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Temporal and Spatial Patterns in Coral Reef Soundscapes and their Relevance for Larval Fish Orientation

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UNIVERSITY OF MIAMI

TEMPORAL AND SPATIAL PATTERNS IN CORAL REEF SOUNDSCAPES AND THEIR RELEVANCE TO LARVAL FISH ORIENTATION

By

Erica R Staaterman

A DISSERTATION

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TEMPORAL AND SPATIAL PATTERNS IN CORAL REEF SOUNDSCAPES AND THEIR RELEVANCE TO LARVAL FISH ORIENTATION

Erica R. Staaterman

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Most coral reef fish adults have limited home ranges, but their pelagic larvae have the potential to disperse over great distances. At the end of the pelagic phase, these larvae must seek appropriate settlement habitat. Which environmental signals do they use to find the reef? It has been suggested that fish larvae utilize a combination of visual, olfactory, and acoustic cues at different ontogenetic stages and different distances from the reef. At least ten experiments in the last decade have tested the response of reef fish larvae to sounds of a coral reef, resulting in more than 650 citations. This dissertation focuses on the potential role of acoustic cues in the orientation behavior of larval reef fish from the open ocean.

First, a biophysical model was used to examine the consequences of orientation behavior if larvae could detect acoustic signals from 1-10 km from the reef. When larvae oriented early during ontogeny and from larger distances, they greatly increased their settlement success and settled closer to home. These findings suggest that early orientation is critical to the survival of fish larvae, which must be active agents of their own dispersal. Second, a time-series of coral reef soundscapes was conducted for two nearby coral reefs in the Northern Florida Keys. The reef soundscapes were highly

variable over daily, lunar, and seasonal time-scales, and the highest amplitudes coincided with new moons of the wet season - the time when the larvae of most coral reef fish species settle. Interestingly, the wind-based contribution to the soundscape also had a lunar period. Third, an acoustic playback experiment was conducted at Dean's Blue Hole in the Bahamas, a relatively "quiet" environment. Larvae from Apogonidae (cardinalfish) and Acanthuridae (surgeonfish) families were exposed to reef sounds recorded in the Bahamas and in Florida and played back at ambient levels. The acanthurid species demonstrated no response to the playbacks, but the apogonids exhibited a disruption of their orientation behavior. This finding suggests that apogonids were able to detect the playbacks, but had no directional response, as was anticipated based on previous studies where sounds were broadcast at higher amplitudes. Finally, an acoustic propagation experiment was conducted in the Upper Florida Keys. Both acoustic pressure and particle acceleration diminished gradually with distance from the reef, but the amplitude of the signal, particularly for particle acceleration, was lower than the detection thresholds of most fish larvae. Furthermore, the particle acceleration field (measured 1-1000 m from the reef) was not highly directional, which may restrict the use of acoustic signals to animals that can detect acoustic pressure.

These findings suggest that most fish larvae in the pelagic zone near Florida reefs would have a difficult time locating the reef using acoustic cues alone. However, this may not be the case for species with particularly sensitive hearing (e.g., those that can detect acoustic pressure), and for reefs with higher-amplitude soundscapes. The results of this study challenge research from the past decades that demonstrated a clear attraction of larval fishes to sounds played-back at high amplitudes. Further work is needed, specifically hearing thresholds in other fish larvae, and particle acceleration measurements over longer time periods and near additional coral reefs, to determine whether the trends found in the Florida Keys are consistent with other parts of the world.

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Although a dissertation is ultimately written by one person, it comes to fruition through the efforts of entire network of people - and they deserve recognition. First and foremost, I want to acknowledge my Ph.D. advisor, Dr. Claire Paris, for all of her help throughout this process. She has provided intellectual, professional, financial, and personal support over the last 5 years and for that I am extremely grateful. Working in her lab has opened doors and afforded me opportunities that I would not have acquired elsewhere.

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CHAPTER 1: GENERAL INTRODUCTION

Orientation Behavior in Larval Fish

Most fishes that live on coral reefs are r-selected species, meaning they produce many offspring to offset high mortality rates and thus guarantee population replenishment (Doherty and Williams 1988). Thousands of larvae hatch in a single clutch; these larvae spend several weeks to several months in the plankton before settling to the reef to begin their juvenile phase. Sensory and swimming capabilities develop during this pelagic period, enabling the larvae to detect and approach settlement habitat (Fisher et al. 2000, Myrberg and Fuiman 2002, Leis 2010). While once considered to be passive drifters, it is now well-accepted that larval fish are active agents of dispersal (Leis 2006). The majority of research on larval behavior has focused on vertical migration, which generally increases retention near the home reef (e.g., Batchelder et al. 2002; Paris and Cowen 2004; Fiksen et al. 2007; Paris et al. 2007; North et al. 2008). But because fish larvae are strong swimmers (Fisher et al. 2005), it essential to consider horizontal swimming behavior as well. The relative importance of environmental cues, and the demographic consequences of horizontal swimming in response to these cues, are not well understood (Leis 2007, Leis et al. 2011).

Although it is likely that fish larvae use a suite of cues – visual, olfactory, and acoustic - at different ontogenetic stages and distances from the reef (Figure 1.1, Montgomery et al. 2001, Kingsford et al. 2002, Myrberg and Fuiman 2002, Leis 2007, Arvedlund and Kavanagh 2009, Leis et al. 2011), this work focuses on the potential role of acoustic cues. In the last decade, a series of experiments have focused on the hypothesis that fish larvae could use acoustic signals – sounds emanating from the reef – to navigate. This hypothesis was first proposed by Stobutski and Bellwood (1998) who observed that fish larvae placed in choice-chambers at night generally swam towards the reef. The authors suggested that they may have been attracted by reef sounds, since visual cues were minimal, and olfactory cues are non-directional (Stobutzki and Bellwood 1998). In 2000, Tolimieri et al. deployed paired light-traps, using speakers to broadcast reef sounds at one light-trap while the other remained silent (Tolimieri et al. 2000). They found that triplefin larvae (a reef fish) were more likely to be caught in sound traps (86%) compared to silent traps (14%), whereas the larvae of pilchard, a pelagic species, showed no preference for noisy or silent traps. Another light-trap study by Simpson et al. (2004) demonstrated that the larvae of several tropical reef fishes were more attracted to noisy light-traps compared to silent light-traps (Simpson et al. 2004). Several years later, a similar experiment was conducted by Simpson et al., but larvae were presented with one of three treatments: “high frequency sounds” (>570 Hz), “low frequency sounds” (<570 Hz), or silence (Simpson et al. 2008). Again, fish larvae generally preferred noisy traps to silent traps. Some Pomacentridae larvae displayed a preference for reef sounds in an experiment in which larvae were introduced to the center of a choice-chamber, and speakers at either end played either silence or reef sounds (Tolimieri et al. 2004, Leis and Lockett 2005). Finally, artificial patch-reef experiments showed that larval pomacentrids were more attracted to high frequencies (Simpson et al. 2005a), and juvenile pomacentrids preferred the sound of a fringing reef compared to the sounds of a lagoon (Radford et al. 2011a).

Clearly these experiments provide compelling evidence that some fish larvae are able to detect and swim towards broadcast reef sounds. However, as intriguing as this evidence may be, certain experimental confounds raise questions about the validity of these results. Most importantly, all of the experiments listed above took place within 500 m of the nearest reef – which is well within the range at which olfactory cues would be available to larvae (Atema et al. 2002, Myrberg and Fuiman 2002, Arvedlund and Kavanagh 2009, Atema 2012). The absence of a control for other sensory modalities makes it difficult to conclude that acoustic cues were the only factor influencing larval behavior. Second, most experiments counted the total number of larvae that moved towards particular experimental areas, without tracking the orientation behavior of individuals. With this type of experimental design, there is no way to know whether schooling behavior took place – whether a group of larvae "followed the leader" (Leis et al. 2009). Third, because these experiments took place near real reefs, the ambient noise levels were relatively high, which required the investigators to use unrealistically high sound levels in their playbacks in order to obtain sufficient signal-to-noise ratios (Mann et al. 2007). Furthermore, in almost every experiment the pressure spectrum of the played-back sounds was not reported; thus it is impossible to know the spectral content of the broadcast sounds. To truly understand the significance of acoustic cues for fish larvae, especially while far offshore, further work is needed. In particular, it is critical to characterize the sounds of the reef itself in order to understand the distance at which fish larvae could detect and respond to acoustic cues.

Shallow-water acoustic habitats

Traditionally, research on underwater sounds focused on deep water basins where most of the variability is explained by physical phenomena (e.g. temperature, wind) (Knudsen et al. 1948, Wenz 1961, 1962, 1972). It wasn't until recently that investigators considered that this "ambient noise" in the ocean could serve as a "signal" for certain organisms (Buckingham 1999, Fay 2009). An emerging type of ecological research called acoustic ecology focuses on the interaction between animals and their habitat's "soundscape" (Schafer 1977). A soundscape includes sounds produced by abiotic factors – such as wind, waves, and rain (Hildebrand 2009), as well as biological factors - the sounds made by animals as they call out for mates, defend their territories, or escape predators (e.g., Myrberg and Fuiman 2002). Soundscapes in both marine and terrestrial environments contain information that can help the animals orient themselves to their surroundings or navigate towards particular areas (Bregman 1990, Fay 2009).

Although several studies have measured coastal soundscapes over short time scales (McCauley and Cato 2000, Lammers et al. 2008, Kennedy et al. 2010, Au et al. 2012, Staaterman et al. 2013, McWilliam and Hawkins 2013), no thorough temporal analysis has been conducted. Yet variability is expected to be highest in these shallow-water environments where soniferous animals are abundant (Urick 1983). In order to identify patterns within an inherently complex system, it is common practice to partition the soundscape (acoustic spectrum) into different frequency bands which are dominated by biological and non-biological sources. Wenz (1962) described three components of the underwater acoustic spectrum: the "low-frequency" spectrum (<10 Hz) caused by turbulence and pressure fluctuations from surface waves, the "non-wind-dependent" spectrum (10-1000 Hz, with peaks between 20-100 Hz), caused by biological sounds and shipping noise, and the "wind-dependent" spectrum (50-10000 Hz, with peaks between 100-1000 Hz), which is driven by the wind (Wenz 1962). Although snapping shrimp tend to dominate reef soundscapes above 2 kHz, sound production and detection for marine fishes is generally below 1 kHz (Higgs et al. 2006, Hildebrand 2009). Therefore, it is essential to tease apart contributions from different spectral bands, particularly in the lowest frequencies, in order to understand the quality and amplitude of acoustic cues that are available to larval fish at different times of the year.

In addition to temporal variability, coastal soundscapes have high spatial variability (Radford et al. 2010, 2014, McWilliam and Hawkins 2013). Not only do acoustic signals diminish with distance from the reef, they can also differ from one area to the next (Radford et al. 2010, 2014, Piercy et al. 2014). For example, Radford et al. (2010) found that different types of coastal environments (sandy beach, urchin-dominated reef, kelp-dominated reef) have distinct acoustic signatures. Similar findings have emerged in terrestrial soundscape ecology, and there has recently been a push to use acoustic information as a tool to assess biodiversity and species composition (Sueur et al. 2008, Depraetere et al. 2012). A few recent studies have examined the propagation of reef sounds in terms of acoustic pressure (Radford et al. 2011b, Piercy et al. 2014) , but have not measured propagation of acoustic particle acceleration, which is the more salient cue for most fishes (Popper and Fay 2011).

There are two types of signals associated with a sound wave: pressure (a non-directional quantity), and particle acceleration (directional along a 180° axis). The physiology of the organism of interest will determine whether one or both of these signals is detectable – in other words, how and what the animal "hears." A sound is created by the vibration of an object within its medium, which creates a propagating sound wave. As this sound wave moves through the water, adjacent water particles are displaced, thus resulting in tiny back-and-forth movements (i.e. "particle displacement" and its derivatives, "particle velocity" and "particle acceleration"). For a monopole source, very close by, in the "near-field" region, particle acceleration falls off steeply (as $\frac{1}{r^2}$, where r is distance) whereas pressure falls off as $1/r$ (Zeddies et al. 2012). Farther from the source, in the "far-field," both particle motion and pressure fall off as $1/r$ (Kalmijn 1988). Thus, while pressure is a scalar quantity that falls off evenly everywhere in the domain, particle motion is an inherently directional quantity (along a 180º axis) that falls off steeply close to the source and falls off with $1/r$ farther from the source. The transition between the near-field and far-field typically occurs at a distance of approximately 1 wavelength from the source (Mann et al. 2007), but this boundary may not be entirely clear; there is often an intermediate zone (Kalmijn 1988, Myrberg and Fuiman 2002). There is a dearth of research on the size of the near-field and the strength of the particle acceleration field emanating from biological sound sources, yet this is critically important for organisms that "hear" this component of the acoustic signal.

Acoustic detection in coral reef fishes

Just as there are two components of a sound wave, in fishes there are two modes of hearing as well: 1) direct stimulation of the inner ear, i.e. "particle-acceleration sensitivity" and 2) indirect stimulation, i.e., "pressure-sensitivity." While the former is the most basal form of hearing, the latter is limited to certain taxonomic groups (Popper and Fay 2011). The density of a fish is similar to that of water; as the sound wave moves through the water and oscillates nearby water particles, the whole body of the fish moves with this oscillation. However, because otoliths are more dense than water, these calcified structures lag behind the movement of the rest of the fish. This lag creates a shearing force in the inner ear where the otolith meets the sensory hair cells, thus triggering an action potential and sending a signal to the brain (Myrberg and Fuiman 2002, Fuiman et al. 2004, Higgs et al. 2006, Lu 2011). Because particle motion is inherently directional (Kalmijn 1988), and because fish have otoliths and sensory epithelia oriented in three axes, through this direct stimulation they should be able to detect the axis of sound propagation (Higgs et al. 2006, Zeddies et al. 2011). However, a 180º ambiguity remains, unless the fish is also able to detect acoustic pressure and can use the phase-lag between pressure and particle motion to identify the direction of the source (Schuijf 1976, Zeddies et al. 2011).

Some fishes have evolved physiological mechanisms to detect acoustic pressure in addition to particle acceleration. These specializations include a set of bones that connect the swimbladder to the inner ear (Weberian ossicles), anterior extensions of the swimbladder, or secondary gas-filled bullae located near the ear (Fuiman et al. 2004, Popper and Fay 2011). When the pressure wave passes by the fish, the swimbladder expands and contracts, which creates a form of particle acceleration within the body of the fish, activating the auditory system via the "indirect path" (Popper et al. 1988). In general, fishes with pressure-sensitive organs can detect a wider range of acoustic frequencies, while those that can only detect particle motion are limited to frequencies less than 1000 Hz (Popper and Fay 2011). Although hearing sensitivity has been described for only a fraction of fish species, this distinction between the two types of hearing is critical for any fish-centric acoustic ecology work.

Given the broad literature on hearing abilities in adult fishes (e.g., Tavolga and Wodinsky 1976; Tavolga *et al.* 1981; Higgs *et al.* 2006; Popper and Fay 2011), it is reasonable to hypothesize that fish larvae, too, may be sensitive to sounds. But only a few studies have addressed the hearing abilities in fish larvae, making it difficult to generalize across species. While the number of inner ear hair cells increases throughout ontogeny, the timing of this proliferation varies among species, and the development of specialized pressure-sensitive organs tends to occur later in ontogeny (Fuiman *et al.* 2004). In zebrafish, for example, hearing bandwidth increases as the Weberian ossicles develop (Higgs *et al.* 2003). In damselfish, the general shape of the audiogram does not change throughout ontogeny, but the smallest juveniles are less sensitive to sounds than adults (Kenyon 1996), due to the fact that they have fewer hair cells. In several other studies using either the auditory evoked potential (AEP) or auditory brainstem response (ABR) techniques, several reef-associated species (a carangid, a serranid, Wright *et al.* 2011), and a pomacentrid (Egner and Mann 2005) showed an increase in hearing sensitivity throughout ontogeny as well. However, it is difficult to generalize these results given the different methodologies, different species, and different frequencies tested (Ladich and Fay 2013). The best approach is to observe larval behavior when presented with stimuli that they would actually encounter (i.e. reef sounds rather than pure tones), at amplitudes equivalent to what they would encounter in their natural habitat.

Dissertation Scope

This dissertation addresses the question: do fish larvae use reef soundscapes to orient towards reefs? My goals were to quantify the acoustic signals near coral reefs, to observe the behavioral response of fish larvae to these cues, and to examine the potential consequences of active orientation behavior.

