underwater sounds to find suitable settlement habitat. I capitalized on the unfortunate loss of large, structure-forming sponges in Florida Bay as a “natural experiment” and compared the assemblages of fish and invertebrate larvae that settled within degraded hard-bottom areas, hard-bottom areas unaffected by sponge die-offs, and hard-bottom sites undergoing active restoration. I also tested whether larvae are specifically attracted to the sounds emanating from healthy hard-bottom habitat. Both habitat quality and moon phase significantly affected the assemblage of larvae that recruited to hard-bottom sites. The \textit{a posteriori} pair-wise npMANOVA indicated that larval assemblages that recruited to healthy areas differed from those that recruited to degraded or restored habitat ($F = 2.955$; $df = 2, 70$; $P = 0.030$). This is particularly evident during full moon when collections of larvae in healthy hard-bottom habitat were double those of degraded or restored habitats. In addition, larvae were more abundant during new moon than full moon. I discovered that both habitat quality and moon phase significantly affect the assemblage of larvae that recruited to hard-bottom sites. A greater number and variety of larvae recruited to healthy areas than to degraded or restored habitat, especially during full moon when larval recruitment in healthy hard-bottom habitat was twice that in degraded or restored habitats.

The various cues that settlement-stage larvae use to navigate to suitable habitats are
often discussed in isolation (Kingsford et al. 2002), so disentangling larval response to one cue versus another can be difficult in the field. I broadcast the sound of healthy hard-bottom at degraded hard-bottom sites to test whether recruiting larvae use soundscapes to locate nursery habitat and found that the playback of healthy hard-bottom soundscapes on degraded hard-bottom sites enhanced larval recruitment, particularly during the full moon. More larvae recruited to sound playback sites during the full moon as compared to silent controls, those differences driven largely by the recruits of a bivalve clam (Lima sp.).

The recruitment of larvae of many marine organisms often peaks around the new moon (e.g., bluehead wrasse Thalassoma bifasciatum [Victor 1986], clownfish Amphiprion polymnus [Jones et al. 2005], the Caribbean spiny lobster Panulirus argus [Acosta et al. 1997], Penaeid shrimp Farfantopenaeus duorarum [Rossler & Rehrer 1971]). I also observed greater numbers of recruits during new moon compared to full moon, consistent with many previous studies. However, it appears that difference in recruitment between the sound playback and silent control sites was driven during the full moon phase (Tables 5). There is almost certainly some bias in the types of larvae that were attracted to the collectors that I deployed in this study. For example, light traps, used to collect a variety of fish and invertebrate species in other studies (e.g., Jeffs et al. 2003; Simpson et al. 2004), have been criticized for being biased toward specific size, age, or taxonomic groups (Gregory & Powles 1985; Brogan 1994; Hernandez & Lindquist 1999; Marchetti & Moyle 2000). The larval collectors I employed mimic the benthic algae in which a variety of hard-bottom associated organisms settle, and have been used previously in studies around the Florida Keys (e.g., Herrnkind & Butler 1994). Still, it’s possible that an artificial collector might have a carrying capacity with respect to settling larvae, so that
once a certain number of larvae settle onto a collector it becomes less attractive to subsequent settlers. If so, then collectors might underestimate recruitment when larvae are at high densities. In addition, healthy hard-bottom areas might offer larvae more settlement sites compared to degraded areas, thus the collectors in degraded habitats might represent prime settlement substrate and attract larvae from a wider area than collectors within healthy hard-bottom areas.

\textit{Habitat degradation and larval settlement: a role for sound}

Most marine fishes and invertebrates have a bipartite life history, wherein adults spawn dispersive larvae (Kingsford et al. 2002) that spend hours to months in the plankton (Scheltema 1986; Leis & McCormick 2002) before locating a suitable environment in which to settle. These larvae use a variety of cues to orient toward and navigate to appropriate settlement habitat (see Kingsford et al. 2002 for review). Many species use multiple settlement cues at once or in sequence (e.g., barnacles [Hills et al. 1998], American blue crab \textit{Calinectes sapidus} [Forward 1989; Forward & Tankersely 2001], Caribbean spiny lobster \textit{Panulirus argus} [Goldstein & Butler 2011], and fishes [Lecchini et al. 2005; Huijbers et al. 2012]).

Among the host of settlement cues, underwater sound is unique. It propagates long distances regardless of current, so sound can carry biologically relevant information to distant larvae (Jeffs et al. 2003, 2005; Radford et al. 2008, 2010). Still, a larva must possess the sensory abilities to detect and respond to different information within the soundscape. Kingsford et al. (2002) reviewed the sensory abilities of a broad range of marine taxa. The literature at that time indicated that the larvae of many organisms in higher taxonomic groups (e.g., cephalopods
[Williamson 1995], lobsters [Jeffs et al. 1997], and fishes [Fay & Popper 1999]) use auditory cues during settlement. However, recent studies have shown that species previously thought to lack the sensory abilities necessary to use underwater sounds do indeed respond to acoustic stimuli. Vermeij et al. (2010) broadcast coral reef noise using underwater loudspeakers and found that coral larvae detect and positively respond to the reef sounds. Lillis et al. (2013) combined field and laboratory trials to determine that Eastern oyster (*Crassostrea virginica*) larvae settle in response to oyster reef soundscapes. Furthermore, Stanley et al. (2011, 2012) showed that megalopae of some New Zealand crabs alter their swimming behavior and experience a decrease in time to metamorphosis in response to acoustic cues produced along rocky shorelines. Their studies also indicated that the behavioral response thresholds of the crab larvae were sensitive enough to detect acoustic settlement cues up to 40 km offshore.