Chapter 2:

To set the stage for this work, I needed to ask: if fish larvae could navigate using acoustic signals, what would be the demographic consequences of this behavior? I used a biophysical model to compare dispersal paths of larvae that possessed orientation behavior to those that did not (Staaterman et al. 2012). I created an orientation module based off of a biased correlated random walk framework (Codling et al. 2004), integrated it into the Connectivity Modeling System (Paris et al. 2013b), and tracked the movement of individual larvae throughout time. I examined the effects of orientation behavior when fish larvae began this behavior early vs. late in their ontogeny, and from a range of distances.

Chapter 3:

Next, it was essential to examine the variability of acoustic cues throughout time, and to reveal biological vs. abiotic contributions to the soundscape. I deployed passive acoustic recorders for 14 months at two nearby reefs in the Florida Keys, and compared acoustic data to environmental data. One of the reefs had historically received nearly an order of magnitude more reef fish larvae than the other reef (Grorud-Colvert and

Sponaugle 2009), so I expected to observe different acoustic patterns at the two sites. I identified patterns on daily, lunar, and seasonal time-scales in different frequency bands. I also examined acoustic complexity and compared results from the two reefs.

Chapter 4:

Field-based behavioral tests were required to understand how fish larvae respond to reef sounds *in situ*. Previous studies presented fish larvae with unrealistically high-amplitude sounds, or focused on groups of larvae, rather than individuals. I conducted a playback experiment in Dean's Blue Hole, Bahamas, using the Drifting *In Situ* Chamber (Paris et al. 2008, 2013a), to observe the response of individual fish larvae from two taxonomic groups: *Acanthurus* spp. and *Astrapogon stellatus*. I tracked individual larvae through time and measured their orientation relative to a cardinal frame of reference and relative to the speakers.

Chapter 5:

To understand the distance at which fish larvae could detect the sounds of a reef, I conducted a propagation experiment and measured both acoustic pressure and particle acceleration. I compared results from a propagation model to field-based playbacks of a point-source. I also measured ambient sounds of the reef with increasing distance and compared the amplitude of the acoustic signals emanating from the reef to previously-published data on fish hearing thresholds.

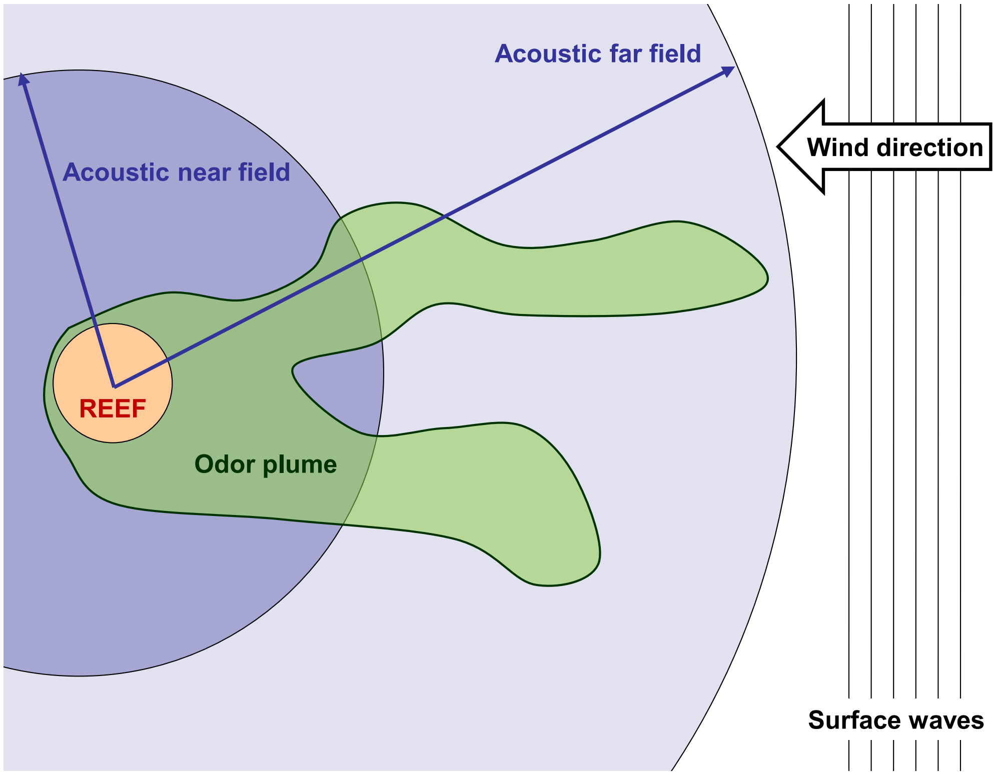

Figure 1.1. Potential environmental signals that could be used by fish larvae as they move from the pelagic zone towards the reef. At a range of distances, a fish larva would likely encounter environmental signals requiring different navigational mechanisms (Staaterman and Paris 2013). Farthest from the reef, orientation is presumably limited to the use of magnetic cues, polarized light, or a sun compass. Closer to the reef, fish may orient using chemical signals when inside the odor plume, or acoustic signals when within the acoustic field. It is likely that fish exhibit some degree of behavioral plasticity and can utilize different cues depending on their proximity to the reef (Kingsford et al. 2002, Leis 2006, Staaterman and Paris 2013). The distance at which the acoustic field becomes detectable to the fish depends upon 1) the frequency components of the reef soundscape, which affects the location of the near-field/far-field boundary; 2) the physical properties of the environment, which affects the propagation of the sound wave; and 3) the detection abilities of the species of interest (Kalmijn 1988, Mann et al. 2007).

CHAPTER 2: ORIENTATION BEHAVIOR IN FISH LARVAE: A MISSING PIECE TO HJORT'S CRITICAL PERIOD HYPOTHESIS[1]

Summary

Larval reef fish possess considerable swimming and sensory abilities, which could enable navigation towards settlement habitat from the open ocean. Due to their small size and relatively low survival, tagging individual larvae is not a viable option, but numerical modeling studies have proven useful for understanding the role of orientation throughout ontogeny. Here I combined the theoretical framework of the biased correlated random walk model with a very high resolution three-dimensional coupled biophysical model to investigate the role of orientation behavior in fish larvae (Staaterman et al. 2012). Virtual larvae representing bicolor damselfish (*Stegastes partitus*) were released daily during their peak spawning period from two locations in the Florida Keys Reef Tract, a region of complex eddy fields bounded by the strong Florida Current. The larvae began orientation behavior either before or during flexion, and only larvae that were within a given maximum detection distance from the reef were allowed to orient. They were subjected to ontogenetic vertical migration, increased their swimming speed during ontogeny, and settled on reefs within a flexible window of 24 to 32 days of pelagic duration. Early orientation, as well as a large maximum detection distance, increased settlement, implying that the early use of large-scale cues increases survival. Orientation behavior also increased the number of larvae that settled near their home reef, providing evidence that orientation is a mechanism driving self-recruitment. This study demonstrates that despite the low swimming abilities of the earliest larval stages, orientation during this "critical period" would have remarkable demographic consequences.

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[1] (Staaterman et al. 2012)

Background

For many reef fish, adults are relatively sedentary, but larvae have the potential of dispersing over long distances. Recent studies have demonstrated that fish larvae are strong swimmers that possess considerable sensory capabilities (Kingsford et al. 2002, Fisher 2005, Leis 2006). These capabilities allow fish to migrate vertically in the water column and also to navigate towards reefs, thus influencing their dispersal paths (Paris and Cowen 2004, Vikebø et al. 2007). It has been further hypothesized that orientation behavior in fish larvae may be a significant determinant of the structure of reef fish populations (Doherty and Williams 1988, Leis 2006). Orientation behavior could be a missing component of Hjort's critical period hypothesis, which focused on the necessity of early feeding behavior for survival (Hjort 1914). Recruitment variability results from a suite of physical and biological processes (Houde 2008), and this work adds another piece to this puzzle by illustrating the critical role of orientation behavior.

Techniques for tracking larval orientation *in situ* by following individual larvae (Leis et al. 1996, Huebert and Sponaugle 2009) or using a drifting behavioral chamber (Paris et al. 2008) are valid over short time periods, but cannot be used to track larvae from birth to settlement. Alternatively, it is possible to test hypotheses about the relative importance of behavior through numerical modeling techniques (Fiksen et al. 2007, Paris et al. 2007). Previous modeling studies that included swimming behavior found that swimming can affect dispersal patterns as well as the number of successful recruits (Wolanski et al. 1997, Porch 1998, Fiksen et al. 2007). In these studies, however, all larvae either swam directly towards their target or had no target, and had no variability in sensory capabilities or the strength of cues. On the other hand, studies that do include stochastic components are primarily theoretical, testing the importance of parameters without using real ocean currents (Codling et al. 2004). The novel contribution of this paper is the fusion of a theoretical framework (Armsworth 2000, Codling et al. 2004) with an existing coupled biophysical model that uses “real world” complex hydrodynamics and habitat data (Paris et al. 2007). Fiksen et al. (2007) emphasized the importance of linking hydrodynamic models with rule-based behavioral models in order to understand why and how certain larval traits have prevailed, revealing optimal strategies as well as broader scale ecological processes controlling fish populations (Fiksen et al. 2007, Vikebø et al. 2007).

Beyond demonstrating the proof-of-concept for this new orientation module, I examined the effects of maximum detection distance, the strength of habitat cues, and the timing of orientation behavior on settlement and dispersal patterns. Larval reef fish may be able to navigate towards reefs using a suite of behavioral modalities at a range of distances (i.e. magnetic, 10-1000 km; olfactory, 0-50 km; acoustic, 0-10 km; visual, 0-100m; Kingsford et al. 2002, Atema 2012). To disentangle the potential utility of these modalities, I used a range of detection distances. Although the development of sensory abilities throughout ontogeny is not well-studied, orientation behavior began either immediately post-hatching or during the flexion period to examine potential consequences of orientation capabilities during the “critical period” of the larval stage (Hjort 1914).

Specific objectives were to 1) create an orientation module to simulate the behavior of fish larvae in realistic turbulent flow conditions, 2) to examine the effects of orientation behavior on settlement and dispersal patterns and 3) to test for differences between early and late orientation, cue strengths, and as different sensory abilities.

Methods

The Connectivity Modeling System

The Connectivity Modeling System (CMS; Helgers and Paris 2011) is a coupled biophysical individual-based model that combines physical parameters such as ocean currents, bathymetry, and turbulence, with biological parameters such as spawning production, pelagic larval duration, ontogenetic vertical migration, mortality, and settlement. The "virtual larvae" are released at given locations and times, and are subjected to physical and biological forcing at each time step until settlement occurs. In previous versions of the CMS where orientation was not explicitly modeled, potential settlement locations were represented by polygons which typically included the reef habitat as well as buffer for a sensory zone. In these cases, the boundary of each polygon represented the edge of the larva's sensory zone and if a competent larva crossed this boundary, its trajectory was terminated and it was considered to have settled on the reef. In a 2005 study, Paris et al. manipulated the size of this sensory zone and found that a larger sensory zone increased settlement (Paris et al. 2005a). However, little is known of the effects that short-range orientation behaviors (those that take place between the edge of the sensory zone and the reef) have on settlement. Therefore, a more realistic scenario would model the paths of larvae within this near-field region of the reef (Armsworth 2000), which is the purpose of the orientation module developed here.

The CMS has an ontogenetic vertical migration algorithm which moves larvae in the water column following observed stage-specific distributions (Paris and Cowen 2004b, Irisson and Lecchini 2008, Irisson et al. 2010). This behavior has been shown to increase local retention (Paris and Cowen 2004), yet before this behavior begins (usually during the flexion period), larvae are subjected to advection from surface currents. Here our goal was to examine the effect of an additional type of larval movement: horizontal swimming behavior. Therefore, vertical migration was included in all simulations, and I tested the effect of adding oriented horizontal swimming behavior to the existing CMS framework.

The Orientation Module

The theoretical framework for the new Orientation Module (OM) is based on the biased correlated random walk described in Codling et al. (2004). From any given position in space, there is a target destination which the larva is "seeking," represented by the centroid of a reef location. The larva's ability to reach the target destination depends on the 1) strength of the cue (or combination of cues, in the real world) emanating from the target, 2) the maximum detection distance, β, 3) the swimming speed, S, of the animal, and 4) its ability to navigate in a turbulent flow. The equations and framework used to develop this orientation module are summarized below, following the notation of Codling et al. (2004):

The direction in which the larva will travel in the present time step, θ, is picked from the von Mises distribution, $f(\theta)$:

$$f(\theta) = \frac{1}{2\pi I_o(k)} e^{k cos(\theta-\theta'-\mu_\delta)}$$

Where θ' is the current direction the larva is facing (based on travel from previous time step to current time step), $I_o(k)$ is the modified Bessel function (Batchelet 1981) based on *k,* a parameter representing the strength of a cue from the habitat. The mean turning angle, μ_δ, is given by:

$$\boldsymbol{\mu_\delta = -\, d_T\, (\theta' - \theta_o)}$$

Here θ_o is the preferred direction, which is the angle between the current position and the center of the reef (the target destination). The sensing ability of the larva, d_T, is given by:

$$\boldsymbol{d_T(x) = 1 - \frac{C}{\beta}}$$

Where *C* is the distance to the center of the nearest reef, and β is a parameter representing the maximum distance at which the animal can detect the reef (Codling et al. 2004).

Thus, each larva at any given time has a choice of possible bearings from the von Mises distribution. The von Mises distribution is transformed into its cumulative density function and a bearing angle, θ, is drawn at random. Using this directional angle, θ, and the swimming speed, *S*, I calculate:

$$u_{orient} = S\cos\theta$$

and

$$v_{orient} = S \sin \theta$$

It is important to remember that this is a biased correlated random walk – biased because it includes a preferred direction, correlated because it remembers its previous direction, and random because the angle is drawn randomly from a distribution.

Fusion of the Orientation Module and the Connectivity Modeling System

The displacement of individual larvae is computed by integrating the total horizontal velocity components, U and V, at each time step. Without orientation behavior, U and V are estimated by interpolating the horizontal velocity components of the ocean currents, u and v, at the larva's location, while also including u_{turb} and v_{turb} terms for the stochastic velocity due to unresolved subgrid-scale turbulence, i.e. U = u + u_{turb} and V = v + v_{turb}. Instead, with orientation, larval movement is directed by U = u + u_{orient} and V = v + v_{orient}, where the terms u_{orient} and v_{orient}, represent the orientation of the larva and include a stochastic component as previously described in the Orientation Module (above).

Simulation scenarios

I conducted an ensemble of simulations to test the effects of orientation behavior on larval settlement to all reefs, the number of larvae that settled within their home region, the length of the pelagic larval duration, and the distance from release location to settlement location. The maximum detection distance β, the strength of the habitat cue k, and the day that orientation began, were manipulated to examine effects on the above mentioned measures. The focal region was the Florida Keys Reef Tract, FL, USA, for which a very high resolution, data-assimilated hydrodynamic model has been developed to resolve the meso- and sub-mesoscale eddy circulation in the region (Figure 2.1; Kourafalou et al. 2009). The focal species was the bicolor damselfish, *Stegastes partitus*, due to extended knowledge of the reproductive strategy, larval traits, and larval behavior of this species (Sponaugle and Cowen 1994, Paris-Limouzy 2001, Paris and Cowen 2004, Paris et al. 2005b). Velocity fields were obtained from nested simulations of the HYbrid Coordinate Ocean Model for 2007 (Figure 2.1; HYCOM, www.hycom.org, Bleck 2002). To maximize the resolution of the current fields, two nested oceanographic models were used. For the child grid I used the very high resolution FLKEYS-HYCOM 1/100 degree (~900 m) grid resolution model (Kourafalou et al. 2009), extending over a domain encompassing the Florida Keys and the Straits of Florida (Figure 2.1, 23-26° N, 79.5-83.3° W). The parent grid covered a larger domain including most of the cost of Florida (21-35°N, 75-87°W) and was represented by the HYCOM-Global 1/12 degree model (Chassignet et al. 2003). Simulations were run offline, with data available every six hours for the child grid and once daily for the parent grid. The CMS utilizes a zero-order stochastic Lagrangian process and operates with a 4th-order Runga-Kutta integration scheme; integration time steps ranged from 6 minutes to 1 hour, depending on the particular simulation (Table 2.1).

After each simulation, I calculated the percent of the 1000 released larvae that settled to reef habitat, for each monthly cohort. These percentages were then averaged across months and compared with Kruskal-Wallis tests. I also calculated the average number of larvae that settled each day throughout the entire 5-month period and the average pelagic larval duration (PLD) for the settling larvae. The distance between each larva's starting location to its settlement location was determined; dispersal kernels for each scenario were calculated as the normalized probability of each dispersal distance. To provide measures of self-recruitment, I counted the number of larvae that settled into reef polygons within either 4 km or 15 km of their release location.

Initial conditions and parameters used

See Table 2.1.

Locations of release sites, settlement sites, and orientation targets

The release location used for the majority of simulations was upstream of the Florida Keys, in the Dry Tortugas (82.795° W, 24.686° N), but some simulations were repeated with a release in the Middle Keys (81.274° W, 24.571° N). Settlement sites were depicted by 2 km x 2 km reef polygons which were created by overlaying a grid onto larger reef polygons derived from the Coral Reef Millennium Mapping Project (Andrefouet 2006; Figure 2.2). Any areas of the grid that contained reef habitat were included as potential settlement sites following Paris et al. 2005. These polygons were smaller than those used in previous studies (Paris et al. 2005a, 2007a, Cowen et al. 2006, Kool et al. 2010) and more accurately represented reef habitat without including a sensory zone. The centroids of these 2 km x 2 km polygons were used as target destinations for the larvae.

Timing of release

Larvae were released throughout five lunar cycles, from April to August of 2007. One thousand larvae were released in each lunar cycle; the number released each day was scaled by the lunar cyclic spawning patterns observed in collections and otolith aging studies of *S. partitus* larvae in this region (D'Alessandro et al. 2007).

Timing of orientation

For each lunar cycle, 3 scenarios were simulated: 1) no orientation, 2) orientation begins the first day after hatching ("early orientation"), and 3) orientation begins during the flexion period (day 6, "late orientation," Paris et al. 2005a).

Timing of settlement

The larvae were allowed to settle any time between the 24th day and the 32nd day after hatching (Paris and Cowen 2004, Rankin 2010). If a larva reached a reef before it was competent (before day 24), it continued to travel. If a larva failed to settle by the end of this competency period, its trajectory was terminated and excluded from further analysis.

Turbulence value

For non-orienting scenarios in the CMS, turbulence was simulated by adding a random kick (i.e. u_{turb} and v_{turb}) to the horizontal and vertical velocity vectors at each time step to represent turbulent diffusion (Okubo 1971) unresolved within the 900 m grid of the hydrodynamic model. The random displacement assumes that turbulence is isotropic in the horizontal direction, which is recommended for oceanographic applications (Brickman et al. 2007). In the orientation scenarios, when the larvae were beyond their maximum detection distance, *β,* the stochastic component of movement was also modeled by this turbulent random kick. The magnitude of the random kick was given by:

$$n\sqrt{\frac{2K}{\Delta t}}$$

where n is a uniform random number between 0 and 1, Δt is the integration time, and K is the horizontal diffusivity coefficient. Based on the resolution of the FL KEYS - HYCOM model, a value of $K = 0.7\ \mathrm{m^2\,s^{-1}}$ was used (Okubo 1971).

Maximum detection distance, β

This value represented the maximum distance at which a larva could detect its target. Armsworth (2000) defined "current-independent cues" as those which propagate radially from the reef center, which is what I modeled here. I tested for differences between three maximum detection distances: 1 km, 5 km, and 10 km, using 6 minute, 30 minute, and 1 hour integration times, respectively (Table 2.1). When larvae were within β, their movement was directed by $U = u + u_{orient}$ and $V = v + v_{orient}$. When larvae were beyond β (i.e., $C > \beta$), then the u_{orient} and v_{orient} terms were replaced with u_{turb} and v_{turb}; the stochastic component of movement was represented by the usual turbulent random kick used in the CMS for sub-grid scale motion.

Vertical migration

A probability matrix for the vertical distribution of larvae over time was used to depict the patterns observed from plankton sampling efforts around Barbados, West Indies, where *S. partitus* is also common (Table 2.2; Paris and Cowen 2004). The matrix placed larvae in 20-m depth bins depending on their developmental stage (hatching, pre-flexion, flexion, post-flexion, Paris et al. 2005b). The distribution of larvae was dictated by this probability matrix, and individual larvae could move at random between two adjacent depth bins once per day.

Cue strength, k

This dimensionless parameter represents the strength of a cue emanating from a reef, which relates to habitat quality (Codling et al. 2004). For most of the simulations conducted here, I chose $k = 4.5$, a value close to the maximum, $k = 5$. I did not repeat the well-developed sensitivity analysis for this parameter conducted by Codling et al. (2004), but did test the effects of k by running a sub-set of simulations with a smaller value, $k = 2.5$. The relationship between the values of k and real measures of habitat quality must be validated with empirical data.

Swimming speed, S

Swimming speeds in coral reef fish larvae increase throughout ontogeny (Fisher et al. 2000, Fisher and Bellwood 2003), thus, I used the nearly-linear equation relating swimming speed to age post-hatching from (Fisher 2005) given by:

$$S(age) = S_{hatch} + 10^{\frac{\log_{10} age}{\log_{10}(PLD)} \log_{10}(S_{settle} - S_{hatch})}$$

where S_{hatch} (1.9 cm s^{-1}) was estimated from Fisher (Fisher 2005) and S_{settle} was the published U_{crit} value (42 cm s^{-1}, Fisher et al. 2005).

Results

Dry Tortugas

Orientation behavior increased settlement in all months, and larvae that oriented early were more likely to settle than those that oriented late (Figures 2.3 – 2.5). The average number of daily arrivals was highly variable, yet early and late orientation from both 5 and 10 km significantly increased daily settlement compared to no orientation (Kruskal-Wallis test, df = 6, $\chi^2 = 255.3$, $p < 0.001$). When percent settlement was averaged across months, only the scenarios with a maximum distance of 10 km resulted in significantly higher settlement for both low and high values of k used (Kruskal-Wallis test, df = 6, for $k = 4.5$, $\chi^2 = 27.02$, $p < 0.001$; for $k = 2.5$, $\chi^2 = 25.3$, $p < 0.001$, Figures 2.4 – 2.5). Larvae that did not orient arrived at settlement habitat significantly later than orienting larvae (Kruskal-Wallis test, df = 6, $\chi^2 = 1665.1$, $p < 0.0001$), and larvae that oriented from 5 km and 10 km distance settled significantly earlier than those that oriented from 1 km. Despite a high degree of variability between monthly cohorts (Figures 2.3 – 2.4), the trends were robust: larger maximum detection distances, early orientation, and larger cue strengths increased the likelihood of settlement (Figures 2.3 – 2.5). Yet, a larger detection distance, β, had a greater effect on settlement than did cue strength, k (Figure 2.5).

In all months, early orientation, together with a larger maximum detection distance, resulted in a higher number of self-recruiting larvae (Figure 2.6). When the home region was defined as 15 km, these differences were only significant for early and late orientation from a maximum distance of 10 km (Figure 2.6A, Kruskal-Wallis test, df = 6, $\chi^2 = 21.75$, $p < 0.001$). However, when the home region was limited to 4 km, none of the orientation scenarios resulted in a higher number of self-recruiting larvae (Figure 2.6B, Kruskal-Wallis test, df = 6, $\chi^2 = 0.58$, $p < 0.99$).

Orientation behavior from all distances significantly decreased the mean dispersal distance of settling larvae for both values of cue strength (*k)* that were tested (Kruskal-Wallis test, df = 6: $\chi^2 = 334.2$, $p < 0.001$ for $k = 4.5$; $\chi^2 = 197.6$, $p < 0.001$ for $k = 2.5$), shifting the peak of the dispersal kernels closer to the release location (Figure 2.7). Early orientation behavior caused larvae to travel smaller distances than late orientation behavior for orientation from 5 km and 10 km.

Middle Keys

Similarly, for larvae released from the Middle Keys, early orientation behavior increased settlement for all months. Early and late orientation significantly increased the number of daily settlers (Kruskal-Wallis test, df =2, $\chi^2 = 66.73$, $p < 0.001$). Yet, when averaged across months, only the early orientation scenario had a significantly greater percent settlement than no orientation (Kruskal-Wallis test, df = 2, $\chi^2 = 11.18$, $p < 0.005$, Figure 2.4).

Self-recruitment for the Middle Keys was highly variable from month to month; there was no significant difference in self-recruitment between the scenarios when the home region was defined as 15 km (Kruskal-Wallis test, df = 2, $\chi^2 = 3.46$, $p < 0.177$) or when it was defined as 4 km (Figure 2.6, Kruskal-Wallis test, df = 2, $\chi^2 = 3.35$, $p < 0.187$). Yet the total number of larvae that settled near home throughout the 5-month spawning period was greater for early orientation compared to no orientation (Figure 2.6).

The dispersal distances of larvae released from the Middle Keys site were highly variable. Orientation increased dispersal in some months, and decreased it in other months. Unlike the Tortugas site, when averaged across months, larvae released in the Middle Keys under both early and late orientation scenarios had significantly longer dispersal distances than non-orienting larvae (Kruskal-Wallis test, df = 2, $\chi^2 = 201.6$, $p < 0.001$).

Discussion

This study demonstrates that orientation behavior increases settlement, decreases dispersal distances, and increases the number of larvae that settle close to home. It builds upon the theoretical framework developed by others (Armsworth 2000, 2001, Codling et al. 2004) but utilizes more realistic ocean circulation conditions, thus demonstrating that in the real world, fish larvae are able to significantly influence their dispersal paths through orientation behavior.

Previous studies have shown that after the onset of vertical migration, most larvae can be retained near their home reef (Paris and Cowen 2004, Vikebø et al. 2007). Before flexion, however, larvae are vulnerable to advection from the currents, especially in the Florida Keys where the Florida Current is strong and currents are highly variable (Figure

2.1). Larvae may be retained if the currents are favorable during this critical period, but because currents are highly variable from month to month, the settlement success of larvae will be highly variable too (Paris and Cowen 2004). This is supported by my data from the no orientation scenarios; in some months nearly 14% of larvae reached reef habitat, while in other months less than 3% settled in viable habitat. With orientation, larval movement was driven by a combination of swimming speed and ambient ocean currents; this interplay led to considerable variability in settlement. Orienting larvae were not guaranteed to reach a reef - the likelihood of settlement depended on the larva's ability to effectively use the ambient current conditions. This variability is reflected in the average number of larvae that settled each day as well as in the monthly settlement levels.

Despite varying daily and monthly levels of settlement, by adding orientation behavior during this critical pre-flexion period, the likelihood of settlement increased tremendously. Although swimming speeds before flexion were extremely slow (1.9-7.5 cm s^{-1}), larvae that oriented early had the highest chance of reaching a suitable reef after *ca.* four weeks of larval duration. Other modeling studies have found similar results, using different mechanisms. For example, Irisson et al. (2004) used an optimization model to demonstrate that the most successful larvae were those that oriented and swam early in their development. In a study by Paris et al. (2005a), "retention zones" around reef habitats represented orientation behavior - if a larva crossed into a retention zone, it was retained. When this behavior occurred earlier, a higher percentage of fish larvae settled within their natal region. The results of this more realistic modeling study corroborated these findings; early orientation limited dispersal (Figures 2.7 -2.8).

The condition of a larva upon its arrival on a reef may be closely tied to the length of time that it spends in the pelagic zone (Searcy and Sponaugle 2001). On average, orienting larvae settled on reefs two days earlier than those that did not orient. These two days can make quite a difference – not only because the fish larvae will be less exhausted upon settlement, but also because those are two fewer days when they are vulnerable to predation (Paris et al. 2007, 2009). Here I did not include mortality, but if I did, I would predict trade-offs between predator-induced mortality incurred while a larva remains nearshore vs. starvation-induced mortality while a larva continues to travel. Furthermore, by including growth rates and metabolic activity, the trade-offs between high swimming activity and early settlement compared to lower swimming activity and later settlement could be investigated. An analysis of the condition of settling larvae would allow a thorough understanding of the benefits of certain behavioral strategies (Fiksen et al. 2007).

The magnitude of difference in levels of self-recruitment between the orientation and no-orientation scenarios for the Dry Tortugas and Middle Keys was markedly different, and it varied depending on the size of the "home region" (Figure 2.6). When home was defined as reefs within 15 km from the natal reef, early orientation with a 10 km detection distance increased the total number of self-recruiting larvae to the Dry Tortugas by nearly one order of magnitude (i.e., 17 times), whereas in the Middle Keys the increase was 7-fold (Figure 2.6). However, when home was limited to a 4 km region, orientation in the Middle Keys led to an order of magnitude increase in self recruitment, while in the Dry Tortugas it led to only a 6-fold increase. Therefore, for larvae in the Middle Keys, where the current is more unidirectional, orientation behavior is absolutely critical in order to settle within a small region of the home reef, whereas in the Dry Tortugas, the benefits of orientation on self-recruitment are less important.

These results reflected the differences in the current regimes and geomorphology at the two sites. In the Dry Tortugas region, larvae were often entrained into a semi-permanent gyre (Kang and Kourafalou 2008) which means that they passed their home region a second time, once they were older and had stronger swimming abilities (Figure 2.2). This gyre allowed more larvae to be retained in this region, resulting in higher self-recruitment (Figure 2.6) and overall smaller dispersal distances (Figures 2.7, 2.8). This corroborates previous work on the relative influence of physical and biological processes to larval fish dispersion (Fiksen et al. 2007, Paris et al. 2007). Paris et al. (2007) showed a sequential shrinkage of larval dispersal kernels and an increase in self-recruitment with eddy activity and deep vertical migrations (Paris et al. 2007). In addition, the reef habitats are highly patchy in this region, which increased the chance of settlement within the larger 15 km region, but not necessarily within the 4 km region. This is because the model dictated that when they reached settlement age, larvae oriented towards the nearest reef they could detect, without a special preference for their natal reef. In the Middle Keys, the meandering Florida Current quickly advected the larvae to the north (Kang and Kourafalou 2008), making early orientation behavior even more critical, especially to reach the reefs within 4 km of home. Because the reefs in the Middle Keys are aligned on a straight line and are thus more fragmented, there are fewer dispersal paths that can lead to settlement habitat, so the probability that larvae settled without orientation behavior was low. Furthermore, many larvae were advected beyond the northern edge of the reef tract before they had the chance to orient and move towards the reefs, which explains why it was only the early orientation scenario that increased overall settlement for larvae released in the Middle Keys. In sum, my results indicate that it is a combination of oceanographic conditions, geomorphology, and orientation behavior that explains the site-specific differences in larval recruitment levels.

When examining the effect that maximum detection distance had on larvae released in the Dry Tortugas, I found that larger detection distances led to an increase in settlement (Figures 2.3-2.5) and self-recruitment (Figure 2.6). This trend was consistent for each month (Figure 2.3). When larvae sensed the reef from farther away, they were able to influence their path and were more likely to find suitable habitat. Interestingly, the change from a 5 to 10 km detection distance made little difference, suggesting that the most advantageous cues in this model operate on a 1-5 km scale, making acoustic cues a likely orientation mechanism. Indeed, these results match the orientation method modeled here, i.e. detection of current-independent cues radiating from a central habitat (Armsworth 2000). In the future, this module could be adapted for use with "current-dependent" (i.e. olfactory) cues, or large-scale (i.e. solar or magnetic compass) cues, as empirical data become available.

In these simulations I used a range of 1 km to 10 km to represent the possible distances at which a fish larva could detect a reef using short-range cues (Kingsford et al. 2002). More empirical data are needed to validate the maximum detection distances used here. In particular, it is important to test the response of fish larvae to these short-range cues *in situ* (Paris et al. 2008, Irisson et al. 2009), in realistic flow regimes such as those used in these simulations. Finally, an understanding of the sensitivity of larval fish to various cues throughout ontogeny is of critical importance, as the timing of orientation was a key factor influencing settlement success and dispersal patterns.

My results raise further questions regarding the abilities of larvae to detect and orient towards reef habitats from a distance. In the simulations described here, a relatively strong habitat cue ($k = 4.5$) was used, representative of a healthy reef, as well as a weaker habitat cue ($k = 2.5$), representing a mediocre reef habitat. The trends were consistent across k-values; but the most important parameters affecting larval settlement were the maximum detection distance and, to a lesser extent, the timing of orientation (Figure 2.5). Here, all reefs were assigned the same k-value. But because the quality of reef habitats varies spatially, an improvement of the Orientation Module should include the ability to parameterize k for individual reefs. This development would allow a more thorough analysis of "homing" behavior, as home reefs could be assigned a very large k-value compared to other reefs. This would allow investigators to determine whether larvae are able to return home with attraction to a strong imprinted cue.