My results indicate that larval recruitment differed among healthy and degraded hard-bottom habitats, and some of the taxa whose recruitment differed among habitats are known to respond to variation in underwater soundscapes. For instance, larvae of the two families of fishes (Syngnathidae and Bleniidae) that showed distinct differences in recruitment among habitats in my study respond to sound (Simpson et al. 2008), some of which may be cues produced by conspecifics. Some members of the Syngnathidae produce high frequency, short duration clicks (Colson et al. 1998; Ripley & Foran 2007) whose function is as yet unknown, but could potentially serve as a localized navigational cue for larvae as high frequency sounds do not propagate as far as low frequency noises. Recent work by Lillis et al. (2013) indicate that larvae of the oyster *Crassostrea virginica* settle in response to habitat-associated sound cues, and this study indicates that the bivalve clam *Lima* might do the same. Testing the response of
individual species that responded to underwater sounds in my study are needed, particularly those species that exhibited the largest differences in recruitment between degraded hard-bottom and healthy hard-bottom and those that were attracted to broadcasted soundscapes. Such studies would expand our knowledge about how larvae use variation in underwater sounds to find appropriate settlement sites. That information is crucial to understanding how anthropogenic effects on underwater soundscapes may directly (e.g., production of additional abiotic sounds) or indirectly (e.g., alteration of biotic sounds via habitat degradation) alter settlement cues necessary for larval recruitment.

In Chapter 2, I demonstrated that habitat degradation also changed underwater soundscapes. The loss of large, structure-forming sponges that house soniferous organisms such as snapping shrimp within their internal canals, as well as other sound producing taxa (e.g., fish, lobsters) that often seek refuge among what were once “forests of sponges”, severely altered the soundscape of degraded hard-bottom. Degraded hard-bottom sites without sponges had significantly lower sound spectra levels across all bands up to 24 kHz. In particular, the loss of snapping shrimp snaps on sponge-less sites drastically reduced the magnitude of sound in the 2 – 5 kHz band. Loss of sound within the higher frequency bands is likely to affect larvae of various taxa differently. For example, Simpson et al. (2008) found that settlement-stage fish larvae (Syngnathidae and Bleniidae) settled preferentially on experimental reefs where high frequency, invertebrate-generated sounds of reef noise were experimentally broadcast. Though knowledge of how the larvae of marine invertebrates use characteristics of habitat-associated soundscape is growing (e.g., Vermeij et al. 2010; Stanley et al. 2011, 2012; Lillis et al. 2014), the extent to which these larvae can differentiate among
distinct frequency bands (e.g., low frequency fish call ~100 Hz versus high frequency pulsed “snaps” ~2 – 5 kHz) has been the focus of recent research (Stocks et al. 2012; Wilkens et al. 2012).

In chapter 2, I described how the restoration of sponge communities on previously degraded resulted in acoustic signatures similar to those of healthy hard-bottom sites lying outside the area impacted by sponge die-offs, both of which differed from degraded, sponge-less hard-bottom. In this chapter, I also experimentally demonstrated that broadcasting sounds from healthy hard-bottom attracts more larvae, primarily a bivalve clam species, than does the sound of sponge-less hard-bottom. Yet, when I directly compared the recruitment of larvae to degraded and restored hard-bottom, they did not differ. Why?

The hard-bottom restoration sites used in my study are 25 m x 25 m areas in which out-planted sponges occupy the center 10 m x 10 m. Acoustic recordings on these sites show signatures similar to those of hard-bottom sites that were unaffected by sponge die-offs, yet we do not know how far these restored soundscapes travel through the water. The sound produced by small, restored “sponge habitat islands” may not propagate far enough to attract settling larvae. On the other hand, the underwater loudspeaker that I used to broadcast healthy hard-bottom soundscapes at its maximum output of 180 dB re 1 µPa would likely transmit sounds much farther than the sounds emanating from the small restored hard-bottom sites. If so, I hypothesize that the experimental broadcast of sounds probably attracted larvae from further away than did the sponges transplanted onto restoration sites, thus explaining the observed differences in larval recruitment between studies that I conducted.

In addition, the design of the playback experiment, wherein healthy hard-bottom sound
was broadcast at one site and a structural mimic was deployed at the silent control, begs the question of whether any sound production, not just playback of “healthy” soundscapes, would attract more larvae. However, Stanley et al. (2012) and Lillis et al. (2013) both used multiple loudspeakers to broadcast sounds of optimal and sub-optimal settlement habitats and found that crab megalopae reduced the time to metamorphosis and oyster larvae settled in response to the sounds of optimal settlement habitat, not sub-optimal habitat.

The logical next steps are to: 1) simultaneously compare larval attraction to the playback of healthy hard-bottom sound versus the playback of degraded hard-bottom sounds, or sound of another environment; and 2) determine the extent to which the soundscapes propagate from restored sites into the void of barren hard-bottom surrounding them. Doing so would permit the calculation of the “sonic footprint” of restoration sites of the type used in this study, which could guide future implementation of restoration efforts so that there is some acoustic overlap among sites.

In summary, this study detailed how habitat degradation altered larval recruitment and showed that habitat-associated soundscapes played a role in driving those differences. Future investigations should examine how the larvae of different taxa respond to acoustic cues, which frequency bands these larvae navigate toward or actively avoid, and at what spatial scales these acoustic cues operate. Furthermore, as the science of restoration ecology burgeons, setting realistic and attainable goals for restoration efforts will become increasingly important. By measuring how restoration not only returns habitat structure, but also how restoration returns ecological function (e.g., sounds used by recruiting larvae) to degraded areas, restoration practitioners will gain a fuller understanding of the key ecological drivers of
impaired ecosystems.
CHAPTER 4

ACOUSTIC-BASED MODEL ESTIMATION OF SNAPPING SHRIMP POPULATIONS AND THE EFFECTS OF A SPONGE DIE-OFF

INTRODUCTION

Humans rely upon ocean ecosystems for goods and services; unfortunately, extractive use of marine resources (e.g., fishing and mining,) and the indirect effects of human habitation (e.g., land-based run-off and climate change) have altered and degraded these ecosystems (Jackson et al. 2001; Pew Oceans Commission 2003; Halpern et al. 2008). Worldwide, marine ecosystems are declining (Suchanek 1994; Valiela et al. 2001; Waycott et al. 2009) and coastal ecosystems are particularly vulnerable to anthropogenic disturbances (Vitousek et al. 1997; Limburg 1999; Lotze & Milewski 2004), threatening their function (Solan et al. 2004; Worm et al. 2006; Diaz & Rosenberg 2008).