In addition, it is important to assess critical thresholds as well as the real meaning of "habitat cue strength." Codling et al. (2004) found that it was possible to miss the reef with a small value of k. In the case of more realistic settings with a series of reefs to choose from and highly variable current fields (Figure 2.1), I found a similar effect: the arrival of larvae to settlement habitat was diminished with a weaker habitat cue. In the future, it would be useful to determine the cue strength threshold in the context of real oceanographic and habitat data (e.g. barrier reefs, oceanic atolls, etc.). Finally, calibration of this parameter by matching the arbitrary scale of $k = 0.5 - 5$ (established by Codling et al. (2004) to meaningful empirical data on the quality of the habitat is critical. With these developments, along with improved empirical data on sensory abilities and behavior, this module could be used to evaluate the critical threshold levels required for fish to detect and orient towards reefs. This Orientation Module could be applied to further investigate the effects of orientation on spatial patterns of settlement and population connectivity.

Conclusions

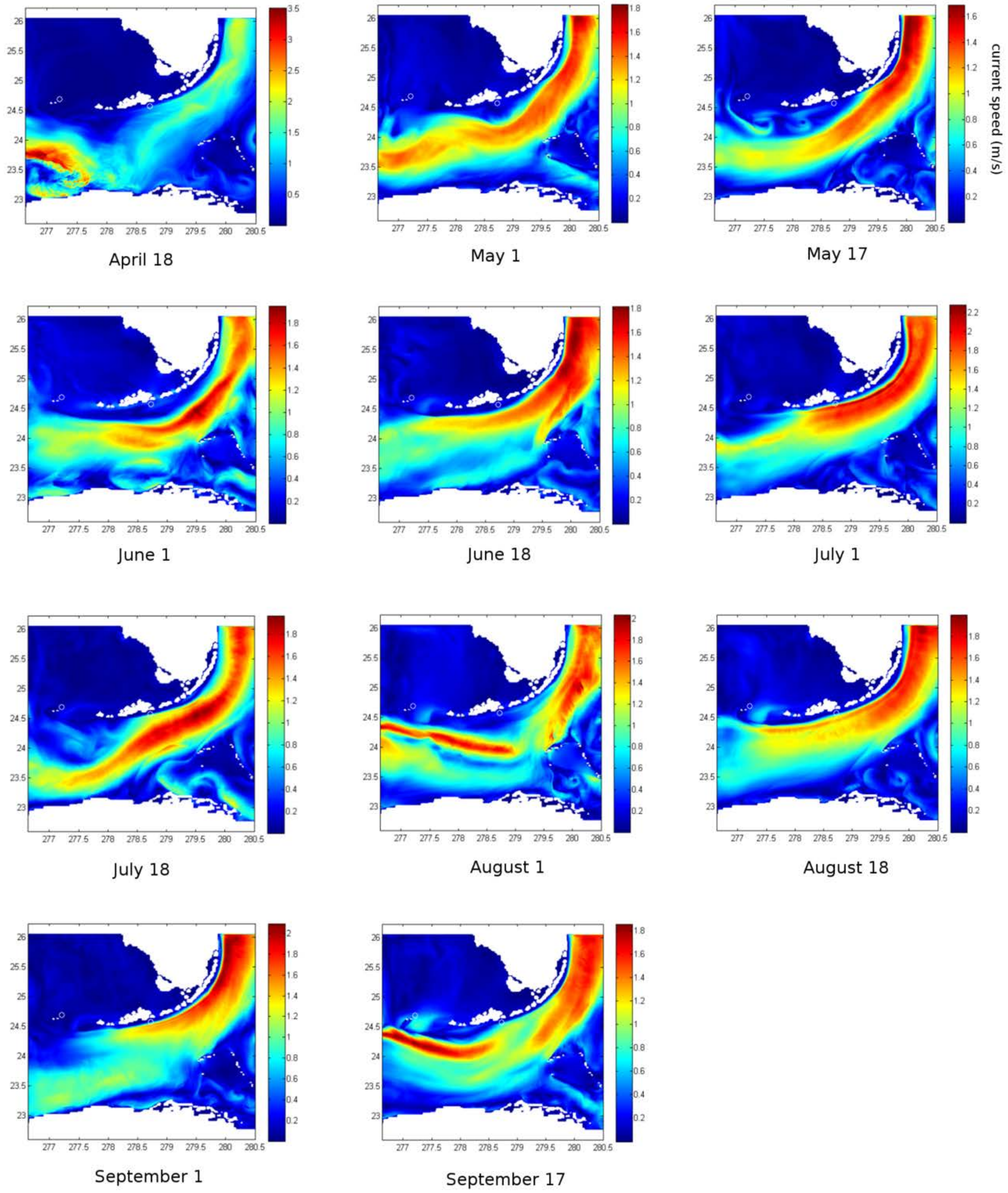
The long-standing assumption that larval fish are passive particles is being overturned. Recent empirical studies have elucidated the sensory and swimming capabilities of these organisms. Using a modeling approach, I showed the demographic consequences of larval navigation. I demonstrated that even with weak swimming speeds, fish larvae that possess strong sensory abilities can influence their dispersal paths and are more likely to successfully find reef habitat, especially when orientation behavior happens early in the pelagic phase. These results provide a missing piece to Hjort's critical period hypothesis: orientation behavior during the "critical period" increases the likelihood that larvae will survive the pelagic phase.

Table 2.1. Summary of scenarios performed. Release patterns were similar for all scenarios. Virtual larvae were released over 5 lunar cycles, from April to August 2007; the number of larvae released each day was scaled with observed spawning production and ranged from 5-126; a total of 1000 particles were released in each lunar cycle. *Stegastes partitus* life history traits were modeled following (Sponaugle and Cowen 1994, Paris-Limouzy 2001, Paris and Cowen 2004, Paris et al. 2005b). β = maximum distance at which larvae could detect the reef, Δt = integration time of the model, k = cue strength.

Release location	Orientation type	β	Δt	k
Dry Tortugas	No orientation	N/A	1 hour	N/A
Dry Tortugas	Early orientation	1 km	6 min	2.5 / 4.5
Dry Tortugas	Late orientation	1 km	6 min	2.5 / 4.5
Dry Tortugas	Early orientation	5 km	30 min	2.5 / 4.5
Dry Tortugas	Late orientation	5 km	30 min	2.5 / 4.5
Dry Tortugas	Early orientation	10 km	1 hour	2.5 / 4.5
Dry Tortugas	Late orientation	10 km	1 hour	2.5 / 4.5
Middle Keys	No orientation	N/A	1 hour	N/A
Middle Keys	Early orientation	10 km	1 hour	4.5
Middle Keys	Late orientation	10 km	1 hour	4.5

Table 2.2. Probability matrix of depths and times driving the ontogenetic vertical migration of *Stegastes partitus* larvae. Numbers represent the fraction of larvae distributed in each depth bin based on empirical data from Paris & Cowen (Paris and Cowen 2004).

Depth (m)	Hatching (day 0)	Pre-flexion (day 1- day 5)	Flexion (day 6 - day 7)	Post-flexion (day 8 - day 32)
3	0.80	0.05	0.05	0.01
10	0.20	0.55	0.35	0.19
30		0.30	0.32	0.33
50		0.06	0.16	0.25
70		0.03	0.09	0.18
90		0.01	0.03	0.04



April 18

May 1

May 17

June 1

June 18

July 1

July 18

August 1

August 18

September 1

September 17

Figure 2.1. Current fields in the The FL KEYS- HYCOM during new moon and full moon periods in the spawning season of 2007. Full moons occurred at the beginning of each month, and new moons during the middle of each month. The magnitude of the current speed, in m s^{-1}, as a combination of *u* and *v* velocities, are scaled to the color bars. The strong meandering Florida Current is visible in all months, though the exact location and magnitude are highly variable from month to month.

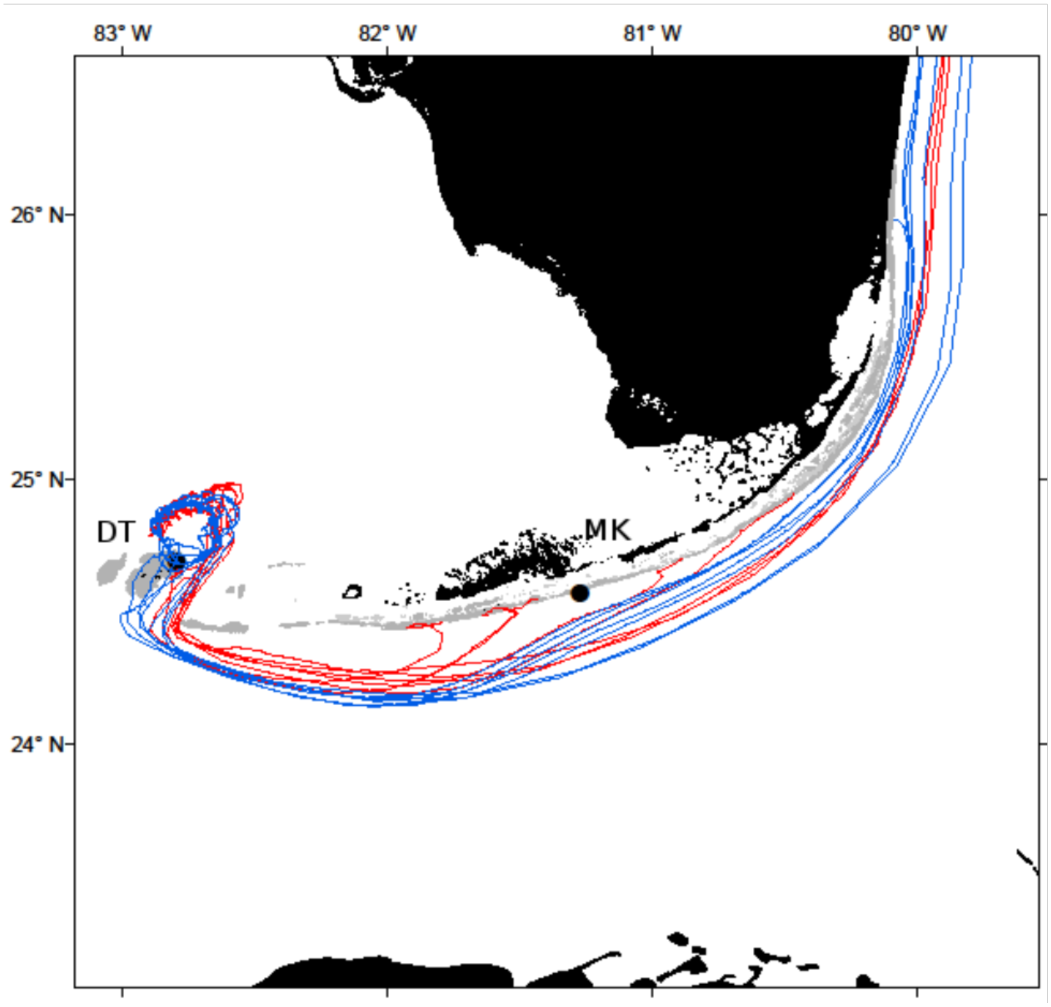


Figure 2.2. The FL KEYS- HYCOM domain included the Straits of Florida and the Florida Keys. Grey regions depict the (2 km x 2 km) reef habitats, black regions depict land. Larvae oriented towards the nearest reef polygon once they passed within their maximum detection distance, *β*. The black dots show the two release locations: the Dry Tortugas (DT) and Middle Keys (MK). Blue lines depict a subset (n = 8) of larval trajectories released in the Dry Tortugas that did not possess orientation behavior. Most of these larvae were advected into a gyre and were eventually swept past the reefs to the north. The red lines show trajectories (n = 8) of larvae with orientation behavior, with a maximum detection distance of 10 km. Once the larvae passed within 10 km of a reef, they began to swim towards the reefs and most were able to settle.

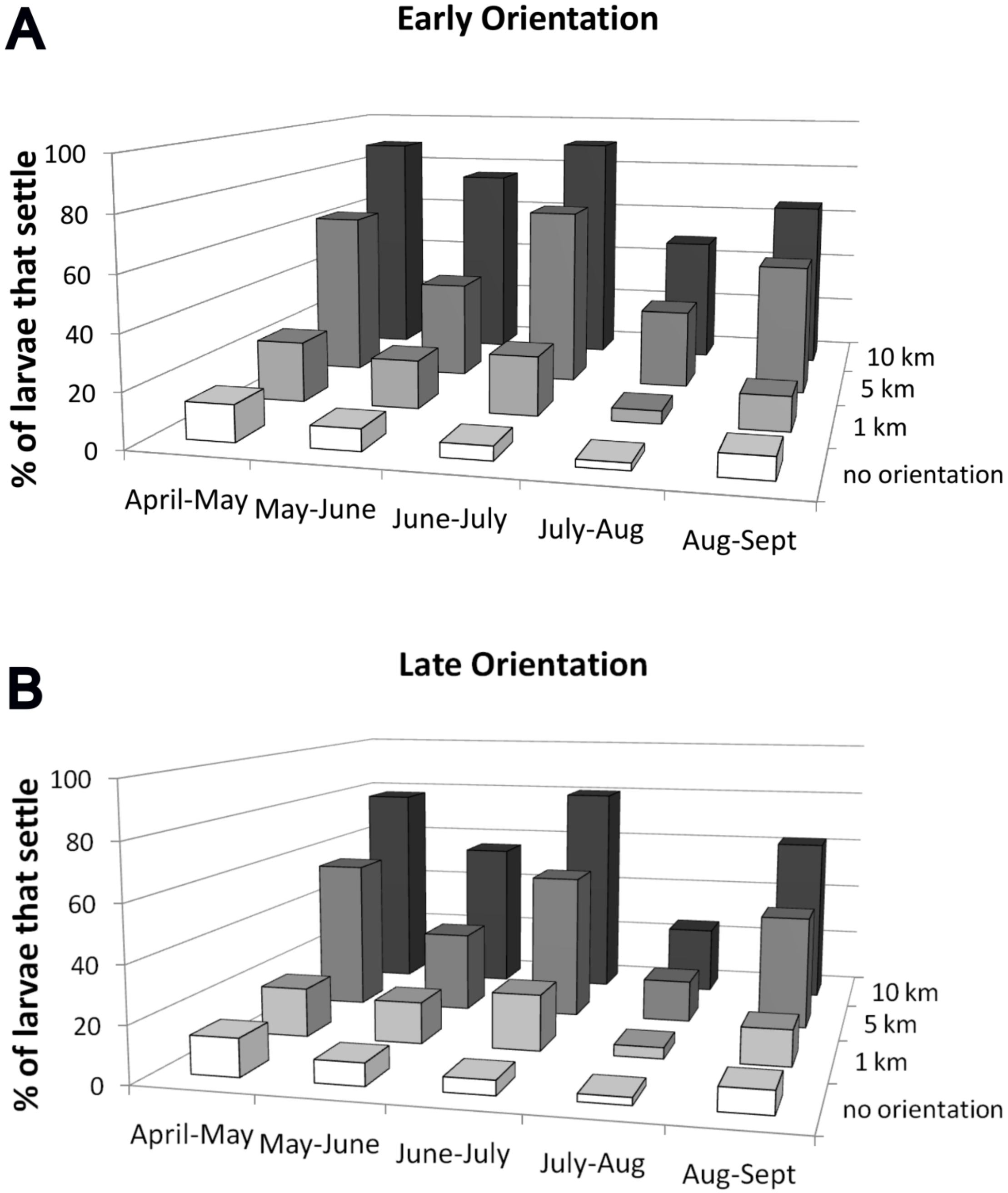


Figure 2.3. Monthly settlement for early orientation (A) and late orientation (B) behavior for larvae released in the Dry Tortugas with cue strength, *k* = 4.5. In each lunar cycle, 1000 larvae were released for each scenario. Although the magnitude of differences in settlement was variable between months, the trends are consistent: both a larger maximum detection distance and early orientation behavior increased the likelihood of settlement.