Habitat monitoring and assessment are key to understanding how ecological communities respond to habitat degradation (Kremen et al. 1994), yet monitoring presents many challenges. It is often time-consuming, expensive (Harris et al. 2015), and prone to human bias (Willis 2001); as when, for example, the avoidance of divers by fishes skews estimates of their biodiversity (Dickens et al. 2011). So the development of accurate and inexpensive monitoring techniques is becoming increasingly important as anthropogenic influences continue to buffet near-shore environments, including structurally complex coastal habitats that are so important as nurseries and foraging grounds (Airoldi et al. 2008).
One promising technique, based on the burgeoning science of soundscape ecology, relies on the measurement of sound to monitor ecosystems (Pijanowski et al. 2011). Although pioneered in terrestrial ecosystems, the study of soundscapes has been extended to the marine environment as a framework for environmental monitoring (Harris et al. 2015). Contrary to the public perception that the sea is a quiet realm - as implied, for example, in Jacques Cousteau’s *Silent World* - the ocean is alive with sound.

Underwater sound, whose sources are physical, biological, and anthropogenic, has been studied for decades. Early studies by Tait (1962) and Cato (1976, 1980) were some of the first to describe variation in underwater noise from rock and coral reefs off New Zealand and Australia. Recent research has confirmed that many of those noises are of biological origin and exhibit diel, lunar, and seasonal variation (Radford et al. 2008a, 2008b). There is also spatial variability in the sounds that emanate from within and among habitats (Cato 1978, 1992; Radford et al. 2008a, 2008b, 2010; Lillis et al. 2014), but only a few studies have used acoustics to assess community structure or habitat characteristics in the marine environment. For example, Lammers et al. (2007) described how acoustic activity is correlated with the structural characteristics of habitats, whereas Kennedy et al. (2010) determined that acoustic variability was positively correlated with the density, biomass, and diversity of organisms on coral reefs.

Though many marine organisms produce sounds and contribute to the biological component of soundscapes (Myrberg 1981; Versluis et al. 2000; Bouwma & Herrnkind 2009; Schärer et al. 2014; Staaterman et al. 2014), few are as ubiquitous as snapping shrimps whose snaps contribute a significant portion of energy to the biological din (Au & Banks 1998; Radford et al. 2008a, 2010; Bohnenstiehl et al. 2016). By rapidly closing the dactyl of its enlarged chela,
a snapping shrimp creates a cavitation bubble that produces a loud pop upon its collapse (Versluis et al. 2000). Snapping shrimps occur throughout temperate and tropical waters (Au & Banks 1998; Cato & McCauley 2002; Radford et al. 2010) and dwell in a variety of habitats, from estuaries to coral reefs (Au & Banks 1998). One group of snapping shrimps within the genus *Synalpheus*, a clade of ~100 species, all live within the canals of tropical sponges (Duffy & McDonald 1999; Duffy 2002). Some species of *Synalpheus* live in colonies of several hundred shrimps all living within the same sponge; a few have developed eusociality, the only occurrence of this extreme form of social behavior known among marine animals. Many species within this genus exhibit direct development in which eggs hatch directly into crawling juveniles (Duffy 2002), which further reinforces the link between shrimps and their sponge home.

Large sponges that harbor snapping shrimps are particularly abundant and important components of tropical hard-bottom communities, such as those found in the Florida Keys (USA). Hard-bottom habitat covers roughly 30% of the near-shore environment of the Florida Keys where dozens of sponge species dominate the benthic animal biomass with a mean density of >80,000 / ha. Many of those sponges, especially large sponges like the loggerhead sponge (*Spheciospongia vesparium*), provide shelter and habitat for fish and invertebrates (Butler et al. 1995), including those that are soniferous (i.e., “sound producers”).

However, the Florida Keys have undergone drastic ecological change in recent decades. In 1991, 2007, and 2013 portions of the Florida Keys - especially Florida Bay, the bay lying between the Florida mainland and the islands of the Florida Keys - were subjected to prolonged thermal stress and a major shift in salinity due to anomalous and persistent weather conditions. These physical stresses resulted in massive and widespread blooms of cyanobacteria whose
radical increase in concentration precipitated the mass mortality of sponges within a 500-km$^2$ area of the bay (Butler et al. 1995). The widespread loss of sponges resulted in a significant reduction of structural complexity in affected areas, leaving barren expanses of open substrate where sponges were once numerous. The ecological effects of such a dramatic shift in the character of these systems are still being studied. Among these being a significant change in the underwater acoustic signature of affected hard-bottom areas (Chapter 2).

Because of the close association between snapping shrimps and sponges, a reduction in sponge density in places such as Florida Bay would also likely reduce snapping shrimp density and abundance. Thus, the present study aimed to: (1) evaluate the efficacy of using remote acoustic monitoring to estimate snapping shrimp density and abundance, and (2) examine how sponge mortality might have affected the distribution of snapping shrimp populations in Florida Bay.

MATERIALS AND METHODS

To evaluate the effect of loss of sponges on snapping shrimp populations, I made acoustic recordings at six healthy hard-bottom sites in Florida Bay outside of the area impacted by the sponge die-off, and at five hard-bottom sites within the area affected by the sponge die-off (Fig. 10). In Chapter 2, I determined that the number of snapping shrimp snaps produced in hard-bottom areas unaffected by sponge die-offs was greater than the number of snapping shrimp snaps produced in hard-bottom areas degraded by sponge die-offs. Therefore, acoustic recordings made outside of sponge die-offs were used as a baseline to characterize the
soundscapes indicative of healthy snapping shrimp populations to which I could compare recordings made within the die-off area.