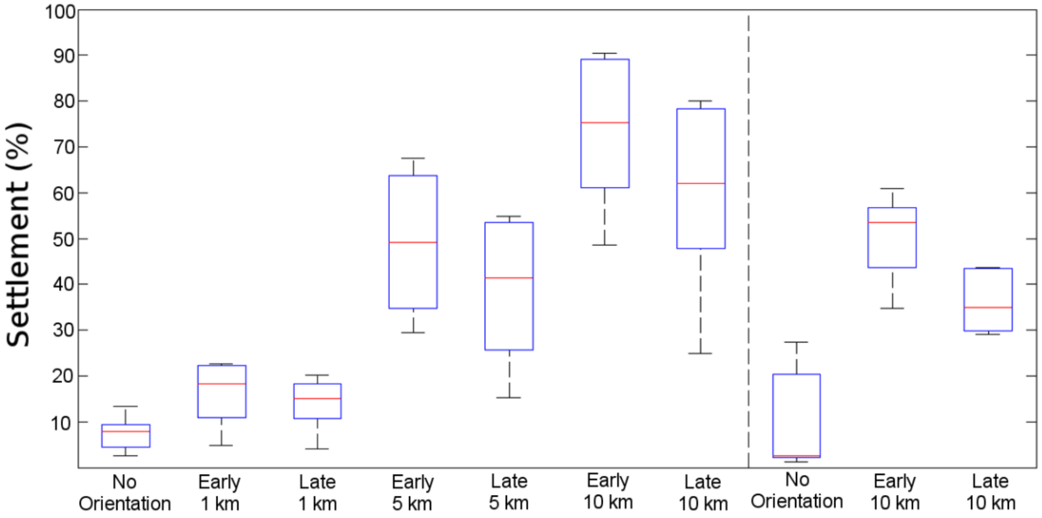


Figure 2.4. Sensitivity analysis on the onset of orientation behavior (early/late) and the maximum detection distance, β. The baseline comparison is the percent of non-orienting larvae that settled on any of the 582 2 km x 2 km reef polygons along the Florida Keys. At total of 1000 larvae were released in each month in each scenario from the Dry Tortugas (left panel) and Middle Keys (right panel), with cue strength, $k = 4.5$. Red line depicts median, blue box shows the 25th- 75th percentiles, black bars depict the edge of range. Simulated larvae were competent to settle between 24 - 32 days after hatching. A larger maximum detection distance, as well as early orientation behavior, generally increased settlement. This trend is evident, but the large ranges reflect the high degree of variability between monthly cohorts (as shown in Figure 2.3).

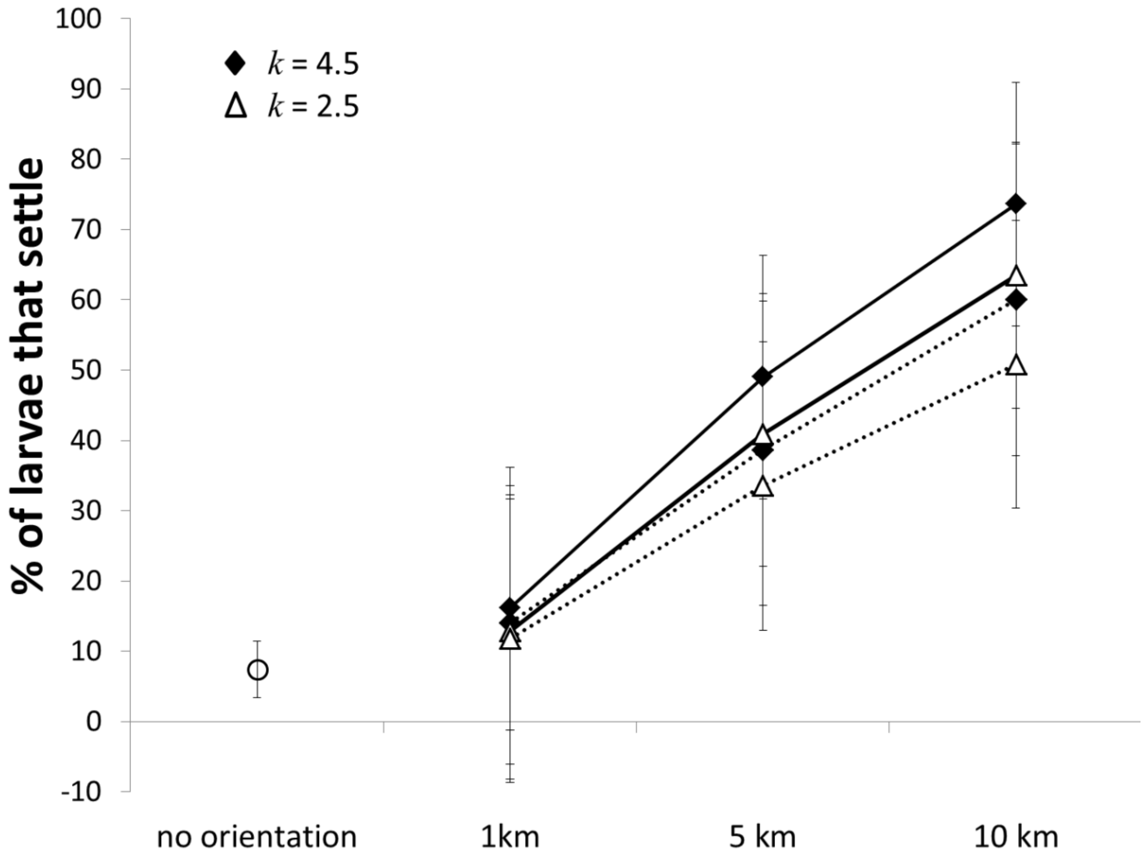


Figure 2.5. Sensitivity analysis for the cue strength, *k*. The mean and standard deviation of the percent of larvae that were released from the Dry Tortugas site that settled. Open circle: no orientation scenario, solid line = early orientation, dotted line = late orientation. A larger detection distance and early orientation had a greater effect on settlement than did cue strength, *k*.

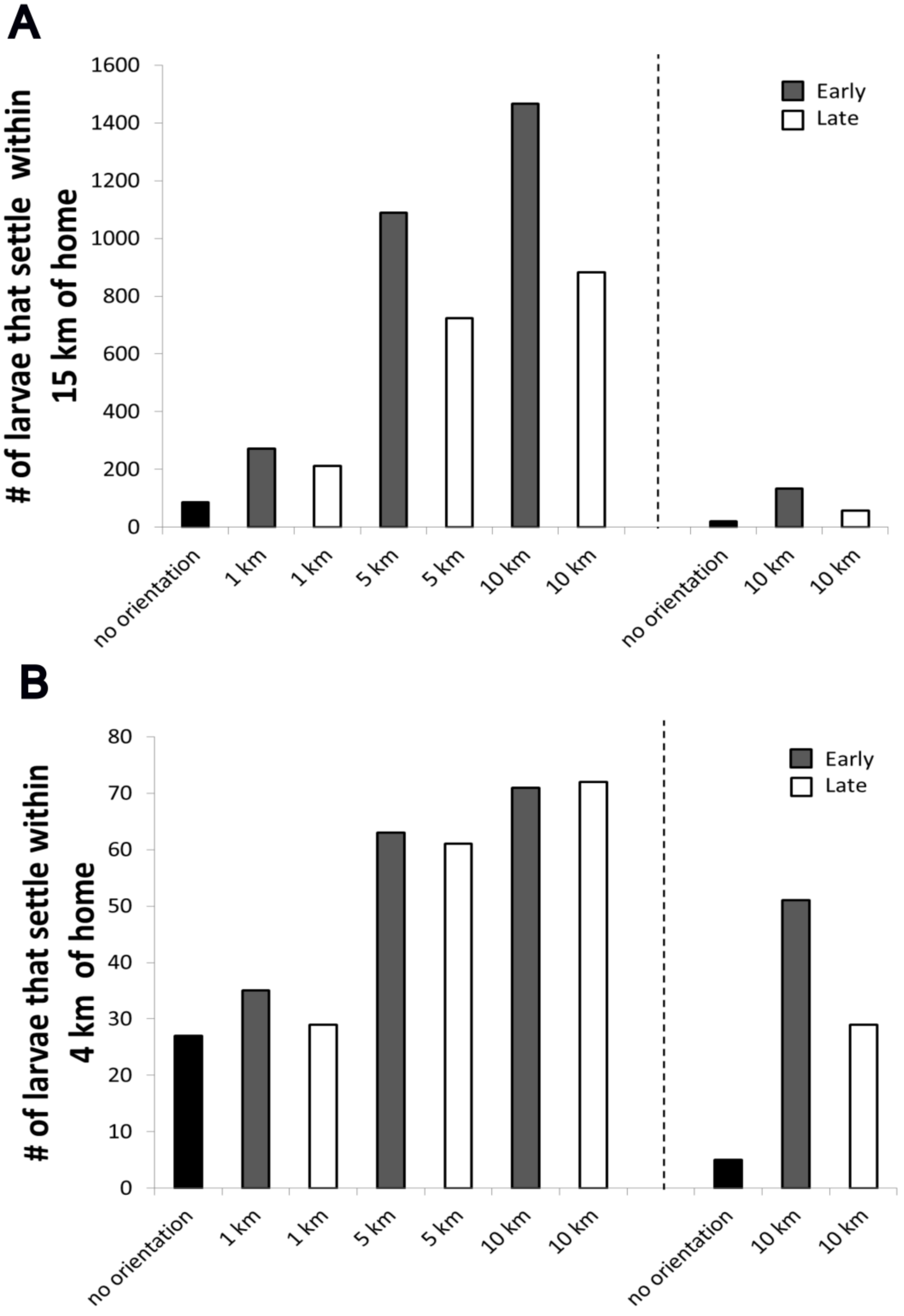


Figure 2.6. Sensitivity analysis of orientation behaviors on homing. Number of larvae that settled to reefs within 15 km of home (A) and 4 km of home (B) throughout the five-month spawning period (April-September 2007), with cue strength, *k* = 4.5. Results from larvae released in the Dry Tortugas appear on the left panel; results from Middle Keys on the right. In general, a larger detection distance and earlier orientation behavior increased self-recruitment. Large site-specific differences in larval settlement may result from a combination of oceanographic processes and geomorphological characteristics. The dispersal kernels for several of these scenarios are shown in Figure 2.7.

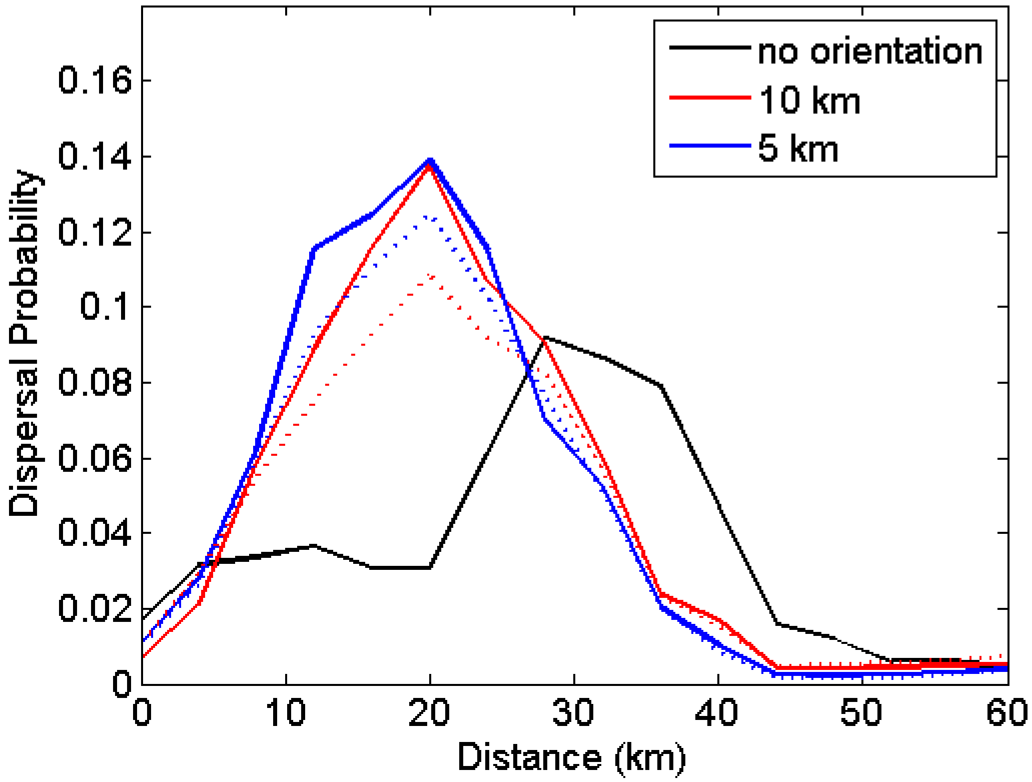


Figure 2.7. Dispersal kernels and orientation: probability density functions of dispersal distances for larvae released from the Dry Tortugas. Values represent the normalized probability for each distance, in 4 km bins. Black line: no orientation; solid lines: *k* = 4.5; dotted lines: *k* = 2.5. Orientation behavior shifted the dispersal kernel closer to the source, returning more larvae to their home region and increasing the probability of settlers (area below the curve). A lower cue strength *k* decreased the probability of settling without changing the modal distance of the kernel.

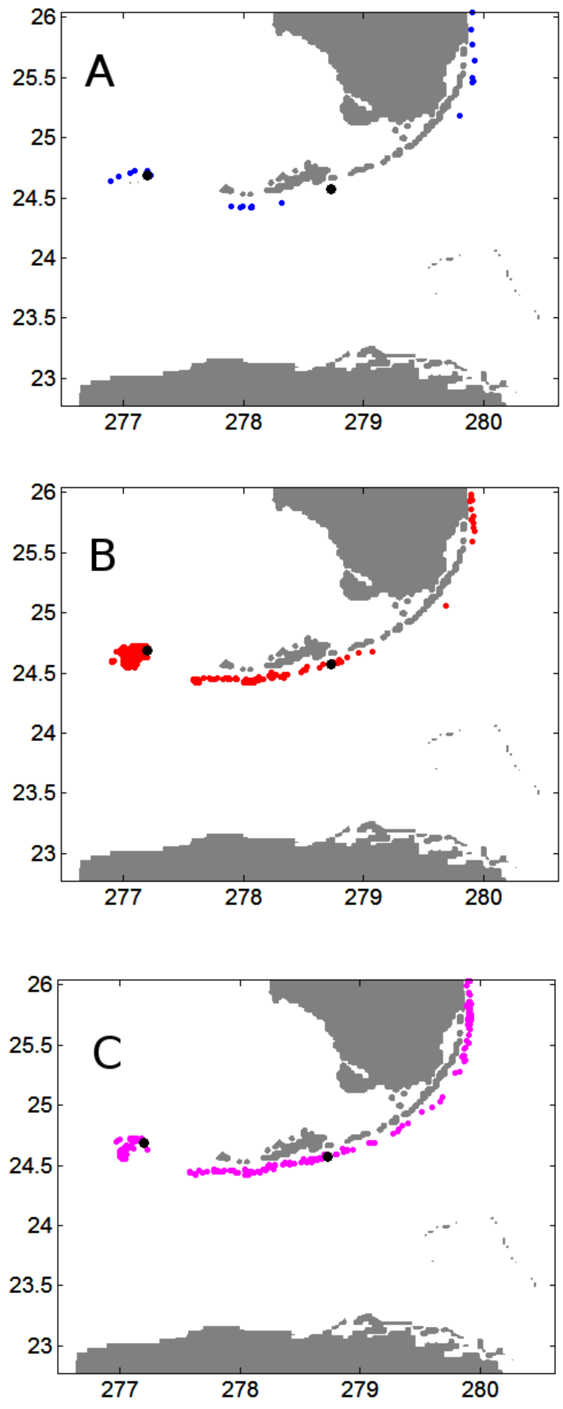


Figure 2.8. Settlement patterns and orientation: for larvae with no orientation (A); with early orientation and a detection distance, $\beta = 10$ km and cue strength, $k = 4.5$ (B); and with late orientation with $\beta = 10$ km and cue strength, $k = 4.5$ (C). Each dot represents the settlement location of one larva released from the Dry Tortugas site from July-August 2007. Larvae only settled to reefs (see Figure 2.2 for location of reef polygons). Larvae typically settled closer to home with early orientation behavior.