Remote acoustic recordings

Habitat recordings were made using the same submersible hydrophone systems employed in Chapter 2 (Fig. 11A). Fifteen-minute recordings were made at noon during either the first quarter or last quarter moon phase at each site, and from these recordings five 10-second subsamples were extracted for further analysis. All recordings were post-processed using MATLAB 2014b software (Mathworks, Inc.). Each 10-second subsample was processed through a MATLAB script written specifically for this study. First, the data were high-pass filtered to 100 Hz to remove extraneous low-frequency interference. The data were then plotted for visual inspection and to determine a snap count threshold level. The threshold is the level above which any transient spike in the data is considered a snapping shrimp “snap” and varies from recording to recording. Using the threshold level, data for individual snaps within the recording were located, extracted, and stored. Once data for individual snaps within a given subsample were extracted, the peak-to-peak pressure level for each snap was calculated. A calibration factor was applied to the raw data to calculate absolute pressure levels, which were converted to decibels relative to 1 microPascal (dB re 1 μPa). These values were later used to calculate sound transmission loss, as described below.
Figure 15. Map of study area showing algal bloom extent and acoustic recording sites
Figure 16. A remote hydrophone system (A), and the in situ sound damping chamber (B)
Estimating snapping shrimp snap rate and snap source level

To determine the cue rate (i.e., snap rate) and to estimate the snap source level, 15 individual sponges of three sponge species (loggerhead sponge, *Spheciospongia vesparium*; sheepswool sponge, *Hypospongia lachne*; yellow sponge, *Spongia barbara*) in which snapping shrimps can be found were acoustically isolated *in situ* using an underwater sound damping chamber. The chamber was constructed of a tin washtub (54 cm dia; 26 cm ht) encapsulated with 5 cm of closed-cell foam and set in a 15 cm thick concrete base to render it negatively buoyant (Fig. 11B). A hydrophone attached to a WAV recorder (see description above) was lowered through a 3 cm dia tube at the center of the chamber, permitting the recording of sound from individual sponges *in situ*.

The effectiveness of the sound-damping chamber was tested in two ways. First, I tested it *in situ* by comparing simultaneous recordings of the soundscape acoustic spectra outside the chamber to the acoustic spectra within the chamber (Fig. 12A). In addition, after recording the number of snapping shrimp snaps as described above, I only counted snaps whose power exceeded a threshold that excluded quieter snaps recorded outside the sound-damping chamber, (Fig. 12B). This was done to ensure the chamber was effectively quieting snaps external to the chamber to reduce false snap counts from sponges recorded within the chamber. Once the chamber was positioned over the sponge, sound levels were recorded for 15 minutes. The sponge was then cut from the substrate and placed in a plastic bag for transport to the laboratory where it was dissected so as to remove and count all of the infaunal organisms, which were primarily snapping shrimps.
For recordings of sponges that housed snapping shrimps, the number of snapping shrimp snaps emanating from that single sponge was calculated as described above. Using the number of snaps and the number of snapping shrimp found within each sponge, cue rate (snaps/10-sec/shrimp) was calculated. For each acoustically-isolated sponge, a calibration factor was applied to the recording and the peak-to-peak sound pressure level (dB re 1 μPa) for individual snaps was calculated. The snap source levels for all individual snaps were averaged to determine the source level used to calculate transmission loss.

*Estimating snapping shrimp distance to hydrophone receiver*

Distance to a sound source (i.e., a snapping shrimp) was estimated using a modified cylindrical spreading model. For each subsample, the previously calculated sound source level and the received sound level (RL) for each snap (see above) was used to calculate the transmission loss of each snap. The transmission loss (TL) of each snap was calculated as:

\[ TL = SL - RL \]

Using the transmission loss for each snap, the distance of each sound source to the hydrophone receiver was calculated using a modified cylindrical spreading model. Sound propagates cylindrically in shallow water habitats like the hard-bottom habitats (< 2m depth) in which I made my recordings. A cylindrical spreading model predicts that the coefficient of transmission loss should be 10 (Urick 1983), but to account for sound wave interference, sound
absorption and scattering at the sea floor, and sound scattering at the sea surface, the coefficient of transmission loss was raised to 15:

\[ TL = 15 \log_{10}(d) \]

From this equation, the distance from the sound source to the hydrophone receiver was calculated:

\[ d = 10^{(TL/15)} \]
Figure 17. (A) shows the comparison between the acoustic spectra outside the sound damping chamber (gray) versus the acoustic spectra within the chamber (black). (B) shows the occurrence of snapping shrimp snaps above a set threshold level (dashed line) outside.
Snapping shrimp population estimation

Using the snap rate calculated within the sound-damping chamber and the estimated distances to snapping shrimp snaps within each of the habitat recordings, snapping shrimp population density was estimated using the program Distance (version 6.2; Thomas et al. 2010). Distance sampling techniques for population density estimation are widely used (Buckland et al. 2005) and have recently been modified to suit point transects wherein distances to sound cues (e.g., bird calls or whale songs) are used rather than distances to animal sightings. This technique allows for easy and inexpensive remote sensing and density estimation of any soniferous organism and have been successfully implemented within the marine environment (e.g., Küsel et al. 2011; Harris et al. 2013). Population density estimation via distance sampling uses a probability density function based on an underlying detection function; this function represents the probability of detecting a cue of interest given its distance from the receiver (Marques et al. 2013). It is assumed that all organisms (or cues) of interest that lie directly on the transect line or point are counted with certainty, and the probability of detection declines with increasing distance from the line or point transect. The distribution of observed detection distances is used to estimate the average probability of detection, and this in turn is used to population density and abundance. In addition, the cue rate (i.e., how often one organism makes one cue of interest) is used to convert cue density and abundance to animal density and abundance (Marques et al. 2009) by multiplying the cue density estimation by the cue rate.

Distance fits several detection functions to the sampling data and uses AIC to determine which model best fits the data. Once a model is selected, Distance provides a summary of the analysis, including a density estimate and 95% confidence intervals around that estimation. For
the present study, a half-normal detection function with cosine adjustment (a standard model within Distance) was fit to the data. This detection function is suggested by Thomas et al. (2010) and was selected over other functions (e.g., a hazard-rate function) because it fit these data best. Distance data were truncated to 50 meters (that is, any snap source estimated to be over 50 meters from the hydrophone receiver was removed from the population density and abundance estimates - about 1% of distance estimates) to avoid adding extraneous adjustment terms to the underlying detection function (Buckland et al. 2001; Thomas et al. 2010). Because distances were truncated, density and abundance estimates of snapping shrimp populations produced by Distance are based on a circular area with a radius of 50 meters, thus resulting in a total coverage area of 7854 m².