CHAPTER 3: CELESTIAL PATTERNS IN MARINE SOUNDSCAPES[2]

Summary

Soundscape ecology is the study of the acoustic characteristics of habitats, and aims to discern contributions from biological and non-biological sound sources. Acoustic communication and orientation are important for both marine and terrestrial organisms, which underscores the need to identify salient cues within soundscapes. Here I investigated temporal patterns in coral reef soundscapes, which is necessary to further understand the role of acoustic signals during larval orientation. I used 14-month simultaneous acoustic recordings from two reefs, located 5 km apart in the Florida Keys, to describe temporal variability in the acoustic environment on scales of hours to months. I also used weather data from a nearby NOAA buoy to examine the influence of environmental variables on soundscape characteristics. Results showed that high acoustic frequencies typically varied on daily cycles, while low frequencies were primarily driven by lunar cycles. Some of the daily and lunar cycles in the acoustic data were explained by environmental conditions, but much of the temporal variability was caused by biological sound sources. The complexity of the soundscape had strong lunar periodicity at one reef, while it had a strong diurnal period at the other reef. At both reefs, the highest sound levels (of ~130 dB re:1 μPa) occurred during new moons of the wet season, when many larval organisms settle on the reefs. This study represents an important example of recently-developed soundscape ecology tools that can be applied to any ecosystem, and the patterns uncovered here provide valuable insights into natural acoustic phenomena that occur in these highly diverse, yet highly threatened ecosystems.

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[2] (Staaterman et al. 2014a)

Background

Acoustic habitats, or “soundscapes,” contain information about environmental conditions, landscape features, and biological composition, and soundscape ecology is an emerging field of research in both terrestrial and marine science (Schafer 1977, Pijanowski et al. 2011b, 2011a, Dumyahn and Pijanowski 2011, Bormpoudakis et al. 2013). The biota living within a given environment can glean critical information from the sounds of their habitat (Bregman 1990). Typical components of a soundscape include “geophony,” the sounds caused by weather and seismological activity, “biophony,” the sounds produced by living organisms, and “anthrophony,” the sounds generated by human activity (Krause 2008, Pijanowski et al. 2011a). In shallow waters, the largest geophonic contributions are caused by wind and rain, which disturb the water’s surface (Wenz 1962, Hildebrand 2009). As in terrestrial environments, in the ocean there are many biophonic contributions to the soundscape, such as sounds made by animals as they call out for mates, defend their territories, or escape predators (Myrberg and Fuiman 2002). Finally, through industrial activity and shipping traffic, anthrophony in the ocean has increased in the last few decades (Andrew et al. 2011) and can interfere with animal communication systems (Clark et al. 2009, Barber et al. 2010, Slabbekoorn et al. 2010). Long-term acoustic recordings are required in order to understand the relative contributions of these sound sources, and to gain insights about the whole ecosystem.

While the geophonic components of underwater soundscapes have been studied for the last half-century (Knudsen et al. 1948, Wenz 1962, Hildebrand 2009) , an emphasis on biophony has been more recent (Slabbekoorn and Bouton 2008, Fay 2009, Pijanowski et al. 2011a, Hawkins et al. 2012, McWilliam and Hawkins 2013). Classical bioacoustic research typically focuses on a single species in isolation, without considering the acoustic properties of the entire habitat (Krause 1987). For example, previous studies in marine bioacoustics have documented unique temporal patterns associated with sound production of damselfish (Mann and Lobel 1995) goliath grouper (Mann et al. 2009), red hind (Nelson et al. 2011), and yellowfin grouper (Schärer et al. 2012), but these sounds were not analyzed within the broader context of their acoustic environments. A holistic picture of the soundscape requires the examination of all sources of biophony, since particular sounds follow distinct patterns and occupy specific frequency ranges, according to the "acoustic niche hypothesis" (Krause 1987). Many of the biological sound sources found in shallow-water, coastal environments remain unidentified (Mann 2012), but because biophony is a major contributor in these habitats (Tavolga et al. 1981, Urick 1983), their soundscapes present complex and exciting research subjects.

Coral reefs, like tropical rainforests, are characterized by high species diversity and thus are expected to have rich acoustic qualities (Rodriguez et al. 2014). Because sound waves experience relatively little attenuation in water compared to air, and sounds travel unidirectionally from their sources (Urick 1983), it has been suggested that reef soundscapes could serve as orientation cues for various types of marine larvae (Montgomery et al. 2006). Understanding the behavioral drivers of larval settlement is necessary for proper management, given the critical role of larval replenishment in marine population connectivity (Armsworth 2002). In the last decade, acoustic playback experiments have demonstrated that larvae from several taxa are capable of detecting acoustic signals and will move towards or will undergo settlement behaviors in response to sounds of their preferred habitat (Tolimieri et al. 2004, Simpson et al. 2005a, Vermeij et al. 2010, Radford et al. 2011a, Stanley et al. 2012, Lillis et al. 2014). While it is likely that a suite of cues are utilized by marine larvae as they seek their benthic home (Paris et al. 2008, Arvedlund and Kavanagh 2009, Pineda et al. 2010, Huijbers et al. 2012, Staaterman and Paris 2013), soundscapes are emerging as important signals. It is even possible that larvae could discriminate between the unique sound signatures associated with specific habitats (Radford et al. 2010, 2014, McWilliam and Hawkins 2013) and make settlement choices accordingly. Therefore, it is critical to characterize spatial and temporal patterns of these soundscapes in order to better understand the acoustic cues that are available to pelagic larvae.

Several studies have recorded coral reef soundscapes over short time scales (McCauley and Cato 2000, Lammers et al. 2008, Kennedy et al. 2010, Au et al. 2012, Staaterman et al. 2013, Radford et al. 2014), and others have attempted to link acoustic qualities of specific reefs with species composition (Kennedy et al. 2010, Staaterman et al. 2013). However, to my knowledge, there has never been a study examining long-term (across one year) patterns at multiple coral reefs. Here, I analyze 14-month recordings from two nearby coral reefs in the Florida Keys, USA, coupled with environmental data collected at a weather station situated between the two sites. The reefs were chosen because they are similar in depth and physical features, so I assume that the geophony of the two soundscapes are similar, but there is one important difference: the number of settlement-stage fish larvae that arrive on one reef is nearly an order of magnitude greater than on the other (Grorud-Colvert and Sponaugle 2009). This observed difference was not detected in biophysical modeling of larval dispersal in the Florida Keys, implying that the dissimilarities are not explained by oceanography, but perhaps by animal behavior (Sponaugle et al. 2012a). If the two sites possess different soundscape qualities, this may affect the orientation behavior of the larval fish in the vicinity of each reef.

This study focused on three central questions: (1) how does the soundscape change over different timescales? (2) what are the geophonic and biophonic contributions to the soundscape? and (3) do the soundscapes of the two reefs differ from one another, and if so, how? I expected to see a strong link between environmental conditions and acoustic measurements, and anticipated that any remaining variability may be attributed to biological sound sources.

Methods:

Study sites

The two sites of the recordings were Sand Island Reef (hereafter “Sand Island”, 25°0’43” N, 80°22’33” W) and Pickles Reef (hereafter “Pickles”, 24°59’23” N, 80°24’88” W) in the upper Florida Keys. The reef framework is comprised of *Acropora* spp. rubble, as well as *Montastraea*, *Porites, Siderastrea, Millepora, Gorgonia*, and *Palythoa* spp. (Ruzicka et al. 2009) and dominant fish families include Scaridae, Haemulidae, Acanthuridae, Labridae, Pomacentridae, Lutjanidae, and Pomacanthidae (Kellison et al. 2012). The reefs are situated on the western edge of the strong Florida Current, which frequently sheds mesoscale and sub-mesoscale eddies (Lee 1975). At Pickles, a recent study by Grorud-Colvert & Sponaugle (2009) found that the most common settlement-stage larvae collected were blennies (Chaenopsidae, Labrisomidae, Tripterygiidae) and gobies (Gobiidae), whereas at Sand Island it was mojarra (Gerreidae), grunts (Haemulidae), jawfish (Opisthognathidae), and blennies (Labrisomidae). Sand Island received significantly greater numbers of fish larvae than Pickles (i.e., the total number of fish collected in the three light-traps deployed at each site), and also had higher diversity of young recruits (i.e., fish that had settled within the lunar month). The highest density of recruits occurred in July during both years sampled (Grorud-Colvert and Sponaugle 2009). Recent surveys of benthic species composition and adult fish found significant differences in the presence of bare substrate, crustose coralline algae, dictyota, fleshy macroalgae, and turf algae, and significantly different numbers of redband parrotfish (*Sparisoma aurofrenatum*) and sergeant major (*Abudefduf saxtalis*) at the two sites (S. Sponaugle & E. D'Alessandro, unpublished data, Table 3.1).

Acoustic data collection:

One passive acoustic recorder, the DSG-Ocean (Loggerhead Instruments, Sarasota, FL), was deployed at each site in December 2010. The DSG-Ocean is a calibrated autonomous recording unit containing an HTI-96 hydrophone (sensitivity: -169.68 and -169.74 dbV/µPa, frequency range: 2 Hz – 30 kHz, High-tech Inc., Gulfport MS) and a 16-bit computer board. Each DSG-Ocean was set to sample 12 seconds every 5 minutes at a rate of 20 kHz (which provides a range of analysis from 1 to the Nyquist frequency, in this case 10 kHz). The instruments were set on mooring systems in a sand patch within the reef framework, in 7m of water and 3.5m from the nearest edge of reef (Figure 3.1). Data were retrieved and batteries were changed every 3.5 months, which caused a ~ 2 hour interruption of the recordings. The total timespan of the recording lasted 412 days, from December 2010-January 2012.

Acoustic Data Processing:

Each 12-second acoustic recording was immediately subjected to two post-processing steps to obtain: 1) the amplitude of the entire sampling bandwidth (1-10 kHz) for each sample, as a Root-Mean-Square (RMS) value, and 2) the distribution of the signal across frequencies, using a Fast-Fourier Transform (FFT, Pierce 1988). A series of FFTs (size: 800 samples, resulting in 25-Hz frequency resolution) were performed and averaged for each 12-second clip. To avoid spectral distortion due to windowing effects, a weighted moving average (weights of ¼, ½, ¼) was applied to all data after transformation into the frequency domain.

In order to identify patterns within an inherently complex system, it is common practice to partition the acoustic spectrum into different frequency bands which are dominated by anthrophony, biophony, and geophony. Wenz (1962) described three components of the underwater acoustic spectrum: the "low-frequency" spectrum (<10 Hz) caused by turbulence and pressure fluctuations from surface waves, the "non-wind-dependent" spectrum (10-1000 Hz, with peaks between 20-100 Hz), caused by biological sounds and shipping noise, and the "wind-dependent" spectrum (50-10000 Hz, with peaks between 100-1000 Hz), which is driven by the wind. While the Wenz-defined spectral components overlap, here I split the data into two non-overlapping frequency bands to focus on the dominant sound sources in each. The "low frequency band" (25-2000 Hz) included the range in which most fish vocalizations occur (Lobel et al. 2010) and covers the known hearing range of most fishes (Tavolga et al. 1981). This band also included contributions from wind, but discarded the very low frequency sounds from surface pressure waves and turbulence (Wenz 1962). The "high frequency band" (2000-10000 Hz) spanned the range that is typically dominated by snapping shrimp (*Alpheus* spp.) and odontocete activity (Hildebrand 2009). Using the sensitivity of the hydrophone and known calibration of the recording system, I report the sound pressure level for the whole bandwidth (hereafter "RMS level") and band level for the two bands (in dB re:1 μPa).

To further examine the acoustic composition of the soundscape, I calculated the "acoustic complexity index" (hereafter "ACI") as described in (Pieretti et al. 2011). This index calculates the difference in amplitude of adjacent time samples in each frequency bin, then sums across all bins, to provide a measure of the changing composition of a soundscape. Higher ACI values are generated by greater variability in intensity (e.g., from multiple sound sources), whereas sounds generated by anthrophony or geophony, which tend to be more constant in intensity, produce low ACI values (Pieretti et al. 2011). I applied this index to the low frequency band at each site (cluster size = 1 second, FFT bins = 160, to match the 25-Hz resolution from the original FFT as described above).

Environmental data collection:

A nearby NOAA buoy (Molasses MLRF1, 25°0'42" N, 80°22'35" W) collected data for wind speed and direction, atmospheric pressure, air temperature, and water temperature (http://www.ndbc.noaa.gov/station_history.php?station=mlrf1); verified tidal data for Vaca Key, FL (24° 42.7' N, 81° 6.3' W, www.tidesandcurrents.noaa.gov) were also retrieved (Table 3.2). The wind was separated into "offshore" and "alongshore" component vectors by shifting the cardinal axis by + 40 degrees (as in Sponaugle et al.

2005). Thus, the “alongshore” vector was parallel to the Florida Keys Reef Tract, and the “offshore” vector was perpendicular to the reefs, aligning with the prevailing wind direction (“Climatic wind data for the United States;” 1998).

Data analysis:

Each time-series was analyzed in both the time domain and frequency domain. Because many biological sounds are known to vary on seasonal and lunar cycles (e.g. McCauley and Cato 2000; Radford et al. 2008), I divided the data into temporal categories using astronomical data from the US Naval Observatory (http://aa.usno.navy.mil/data/docs/). I defined these categories as “wet season” (May 20-Oct 17), “dry season” (Oct 18-May 19), “new moon” (< 14% illuminated, spanning ~6 days), and “full moon” (> 86% illuminated, spanning ~6 days). I calculated the mean and standard deviation of each series for these time periods (Table 3.3). For the acoustic data, I also calculated the hourly amplitude for each day in order to observe the time of day when peak sound levels and maximum acoustic complexity occurred.

When periodic phenomena are sought among noise, Fourier analysis and autocorrelation functions can be used to determine which periods best explain the variance in the series (Wenz 1961, Legendre and Legendre 1998). To do this, I first conducted a resampling routine on the acoustic and wind data to match the sampling frequency of the environmental data (once/hour, Table 3.2), then I either de-trended or centered the data, applied a filter, and calculated the autocorrelation and power spectral density. When two series’ power spectra possess peaks at similar frequencies, e.g. one cycle/day, this means that both series have a regular cycle at that frequency, but it doesn’t necessarily mean that the peak occurs at the same time of day or that there is any causal relationship. Therefore, I isolated the peaks from each series' power spectra to compare the phase angles from shared peaks (Pierce 1988).

To disentangle the effect of wind on ocean sounds, I conducted an ANCOVA using offshore wind as a covariate to test for differences between the sites during particular seasons and moon phases. Because the wind was autocorrelated up to 9 days, but the new and full moon periods were separated by 14 days, I was able to maintain the assumption that the acoustic samples were independent for the ANCOVA. In other words, I assumed that any wind-dependent contribution to the soundscape would have the same autocorrelation lag as the wind itself, which allowed me to test for differences between moon phases and seasons while controlling for wind as a covariate. Continuous variables were checked for equal variances using a Levine's test, and for normal distribution using Q-Q plots. After fitting the model, adjusted means for each site were generated and plotted.

Finally, I both listened to and visualized the raw acoustic data to better understand differences between the soundscapes at the two sites. A spectrogram can be read like a musical score; time is represented on the x-axis, acoustic frequencies on the y-axis, and colors represent the amplitude of the sounds at particular frequencies. One-month and short-term spectrograms from each site are included to exemplify the typical biophony at each site.

Results

General trends in the time series:

At both sites, RMS level increased between March to June, and the highest amplitudes occurred between May and August (Figure 3.2A). The dry season was characterized by sharp peaks that lasted several days, whereas large lunar differences were evident in the wet season. While both sites had similar RMS levels during full moons of the wet season – which were the quiet times – during new moons, the amplitude was greater at Sand Island than at Pickles (Figure 3.2A, Table 3.3). There was a seasonal trend in the high frequency band (Figure 3.2B), with highest amplitudes occurring during the wet season, and Pickles had greater amplitudes than Sand Island throughout most of the year. In the low frequency band (Figure 3.2C, Table 3.3), both sites exhibited an increase in amplitude at the end of the dry season, and Sand Island had greater amplitudes during the majority of the wet season. The highest acoustic complexity occurred during the end of the dry season, and Pickles had higher complexity than Sand Island throughout the whole year (Figure 3.2D, Table 3.3).

Clear dawn and dusk peaks were evident in the high band at both sites (Figures 3.3A & 3.3B), which coincided with the changing duration of daylight throughout the year. In the low band, there was an increase in amplitude during new moons of the wet season (Figures 3.3C & 3.3D), which can be seen as horizontal yellow lines spanning the whole day. Acoustic complexity for the low band was highest during nighttime hours at both sites, with the highest complexity occurring during nights between January – July (Figures 3.3E & 3.3F). At both sites, the lowest acoustic complexity occurred during morning hours, especially between June – November. Pickles had higher amplitudes than

Sand Island for the high band dawn and dusk choruses, as well as greater acoustic complexity. Sand Island had greater lunar-associated increases in amplitude for the low band than Pickles (Figures 3.3C & 3.3D).