Snapping shrimp population density (shrimp/m²) was estimated for each site, and the difference in shrimp density between healthy hard-bottom sites and degraded hard-bottom sites was tested using a nested ANOVA (site nested within habitat type). Pooled data for all sites within either the healthy hard-bottom area or the degraded hard-bottom area were used to estimate population density for healthy and degraded areas. Upper and lower 95% confidence interval density estimates were multiplied by the coverage area to obtain upper and lower snapping shrimp abundance estimates. In addition, number of snapping shrimp snaps per 10-second subsample and average distance to snap source were analyzed using nested ANOVAs (site nested within habitat type) to determine differences in those estimates between healthy hard-bottom and degraded hard-bottom areas.
RESULTS

*Sponge infaunal shrimp communities, snap rate, and snap source level*

At least one individual of each sponge species harbored snapping shrimp of the genus *Synalpheus*, but the occurrence and abundance of snapping shrimp varied among sponge species (Table 6). Every loggerhead sponge housed snapping shrimp in high abundance (mean number of shrimp per sponge: 28 ± 24.15 s.d.) and 80% of the sheepswool sponges housed snapping shrimps albeit at lower abundance (13.5 ± 14.65), whereas only 20% of the yellow sponges housed any snapping shrimp and only in low numbers (1.69 ± 5.72). The number of snapping shrimp within a given loggerhead sponge scaled linearly with sponge volume ($r^2=0.703; p < 0.001$) but the relationship between sheepswool ($r^2=0.217; p = 0.244$) and yellow sponge ($r^2=0.034; p = 0.91$) volumes and number of snapping shrimp within each sponge were weak and non-significant (Fig. 13). However, these differences could be attributed to a wider size range for larger loggerhead sponges compared to sheepswool and yellow sponges, which are smaller with less size variability. The number of snaps per shrimp per ten-seconds was 0.014 ± 0.023 (mean & sd), and the average peak-to-peak source level of all snaps was 130 dB re 1 μPa over 100 – 24,000 Hz.
Figure 18. Sponge volume versus number of snapping shrimp found within individual sponges
Table 6. Summary of infaunal shrimp communities within individual sponges.

<table>
<thead>
<tr>
<th>Sponge Species</th>
<th>Sponge Volume (cm$^3$)</th>
<th>Number of snapping shrimp</th>
<th>Number of snaps</th>
<th>Number of snaps/shrimp/10-sec</th>
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<tr>
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<td>0</td>
<td>0.0000</td>
<td></td>
</tr>
<tr>
<td>3002.75</td>
<td>23</td>
<td>5</td>
<td>0.0036</td>
<td></td>
</tr>
</tbody>
</table>
Number of snapping shrimp snaps and distance to snap source

Habitat type significantly affected the number of snapping shrimp snaps per ten-seconds, as well as the average distance to a snap’s source. The average number of snapping shrimp snaps per ten-seconds in healthy hard-bottom areas (241 ± 26.67; mean & se) was significantly greater ($F_{1,9} = 72.9$, $p < 0.001$) than the average number of snapping shrimp snaps per ten-seconds in affected hard-bottom areas (35 ± 5.98; mean & se). Conversely, the average distance to a snap’s source in degraded hard-bottom areas (18.24 ± 0.86 m; mean & se) was significantly greater ($F_{1,9} = 57.38$, $p << 0.001$) than the average distance to a snap’s source in healthy hard-bottom habitat (6.94 ± 0.15 m; mean & se).

Snapping shrimp population density and abundance estimation

Snapping shrimp population density estimates also differed significantly among habitat types ($F_{1,9} = 13.84$, $p = 0.002$); those within healthy hard-bottom areas (2.68 shrimp per m$^2$ ± 0.68; mean & se) were greater than estimates of shrimp density within degraded hard-bottom areas (0.057 ± 0.013; mean & se). Abundance estimates varied among sites, but degraded sites exhibited lower abundance estimates than did healthy sites (Table 7). The lowest abundance estimated at degraded sites was 23 shrimp within the hydrophone coverage area (7854 m$^2$), and the highest abundance estimated at degraded sites was 7,657 shrimp within the hydrophone coverage area, whereas the estimated abundance of snapping shrimp within healthy sites was one to two orders of magnitude greater than estimates within degraded sites. The lowest estimate within healthy sites was 471 shrimp, and the highest estimate was 341,248 shrimp within the hydrophone coverage area.
Table 7. Estimated snapping shrimp population densities and abundances

<table>
<thead>
<tr>
<th>Site</th>
<th>Type</th>
<th>Density (shrimp/m²)</th>
<th>Lower Density Estimate</th>
<th>Upper Density Estimate</th>
<th>Lower Abundance Estimate</th>
<th>Upper Abundance Estimate</th>
</tr>
</thead>
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<tr>
<td>A06</td>
<td>Degraded</td>
<td>0.101</td>
<td>0.011</td>
<td>0.975</td>
<td>86</td>
<td>7,657</td>
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<tr>
<td>A07</td>
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<td>0.006</td>
<td>0.525</td>
<td>47</td>
<td>4,123</td>
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<td>Healthy</td>
<td>4.602</td>
<td>0.487</td>
<td>43.449</td>
<td>3,824</td>
<td>341,248</td>
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<tr>
<td>Burnt Point</td>
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<td>3.856</td>
<td>0.408</td>
<td>36.418</td>
<td>3,204</td>
<td>286,026</td>
</tr>
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<td>0.128</td>
<td>11.601</td>
<td>1,005</td>
<td>91,114</td>
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<tr>
<td>Lignum Vitae</td>
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<td>0.004</td>
<td>0.317</td>
<td>31</td>
<td>2,489</td>
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<tr>
<td>Old Dan Bank</td>
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<td>0.027</td>
<td>0.003</td>
<td>0.257</td>
<td>23</td>
<td>2,018</td>
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<td>Rachel Bank</td>
<td>Healthy</td>
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<td>0.060</td>
<td>5.337</td>
<td>471</td>
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<td>0.197</td>
<td>17.669</td>
<td>1,547</td>
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<td>S70</td>
<td>Degraded</td>
<td>0.069</td>
<td>0.007</td>
<td>0.651</td>
<td>54</td>
<td>5,112</td>
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<td>Vaca Key</td>
<td>Healthy</td>
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<td>0.421</td>
<td>37.388</td>
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<td>2.167</td>
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<td>0.063</td>
<td>0.007</td>
<td>0.600</td>
<td>54</td>
<td>4,712</td>
</tr>
</tbody>
</table>

DISCUSSION

Habitat degradation disproportionately affects coastal marine ecosystems (Vitousek et al. 1997; Limburg 1999; Lotze & Milewski 2004) and Florida Bay, where this study took place, is no different. Extensive, persistent cyanobacteria blooms have repeatedly decimated hard-bottom sponge communities (Butler et al. 1995; Stevely et al. 2011), resulting in markedly
different soundscapes including fewer snapping shrimp snaps within degraded hard-bottom areas (Chapter 2). The present study confirms that there are indeed fewer snapping shrimp snaps per ten-second subsample at degraded sites. I also estimated distances among individual snaps and found that the distance to a snap’s source (i.e., the distance from a snapping shrimp to the hydrophone) was greater on degraded sites than on healthy sites. This increase in distance to a snap source coincides with a reduction in the number of large, canal-bearing sponges in which the majority of snapping shrimp can be found. Furthermore, shrimp abundances estimated using distance-sampling techniques indicate that degraded hard-bottom sites harbor fewer snapping shrimp and that these populations are less dense.

Many snapping shrimp species within the genus *Synalpheus* dwell commensally within a diverse array of tropical and sub-tropical sponge species (Duffy 1992). However, living within sponges has some consequences on the shrimps, most notable is a limitation on shrimp size imposed by the canal structure of the host sponges. Duffy (1992) found no evidence of shrimp-induced canal excavation among the four tropical sponge species in which snapping shrimp were found (including the loggerhead sponge), and thus concluded that shrimp size must be limited by the canal size of the host sponge. Of the four sponge species Duffy (1992) dissected, the loggerhead sponge exhibited the greatest variability of canal widths (Figure 1 in Duffy 1992). Though I did not measure the canal structure of the three sponge species I dissected for this study, I observed that the loggerhead sponges had more well-developed canals compared to either the Sheepswool sponges or the Yellow sponges. This difference in canal structure could likely affect the numbers of snapping shrimp found within individual sponges (Table 6 & Fig. 13).
Passive acoustics and distance sampling as monitoring tools

As the world’s ocean ecosystems – particularly coastal ecosystems – continue to degrade (Jackson et al. 2001; Lotze & Milewski 2004), effective monitoring to determine the health of a target population or habitat is becoming increasingly important (Kremen et al 1994; Watanabe et al. 2002; Airoldi et al. 2008). Passive acoustic monitoring provides a suite of tools to answer scientific and management questions and avoids many downfalls of other surveying methods (Willis 2001; Dickens et al. 2011; Harris et al. 2015).

Monitoring of marine mammals and fishes via passive acoustics has increased in recent years (Moore et al. 2006; Mellinger et al. 2007; van Opzeeland et al. 2008; Luczkovich et al. 2008). Many species of marine mammals and fishes produce distinct sounds. For example, whales are often not amenable to visual survey methods but can be monitored using passive acoustics. Antarctic blue whales produce characteristic long (~20 sec) tonal calls that downsweep from 28Hz to 18Hz (Sirović et al. 2004, 2009), whereas Antarctic fin whales produce short (~ 1 sec) calls downswept from 28Hz to 15Hz, often with a short following call around 89Hz (Sirović et al. 2004). In fact, combined visual and passive acoustic surveys have shown that the passive acoustic surveying techniques detect as many as ten times more cetaceans than the visual surveys (McDonald & Moore 2002; Sirović et al. 2004; Barlow & Taylor 2005). In addition, passive acoustic monitoring can continue throughout the night and in conditions that would make visual surveys impossible (Mellinger & Barlow 2003; Mellinger et al. 2007).
However, if passive acoustic monitoring is to serve as a robust monitoring technique, it must also provide information such as population density or abundance. Several studies on cetacean abundance have combined line-transect surveys and passive acoustics to estimate the population density of the species-of-interest within a given geographic area (McDonald & Fox 1999; Barlow & Taylor 2005; Moretti et al. 2006; Mellinger et al. 2004; Marques et al. 2009). Marques et al. (2009) extended distance sampling techniques (i.e., estimating a detection function based on an animal-of-interest’s distance to a point or line transect) to point transects of cue counts of Blainville’s beaked whale and estimated the detection function using digital acoustic tag (DTag) data from a previous study (Johnson & Tyack 2003). Extending the work of Marques et al. (2009), Küsel et al. (2011) estimated the population density of Blainville’s beaked whale using a single fixed hydrophone rather than an array of hydrophones and estimated distance to each whale call from the hydrophone by estimating the detection function and enlisting the passive sonar equation (equation 2 in Küsel et al. 2011). The density estimate of beaked whales in the Küsel et al. study was nearly three times higher than the estimate of Marques et al., however, re-analysis of the Marques et al. estimate based on one hydrophone (rather than an array of 82, as was in the original study) brought the two estimate closer together.

Similar to Küsel et al. (2011), I used the passive sonar equation to estimate distances to the source of each snapping shrimp snap. Unlike Küsel et al. (2011) who had available previous estimates of beaked whale population density based on an accurate method of estimation (Marques et al. 2009) with which they could compare their methods, I had no comparable data on snapping shrimp density with which to compare my estimates. To estimate distances to snap
sources more accurately, and thus estimate the detection function more accurately, I could in the future employ hyperbolic localization techniques. For that method, multiple hydrophones are deployed in an array and arrival-time differences of a sound of interest are determined among hydrophones so as to more precisely ascertain the sound source (Spiesberger & Fristrup 1990; Spiesberger 1999, 2001). In this study I used a single hydrophone receiver at each site and the passive sonar equation to estimate distance to a sound source. However, I could not localize that source, which would have been possible with an array of four or more hydrophones and hyperbolic localization techniques. However, the cost of obtaining and deploying a multiple hydrophone array was beyond the limits of the present study.