I refer readers to the Appendix for plots of all environmental data in the time and frequency domains, and limit the focus here on the wind and tidal data. The greatest wind speeds occurred in the dry season (Table 3.3), when there were short (5-8 day) peaks. In the wet season, there appeared to be some lunar periodicity (Table 3.3, Figure A3); the offshore wind was greatest during new moons, whereas during full moons the wind dropped the lowest speeds observed all year (Table 3.3, Figure A3). The power spectrum for offshore wind revealed a peak at once per sidereal month and once per solar day (Figures A3-B). The tidal data exhibited a clear seasonal pattern as well as a strong peak at a frequency of once and twice per lunar day (Figures A7-B).

Periodic components of the data:

Each variable was autocorrelated at different lag times (Figure 3.4). The wind data had fairly low lag time of up to 9 days, while larger-scale environmental descriptors like air temperature and water temperature had a seasonal pattern, apparent as very long lag times (>60 days, Figure 3.4). Vertical bands are indicative of highly periodic data, which was observed for the tides, ACI, and high frequency bands at both sites (Figure 3.4), and can be better understood by examining the power spectra. The low frequency band at both sites had peaks at once per sidereal month (27.32 days), which is the time it takes for the moon to make one complete orbit around the earth. The ACI for Sand Island, but not Pickles, had peaks at once per sidereal month as well as once per synodic month (29.5 days), the time from one new moon to the next (http://asa.usno.navy.mil). ACI at both sites also had peaks at twice per lunar day (24 hr 50 min, or 89400 seconds). The low band at both sites had peaks at once and twice per lunar day (peak was greater at Pickles), and once per solar day (24 hr 0 min, or 86400 seconds, peak was greater at Pickles). Finally, peaks at once and twice per solar day in the high band and ACI were pronounced at both sites, with larger peaks at Pickles.

Geophony:

Since the offshore wind shared peaks with the low band at periods of once/sidereal month and once/solar day, I isolated the peaks from the power spectra and compared their phase. The wind and low band at both sites were in phase at a period of once per sidereal month, but the magnitude of the lunar difference in the acoustic data exceeded that of the wind. The once/day peaks in the wind and acoustic data were not in phase. I performed similar steps for peaks shared between the tides and low band at once and twice per lunar day, and I found that the tides were not in phase with the acoustic data.

For the low band, after controlling for offshore wind, the ANCOVA revealed a significant interaction between season and site ($F_{1,19585} = 13.8$, $p<0.01$), as well as moon phase and site ($F_{2,19585} = 8.03$, $p<0.01$), but there was no significant interaction between season, moon phase, and site ($F_{2,19585} = .07$, $p = 0.94$, Figure 3.6). In addition, there was a significant interaction between offshore wind and site ($F_{1,19585} = 83.8$, $p<0.01$). For the high band, when controlling for offshore wind, there were no significant interactions between season and site ($F_{1,19763} = 0.67$, $p = 0.41$) or moon phase and site ($F_{2,19763} = 1.6$, $p = 0.20$) or season, moon phase, and site ($F_{2,19763} = 0.92$, $p = 0.40$, Figure 3.6).

Biophony:

Lunar patterns were evident in the spectrograms for the low band at both sites (Figure 3.7, see also Figures A9 & A10). At Sand Island, the acoustic complexity also had a lunar phase (Figures 3.5A & 3.7A), which matched the pattern in the most prevalent sounds at this site: “growls” and “thumps” (Figure 3.8A-B) which often occurred together, and were most prevalent during quarter moon and new moon periods. The dominant frequency of the growls was 25-50 Hz (duration: 0.4- 0.8 sec, freq range: 25-350 Hz), and the dominant frequency of the thumps was 75-95 Hz (duration: 0.1- 0.15 sec, freq range: 25-1600 Hz). While many fish calls remain unidentified (Mann 2012), given the known general characteristics of fish vocalizations (Lobel et al. 2010), it is not unreasonable to assume that many of the percussive, thump-like, growl-like, and grunt-like sounds observed at the two sites were produced by fishes (Figure 3.8). At Pickles, although both growls and thumps were audible and also exhibited a lunar pattern, they were less prevalent and generally lower in amplitude than at Sand Island. Instead, the low frequency band at Pickles comprised a wider variety of fish vocalizations, such as grunts and damselfish, in the range of 200-1600 Hz (Lobel et al. 2010), (Figures 3.7D & 3.8C-D). The one-month spectrogram showed that these fish sounds were most common during the night, when acoustic complexity was also highest (Figures 3.7C-D, 3.3F, A9); this finding is consistent with the once/day peak in the Power Spectrum for the low band at Pickles (Figure 3.5B).

Discussion:

The information obtained from the recordings of these two reefs reveals just how little is known about the soundscapes of ocean habitats, which are highly variable across space and time. The 14-month duration allowed me to disentangle the relative contributions of geophony and biophony to the soundscapes of these reefs over a range of timescales. The tools applied here can be used for long-term acoustic recordings from any type of ecosystem. Although the primary focus was not on spatial differences (one recorder per reef), it is still useful to make comparisons between the two sites if for no other reason than to demonstrate that it is difficult to make generalizations about soundscapes from single-location or single-moment recordings.

*Patterns and contribution of wind and tide*s

As the dry season transitioned to the wet season, wind speeds generally decreased while sound levels increased (Table 3.3, Figures A1-3, Figure 3.2). The low frequency band, which contains most of the wind-generated sound (Wenz 1962) had sharp peaks in the winter, but these high-wind events were not periodic phenomena (Figure 3.4). Currents due to tidal flow or high winds can affect measurements of underwater soundscapes (Urick 1983) by generating "self-noise" on a mooring system. At the frequency of once/solar day, the offshore wind had a peak due to the afternoon sea breeze (Winsberg 2003), but by isolating peaks from the power spectra and comparing phases, I found that the sea breeze did not coincide with the once/day acoustic peak. I also found that the once and twice per lunar day acoustic peaks were not in phase with the tides

(Figures 3.4-3.5, A7). Thus, the diurnal acoustic patterns must be caused by other sound sources, which was verified by listening to the recordings and examining the acoustic complexity.

The lunar period in the offshore wind during summer months, which was in phase with the low frequency band, was surprising. Although the atmosphere can experience tidal cycles similar to the ocean tides (Sandford et al. 2006), these cycles occur with the period of a synodic month, rather than a sidereal month. The reason for the once/sidereal month peak in the offshore wind data is unknown, but seems to be a coincidence that occurred only in 2011, as it was not apparent in 2010 or 2012 (NOAA MLRF1 buoy data). To further explore the relationship between the wind and the acoustic data, I generated a series of predicted sound pressure levels from the measured wind speed, based on relationships in Knudsen et al. (1944). While some of the lunar variability was attributed to the wind, the observed sound levels exceeded those that were predicted by the wind, especially during the new moons at Sand Island (Figure A9). When including the wind as a covariate, I observed differences in the low band both within and between sites, especially during the wet season (Figure 3.6). These discrepancies indicate that the wind was not the sole source of sound that varied on a lunar cycle. This was verified with the spectrograms, which clearly showed that certain fish vocalizations (e.g. the “growl”) also followed lunar periods (Figure 3.7, see later sections of discussion). Therefore, I can conclude that although the wind did affect the soundscapes, it was not the sole contributor to the low band and does not explain all of the variance observed. It would be interesting to investigate whether some of the biological patterns I observed were caused by a reaction to elevated noise levels due to wind (i.e. the “Lombard Effect” (Locascio and Mann 2005, Parks et al. 2011).

Patterns and contribution of other non-biological sound sources:

Other sources of ocean noise include thermal agitation, pressure fluctuations on the surface, turbulence, rain, seismic activity, and shipping traffic (Wenz 1962). Thermal agitation is not expected to be a major contributor at frequencies < 10 kHz, and pressure fluctuations and turbulence primarily affect frequencies < 25 Hz, which was discarded from the frequency analysis (Wenz 1962). Therefore, within the range sampled for this study (25-10000 Hz), I would not expect these sources to be major components of the soundscape. Unfortunately there was no record for rain near the site of the recorders, so I assumed that the two sites experienced similar conditions, and that rain events would not represent a primary contribution to the different periodic patterns observed in the data. For both distant shipping and seismological activity, which can affect underwater soundscapes in low frequencies, I assumed that these sound sources would be far enough from the reefs that they would affect the two sites similarly. Finally, local boat traffic may have differentially affected the sound levels at the two sites. Because the recordings were 12 seconds in length but were spread 5 minutes apart, when a small boat passed overhead, it was detectable on just one recording (E. Staaterman, personal observation). Therefore, I assume that the sporadic presence of boats would be diluted by the large number of datapoints. While anthropogenic activity would be interesting to characterize, it was not the primary objective of this study and will instead be investigated in future research. Finally, many of the sources listed above are not periodic phenomena, and while they are interesting to examine, here I maintain the focus on the cyclical elements of coral reef soundscapes.

Patterns and contribution of biological sound sources:

A seasonal pattern was observed for the high band and for acoustic complexity, and to a lesser extent, the low band. Acoustic complexity was greatest at both sites during the transition to from the dry to wet season, when many soniferous marine fish begin their spawning activities (Lobel et al. 2010). Snapping shrimp activity is typically highest in the spring and summer, especially during dawn and dusk (Lammers et al. 2008, Radford et al. 2008, Figure A10). Here, the amplitude in the high band mirrored the seasonal change in daylight (Figure 3.3), making it clear that snapping shrimp activity has a strong relationship to light levels. Odontocete sounds may have also contributed to the high band (Hildebrand 2009), but these signals would be short in duration and transient in nature, and this study demonstrated a highly periodic component that is linked to the daily activity of snapping shrimp.

After accounting for the wind, both sites had greatest amplitudes in the low band during new moons, and the magnitude of the variation was greater in the wet season than the dry season (Figure 3.6, Table 3.3), a finding that is consistent with Radford et al. (2008). In low latitudes, many soniferous marine animals are active during wet season new moons (Breder 1968, Cato 1978, McCauley and Cato 2000, McCauley 2012). However, it was surprising that the lunar cycle in the low band occurred at once per sidereal month, rather than once per synodic month, which is more typical of biological rhythms (Morgan 2000). While mice show activity cycles on a period of once per sidereal day (Brown 1975), and growth rates of some plants seem to follow period of once per sidereal month (Kollerstrom and Staudenmaier 2001), to my knowledge, a lunar-sidereal period in marine animal behavior has not been previously described. The fact that the ACI at Sand Island did have a peak at both once per sidereal and once per synodic month (Figure 3.5), and the spectrograms revealed quiet periods during the entire week of the full moon (Figure 3.7), indicates some degree of periodicity on both of these scales. However, the biological reason underpinning this phenomenon, and the behavioral distinction between sidereal and synodic periods, deserves further study.

Remarkably, the loudest time periods on these two reefs in the Florida Keys coincided with the time when most larval fish recruit to coral reefs (D'Alessandro et al. 2007, Sponaugle et al. 2012b). While the results from this study cannot necessarily imply a causal relationship, this association is significant, given the surge of recent work on the attraction of larval fish to reef sounds (Simpson et al. 2005a, Radford et al. 2011a). Are larval fish more likely to settle on reefs during new moons because they can detect the reef acoustically, and there is a stronger signal during these periods (Cato 1978)? Or does the arrival of the larvae itself produce an acoustic signal (e.g. Kasumyan 2008, Staaterman et al. 2014) that I detected in the recordings? The findings from this study open interesting questions that warrant future research.

On a daily time scale, peaks in the low band and acoustic complexity occurred at once per solar day, and once and twice per lunar day (Figure 3.5). Sound-producing individuals are vulnerable to detection from predators, but this risk is lessened at night, especially during moonless nights. Acoustic complexity was highest at night at both sites (Figure 3.3E-F), indicating that more animals were acoustically active during this time.

Because the once and twice/lunar day peaks in the low band were not in phase with the tide, these sounds must be of biological origin. Perhaps the animals adjusted their calling rates or feeding activity based on ambient light levels, enacted behaviors based on an endogenous clock (Morgan 2000), or sensed when the moon reached the same position in the sky from one night to the next.

Differences between sites:

Both sites followed similar patterns, but in general Sand Island had greater amplitudes in the low frequency band, while Pickles had greater amplitudes in the high band, and Pickles had higher acoustic complexity. Within the low band, the primary biophonic contributions at Sand Island were the very low frequency "growls" and "thumps" which took place throughout the entire day but were almost entirely absent during full moon periods (Figure 3.7B). These sounds were likely produced by fishes, although the species are unknown. Within the low band at Pickles, greater acoustic complexity, especially at night, can be seen in the 200-1600 Hz range on the spectrograms where several sounds were audible simultaneously (Figures 3.7D, 3.8C-D). This was one of the first studies to apply the newly-developed acoustic complexity index to marine soundscapes; there was strong agreement between ACI and the visual patterns of the soundscapes (Figure 3.7), demonstrating that this may indeed be a viable metric in marine systems. To summarize: a high amplitude, very low frequency, lunar signal emanated from the Sand Island site, while a more complex, diel signal emanated from the Pickles site.

I did observe differences in both the types of sounds and temporal patterns of these two reefs' soundscapes, but I must acknowledge the caveat that these were single-site recordings within each reef. Therefore, it is difficult to know whether the findings shown here are representative of the entire reef, or just particularly noisy or quiet regions of the reef. In the future, multiple hydrophones should be used over shorter time scales to ground-truth the patterns gleaned from single-point recordings and to understand whether they can be generalized to describe entire acoustic habitats (Freeman et al. 2014).

Nonetheless, recent surveys of benthic species composition and adult fish did uncover some significant differences in the biological composition of the two sites, which may be linked to their acoustic qualities. Sand Island had significantly more rubble, fleshy macroalgae, and turf algae than Pickles, while Pickles had more bare substrate, crustose coralline algae, and *Dictyota* spp. (S. Sponaugle and E. D'Alessandro, unpublished data, Table A1). Although there were no significant site differences in terms of live coral cover, the relationship between acoustic qualities and other substrates (e.g. rubble, algae) should be explored further, as certain acoustic characteristics could be used as habitat indicators (Kennedy et al. 2010). Some soundscape differences may be explained by differences in the abundance of soniferous fishes. There were significantly more sergeant majors (*Abudefduf saxtalis*) at Sand Island than Pickles (S. Sponaugle and E. D'Alessandro, unpublished data); because this species is known to vocalize in the lowest frequencies (Maruska et al. 2007), this may have contributed to the greater amplitudes observed at this site. In contrast, Pickles had more redband parrotfish (*Sparisoma aurofrenatum)*, and the feeding sounds of parrotfish are important sources of mid-frequency noise on coral reefs (Lobel et al. 2010, Munger et al. 2011). Although not statistically significant, the Pickles site had more bluestriped, French, and smallmouth grunts (*Haemulon* spp.) than Sand Island (S. Sponaugle & E. D'Alessandro, unpublished data). Grunts are known to produce sounds in the range of approximately 100-1600 Hz, which is the range in which the Pickles site had higher acoustic complexity and a greater apparent number of sound sources (Lobel et al. 2010). While passive acoustic monitoring holds great promise as an ecological assessment tool (Luczkovich et al. 2008, Sueur et al. 2008, 2012, Pieretti et al. 2011, Gasc et al. 2013b), more work is required in order to carefully link ecological and acoustic measures.

Larval fish recruit to Florida reefs during the new moon periods of the wet season (D'Alessandro et al. 2007), when Sand Island had higher amplitudes than Pickles. Greater numbers of settlement-stage larval fish have been observed to arrive at Sand Island compared to Pickles (Grorud-Colvert and Sponaugle 2009). The low frequency, high amplitude growls and thumps would propagate a great distance and, depending on the hearing abilities of the fish species, could provide a reliable signal to guide the larvae towards the coast (Tavolga et al. 1981, Mann et al. 2007). This signal was present at Pickles as well, but was lower in amplitude than at Sand Island, which may explain the smaller number of larval fish that have been captured (Grorud-Colvert and Sponaugle 2009). In a study that used high-resolution biophysical modeling to map the trajectories of fish larvae in the Florida Keys, the authors did not find a significant difference in the number of larvae that arrived at these two sites (Sponaugle et al. 2012a). This finding suggests that the site differences are not explained by oceanographic features, but may be explained by a behavioral response from the fish. The hypothesis that the unique soundscapes of these two sites play a role in fish recruitment warrants further investigation through playback experiments. Specifically, it would be interesting to test whether larval fish have a preference for louder signals (e.g., Sand Island) or more complex signals (e.g., Pickles).