Because of the association between snapping shrimp and sponges on hard-bottom communities, estimating snapping shrimp populations and mapping the resultant clusters of snapping shrimp snaps onto a 2-D coordinate system—rather than just counting snaps—allows for a conservative estimation of sponge biomass and location within a hard-bottom area. For example, using the shrimp number and sponge volume data collected while determining cue rate and fitting a simple linear model, we can predict sponge volume (a proxy for sponge biomass) on a given site. This method might work particularly well for estimating loggerhead sponge biomass, given the significant positive relationship between loggerhead sponge volume and number of snapping shrimp found within a sponge (Fig. 9), as well as the significant positive relationship between total loggerhead sponge volume on a given site and the number of snapping shrimp snaps produced on that site (Fig. 10). These predictions would, obviously, lack the resolution and accuracy of diver surveys in which sponge species and size were mapped on a site. In addition, sources of error for the hyperbolic localization of sound sources (e.g.,
variations in the speed of sound due to water temperature) would increase the variance around source position estimates.

Figure 19. Total loggerhead sponge volume on a given site versus number of snaps per 10 seconds
The use of rapid acoustic monitoring techniques to estimate snapping shrimp abundance and sponge biomass also provides insight into the structure of the habitat in an area. Few studies have linked acoustic metrics to habitat structural complexity and biodiversity (Lammers et al. 2007; Kennedy et al. 2010). Because of the close association between snapping shrimps and sponges, mapping the clusters of snapping shrimp snaps, and hence the sponges in which they dwell, might provide a rapid method to determine the sponge biomass and the structural complexity of that site. Furthering our understanding of how physical and biological characteristics interact with the acoustic environment may provide even more benefits. For example, the larvae of some marine fishes and invertebrates respond to habitat-associated sound cues (Tolimieri et al. 2000, 2004; Simpson et al. 2005, 2008; Stanley et al. 2009, 2011, 2012; Vermeij et al. 2010 – among others), and integrating small-scale acoustic and structural variation may help in identifying and predicting patterns of larval recruitment.

In summary, I estimated how the loss of marine sponges from near-shore hard-bottom communities affected snapping shrimp populations by employing remote acoustic recording techniques and distance sampling theory. Areas that suffered sponge die-offs exhibited fewer snapping shrimp snaps and, as a consequence, the estimated snapping shrimp population density and abundance estimates were lower in these areas. This method can hopefully provide rapid assessment of habitat structure and quality, particularly for habitats in which soniferous organisms are associated with structure-forming species.
CHAPTER 5

CONCLUSIONS

As anthropogenic factors continue to degrade ocean ecosystems, understanding how degradation affects ecological traits and processes and monitoring and rapidly assessing habitat quality are becoming increasingly important. For example, there is a large body of evidence which indicates that changes in biological diversity (e.g., the genetic diversity of a population, the functional diversity within a guild of primary producers, or the species diversity within a habitat) alters ecological processes and ecosystem functioning (Loreau et al. 2001; Worm et al. 2006; Hooper et al. 2012). However, few studies have examined the biodiversity-ecosystem functioning link within the framework of restoration ecology (Wright et al. 2009). Employing restoration techniques as tools to study the interactions of ecological traits and ecological processes will expand scientific knowledge and our understanding of interactions within ecosystems. Furthermore, incorporating the interactions of ecological traits and processes in the establishment of ecological benchmarks with which to measure the efficacy of restoration will help set realistic, attainable goals for restoration efforts.

Many studies have examined underwater soundscapes (Cato 1976, 1978; Radford et al. 2008, 2010), however, this is the first study to examine the effects of habitat degradation and subsequent restoration on the process of soundscape production. In Chapter 2, I showed that the seascapes of Florida Bay and near-shore waters of the Florida Keys exhibited distinct soundscape characteristics. In particular, seagrass meadows exhibited fewer snapping shrimp
snaps and lower acoustic spectra levels than did mangrove or hard-bottom habitats. Degraded hard-bottom habitat exhibited spectra similar to seagrass habitat and significantly fewer snapping shrimp snaps than hard-bottom unaffected by sponge die-offs. Furthermore, hard-bottom sites restored via sponge outplanting exhibited acoustic characteristics similar to healthy hard-bottom, indicating that restoration can aid in the recovery of degraded soundscapes in these sponge-dominated hard-bottom areas.

This study linked the loss of ecological traits to changes in the process of soundscape production and showed that sponge community restoration aids in returning natural soundscape production in hard-bottom areas. However, this study does not disentangle the effects of the loss of multiple ecological traits (in this case, biodiversity and habitat structure).

A growing body of evidence suggests that the loss of biodiversity or changes in ecological community composition negatively affects ecosystem functioning (Schulze & Mooney 1993; Kinzig et al. 2002; Loreau et al. 2002; Hooper et al. 2005), and monitoring biodiversity has become imperative due to widespread habitat degradation and climate change (Convention on Biological Diversity 2010). Conventional survey techniques are time-consuming, expensive, and often biased (Sueur et al. 2008), particularly in the marine realm (Willis 2001; Dickens et al. 2011; Freeman et al. 2013). Ecosystem monitoring is a central tenet of soundscape ecology, and many studies have focused on developing acoustic indices that act as proxies for biodiversity (e.g., the acoustic complexity index [Pieretti et al. 2011]). Harris et al. (2015) examined the relationship between traditional diversity indices and three acoustic diversity indices (the Acoustic Entropy Index [Sueur et al. 2008], the Acoustic Richness Index [Depraetere et al. 2012], and the Acoustic Complexity Index [Pierreti et al. 2011]) and found that, with an appropriate
spectral resolution, the Acoustic Entropy Index and the Acoustic Complexity Index showed significant positive correlations with traditional diversity measures. Harris et al. (2015) also postulated that a more complex soundscape could be indicative of an area with greater physical complexity, which could attract higher species diversity to that area. Understanding the linkages among habitat complexity, biodiversity, and soundscape complexity requires further research, and the tools of restoration ecology can aid in examining these interactions. For example, planning future restoration efforts to test biodiversity effects on soundscape production (e.g., by outplanting monocultures of sponges versus outplanting a diverse assemblage of sponges) would help tease these effects apart.

Furthermore, conservation efforts have recently begun to shift their focus to not only include the preservation of intact systems, but also to include the restoration of degraded systems (Dobson et al. 1997; Young 2000; Suding et al. 2004). Two major hurdles of restoration efforts are 1) the setting of feasible and scientifically valid goals (Cairns 2000), and 2) the quantitative evaluation of restoration progress. Ecosystem monitoring is a central tenet of soundscape ecology (Pijanowski et al. 2011b), and ecological restorationists can use soundscape ecology to inform ecological restoration decisions.

Degradation of hard-bottom habitats of Florida Bay also altered the process of larval settlement and recruitment. In Chapter 3, I compared larval assemblages at sites within degraded hard-bottom and at sites within healthy hard-bottom areas to test the effect of habitat degradation on larval recruitment. Assemblages of larvae within healthy hard-bottom areas showed a greater number of recruits, particularly of several gastropod and bivalve mollusk species. Analysis of larval communities settling on restoration sites shows no significant
difference between those sites and sites within degraded hard-bottom areas, indicating that sponge outplanting alone might not return larval recruitment to degraded areas. Moreover, the playback of healthy hard-bottom soundscapes within degraded areas prompted greater larval recruitment at playback sites, particularly during the full moon. A clam species, *Lima* sp., exhibited greater recruitment at healthy hard-bottom sites, as well as at sites where healthy sounds were played back, indicating that this species likely uses underwater sounds as a cue to find suitable settlement habitat.

The results of Chapter 3, in conjunction with the results of Chapter 2, indicate that habitat degradation alters both the ecological processes of soundscapes production and larval settlement and recruitment, yet subsequent habitat restoration does not necessarily return these functions equally. There is a discrepancy between the soundscapes of restored hard-bottom and the soundscapes that were experimentally broadcast, likely in amplitude. However, the tools of soundscapes ecology could be used to determine the acoustic footprint of restoration sites – that is, the area over which the soundscapes emanating from restored hard-bottom broadcast biological information to relevant taxa. Future restoration efforts could aim to establish new restoration sites with overlapping acoustic footprints, and thus create a more natural sound field over a broader area than just the small site onto which sponges were outplanted.

Lastly, in Chapter 4 I employed the passive sonar equation to estimate distances to snapping shrimp snaps from a single hydrophone receiver and distance sampling theory to estimate population densities and abundances of snapping shrimps within healthy and degraded hard-bottom areas. The loss of large, canal-bearing sponges (such as *Spheciospongia*
vesparium) reduced snapping shrimp populations within areas subjected to sponge die-offs.

Snapping shrimp snaps are a conspicuous feature of hard-bottom soundscapes, and the loss of these shrimps from degraded hard-bottom areas greatly alters the soundscape emanating from that area.

In summary, these studies examined how habitat degradation affected the ecological processes of larval recruitment and soundscape production, and how restoration aids the recovery of these processes. Figure 15 highlights the connectivity among the chapters of this dissertation by displaying common words within each chapter and sizing them according to frequency. More research on the interaction between soundscapes and larval recruitment is yet to be done, however. Restored hard-bottom sites exhibited similar soundscape spectra to healthy hard-bottom sites, yet larval recruitment on restoration sites remained lower than healthy sites. Why is there a discrepancy between the return of the ecological processes of soundscape production and larval recruitment? By carefully designing future restoration efforts, we can tease apart how the biodiversity of foundation species (in our case, sponges) affects the return of these ecological functions and why the return of soundscapes does not coincide with a return of larval recruitment. Examining how sponge restoration efforts are returning other ecological functions (e.g., filtration or nutrient cycling) will provide a more holistic picture of the ecology of hard-bottom.

As the human population continues to grow, our demand on the environment to provide goods and services will also increase. Direct and indirect anthropogenic disturbances degrade the functioning of natural ecosystems by altering the underlying ecological processes. Restoration ecology not only provides tools to curb habitat degradation, but it also provides
ecologists tools to study ecological theory and tease apart interactions among various ecological processes.
Figure 20. A word cloud emphasizing the connectivity of dissertation chapters. The size of words indicates their relative frequency within an individual chapter.
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## APPENDIX A

### FIELD SITES GPS LOCATIONS

<table>
<thead>
<tr>
<th>Site Name</th>
<th>Chapter</th>
<th>Site Type</th>
<th>Latitude</th>
<th>Longitude</th>
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</tr>
<tr>
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<td>Degraded</td>
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</table>
The studies presented in this dissertation were designed by John R. Butler, with guidance and input from Dr. Mark J. Butler, as well as committee members Drs. Jenni Stanley, Holly Gaff, and Eric Walters. All data for these experiments were collected and analyzed by J. Butler. Chapter 2 (Characterizing soundscapes) was carried out in close collaboration with Dr. Stanley, and Chapter 4 (Estimating snapping shrimp populations) was conducted as a Modeling and Simulation Fellow under guidance of Dr. Gaff. All manuscripts resulting from these works were written by J. Butler, with editing and creative assistance from co-authors.

Three manuscripts are the expected outcome from this dissertation. The manuscript resulting from Chapter 2 is in review at the *Journal of Experimental Marine Biology and Ecology*, co-authored with Drs. Mark Butler and Jenni Stanley. The manuscripts from Chapters 3 and 4 are in preparation. The manuscript from Chapter 3 is co-authored by Dr. Mark Butler and aimed at publication in *Ecology*, and the manuscript from Chapter 4 is co-authored by Drs. Mark Butler and Holly Gaff and is aimed at publication in *Ecological Indicators*. 
VITA

John Richard Butler
Department of Biological Sciences
Old Dominion University
Norfolk, VA 23529

Education

Current  Ecological Sciences PhD – Old Dominion University, Department of Biological Sciences, Norfolk, VA

B.S.  Zoology, 2009 – University of Florida, Department of Biology, Gainesville, FL

Employment

2014 – 2015  Modeling and Simulation Fellow, Virginia Modeling and Simulation Center, Old Dominion University

2010 – 2014  Graduate Teaching/Research Assistant, Department of Biological Sciences, Old Dominion University

2009 – 2010  Research Technician, Department of Biology, University of Florida

Honors and Awards

1st place, Master’s Student Presentation, Biology Graduate Student Organization Annual Symposium, Old Dominion University

Virginia S. Bagley Endowed Scholarship, Department of Biological Sciences, Old Dominion University

Harold G. and Vivian J. Marshall Scholarship, Department of Biological Sciences, Old Dominion University

Biology Graduate Student Organization, Old Dominion University, Travel Award

Student Engagement and Enrollment Services, Old Dominion University, Travel Award