Conclusions

The long duration of these acoustic recordings, along with the availability of environmental data, allowed me to disentangle the relative contributions of geophony and biophony to these reef soundscapes. The low band, which spans the auditory range of fish, had the greatest amplitudes during new moons of the wet season, coinciding with peak larval fish recruitment periods. Acoustic complexity was greatest at night and during the transition between the dry and wet season, when many fish are beginning their reproductive activities for the year. One reef had a high amplitude, low-frequency, acoustic signal with strong lunar periodicity, whereas the other reef had a lower-amplitude, more complex signal with strong diurnal periodicity. In addition, the high frequency band at both sites was highly periodic at cycles of once and twice per day, corresponding to dawn and dusk snapping shrimp activity. The patterns uncovered here provide insights into the potential role of coral reef soundscapes in the orientation behavior of pelagic larval fish. This work highlights the fact that long-term recordings, coupled with the analytical tools applied here, can be used to uncover natural patterns of acoustic signals that are relevant to resident animals in any marine or terrestrial habitat. Finally, this study contributes to the growing field of soundscape ecology by providing critical baseline data in the face of our changing oceans.

Table 3.1. Site Descriptions SCUBA divers surveyed the sites using ten 25m x 2m transects, between December 2010 and January 2011 (S. Sponaugle & E. D'Alessandro, unpublished data). The abundance of ninety-two species of fish, and the presence of 22 substrate types at each 50-cm mark, were recorded. T-tests were used to compare mean differences of fish abundance and substrate presence at the two sites. The table reports only the fish and substrate types that were significantly different between the two sites.

Variable	Mean difference Sand Island - Pickles	Lower CI	Upper CI	P-value
Bare	-5.10	-7.85	-2.34	<0.01
CCA	-5.50	-9.20	-1.89	<0.01
Dictyota	-10.20	-13.50	-6.94	<0.01
Other fleshy macroalgae	0.90	0.10	1.70	<0.05
Rubble	5.00	3.21	6.78	<0.01
Turf algae	6.90	0.51	13.30	<0.05
Redband parrotfish	-1.10	-1.95	-0.24	<0.05
Seargent major	7.00	0.11	13.89	<0.05

Table 3.2. Data sources, units, sampling rates, and number of samples.

Data type	Measurement units	Sampling frequency	Original #of samples	# of samples after re-sampling
Raw acoustic data Pickles Sand Island	µPa	12 seconds every 5 min (12 times/hour)	118788	9899
Acoustic Complexity Pickles Sand Island	ACI	One sample for every acoustic recording	118788	9899
Wind Total magnitude & direction Offshore vector Onshore vector	m/s	6 times/hour	59394	9899
Temperature Water Air	ºC	Once/hour	9899	9899
Atmospheric pressure	hPa	Once/hour	9899	9899
Tides Mean lowest water level	m	Once/hour	9899	9899

Table 3.3. Mean and standard deviation of each time series for the defined time periods: wet season (May 20-Oct 17), dry season (Oct 18-May 19), and the new and full moons of each of these seasons.

		Dry Season			Wet Season		
Data source		Overall	New Moons	Full Moons	Overall	New Moons	Full Moons
Pickles	RMS	124.4 ± 4.7	126.1 ± 4.1	123.9 ± 4.7	124.1 ± 4.6	126.1 ± 4.4	121.1 ± 3.8
	Low Band	113.2 ± 5.6	115.1 ± 5.1	112.2 ± 5.2	112.5 ± 5.4	114.4 ± 4.9	109.3 ± 4.9
	High Band	115.4 ± 1.4	115.8 ± 1.4	115.2 ± 1.5	116.4 ± 4.6	116.7 ± 1.1	115.9 ± 1.3
	ACI	738.9 ± 18.8	739.5 ± 18.7	738.3 ± 18.4	726.0 ± 16.6	726.1 ± 17.3	727.7 ± 17.5
Sand Island	RMS	123.3 ± 5.6	124.2 ± 5.1	123.1 ± 5.4	126.2 ± 5.9	129.3 ± 5.1	121.3 ± 4.7
	Low Band	113.4 ± 4.5	114.3 ± 4.44	112.9 ± 4.0	114.8 ± 4.6	117.2 ± 4.1	111.2 ± 3.8
	High Band	114.3 ± 1.7	114.7 ± 1.5	114.2 ± 1.7	115.8 ± 1.1	115.9 ± 1.1	115.5 ± 1.2
	ACI	704.9 ± 14.3	709.9 ± 12.4	703.7 ± 13.3	702.0 ± 13.0	704.1 ± 13.9	696.1 ± 11.6
Wind	Total speed	6.4 ± 2.8	6.4 ± 2.7	6.3 ± 2.6	4.8 ± 2.6	5.6 ± 2.4	3.2 ± 2.2
	Along-shore vector	3.9 ± 2.7	3.4 ± 2.5	4.1 ± 2.8	2.9 ± 2.3	3.3 ± 2.2	2.1 ± 1.9
	Offshore vector	4.4 ± 2.6	4.8 ± 2.6	4.0 ± 2.2	3.4 ± 2.2	4.1 ± 2.2	2.0 ± 1.7
Temp-erature	Air	22.6 ± 3.4	23.8 ± 1.9	22.7 ± 2.7	28.2 ± 1.2	28.1 ± 1.3	28.4 ± 1.2
	Water	24.3 ± 1.9	24.5 ± 1.7	24.5 ± 1.7	29.4 ± 1.1	29.3 ± 1.1	29.5 ± 1.1
Pressure		1018.1 ± 3.7	1018.0 ± 3.0	1018.8 ± 4.1	1014.7 ± 2.22	1014.9 ± 2.3	1014.5 ± 2.3
Tides		0.15 ± 0.14	0.14 ± 0.13	0.19 ± 0.15	0.27 ± 0.12	0.27 ± 0.15	0.29 ± 0.11

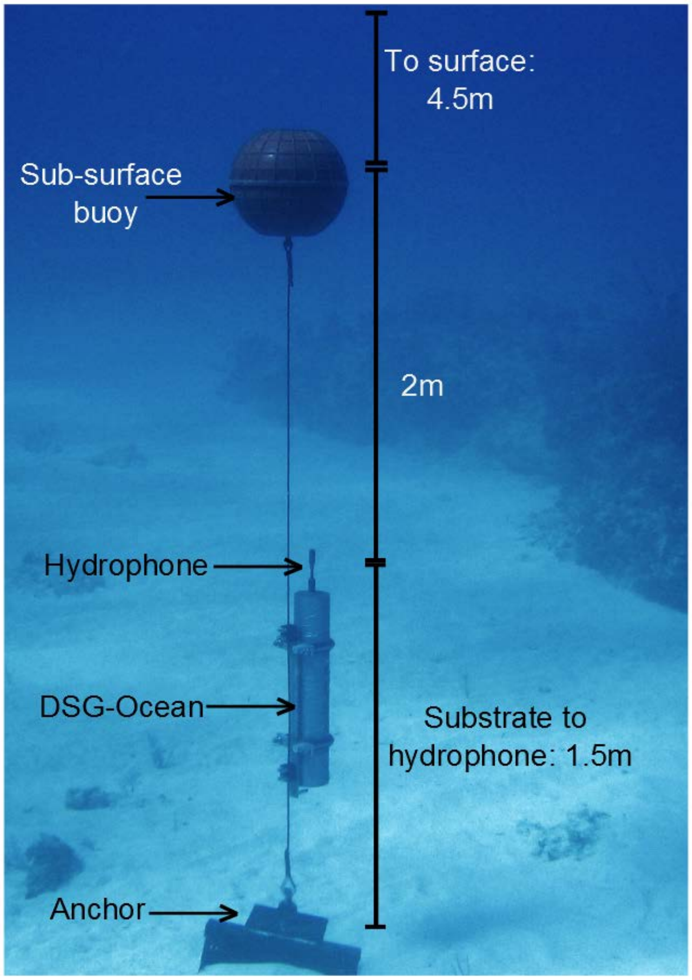


Figure 3.1. Each DSG-Ocean was set on its mooring from December 2010 to January 2012. Twelve seconds were recorded every 5 minutes at a rate of 20 kHz.

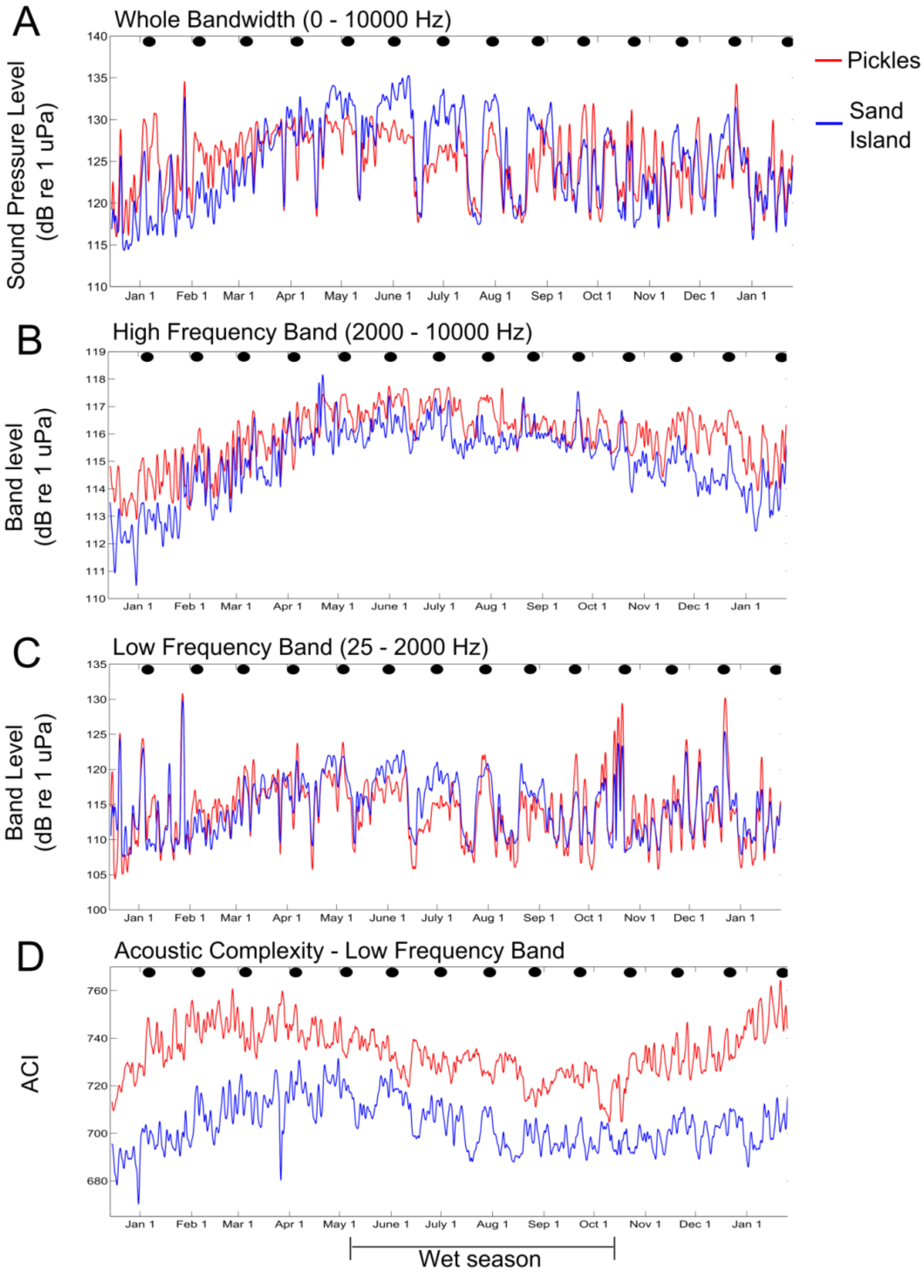


Figure 3.2. A: RMS level for the whole bandwidth (1-10 kHz); B: band level for the low frequency band (25-2000 Hz); C: band level for the high frequency band (2,000-10,000 Hz), D: Acoustic Complexity Index. All data were smoothed with a 50-pt Hanna filter. Acoustic amplitudes were greatest during the wet season, but acoustic complexity was greatest at the end of the dry season. Lunar periodicity can be observed in the RMS level (A), low frequency band (C), and ACI (D), during the wet season, and the magnitude of the lunar fluctuation was generally greater at Sand Island than at Pickles.

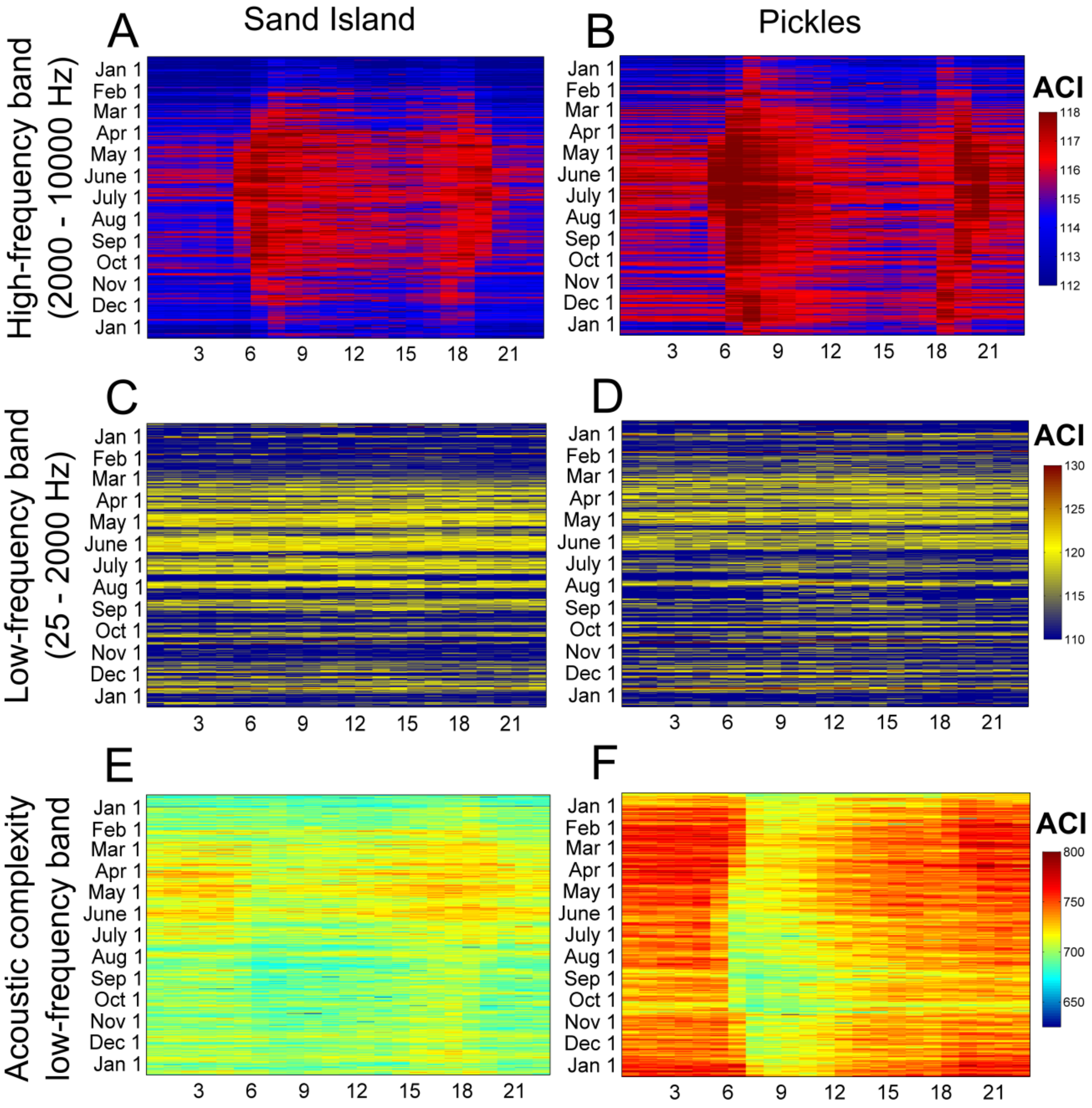


Figure 3.3. Amplitude of the high (A-B) and low (C-D) bands (color bar in dB re: 1 μPa) as well acoustic complexity for the low band (E-F, color bar in ACI) for each hour of the day at the two sites. In the high band, clear dawn and dusk peaks can be observed, shifting with the changing daylight throughout the year. In the low band, horizontal yellow bands correspond to the increase in amplitude during new moon periods of the wet season. Acoustic complexity was high during nighttime hours throughout the year; it was greatest during the end of the dry season and lowest towards the end of the wet season.

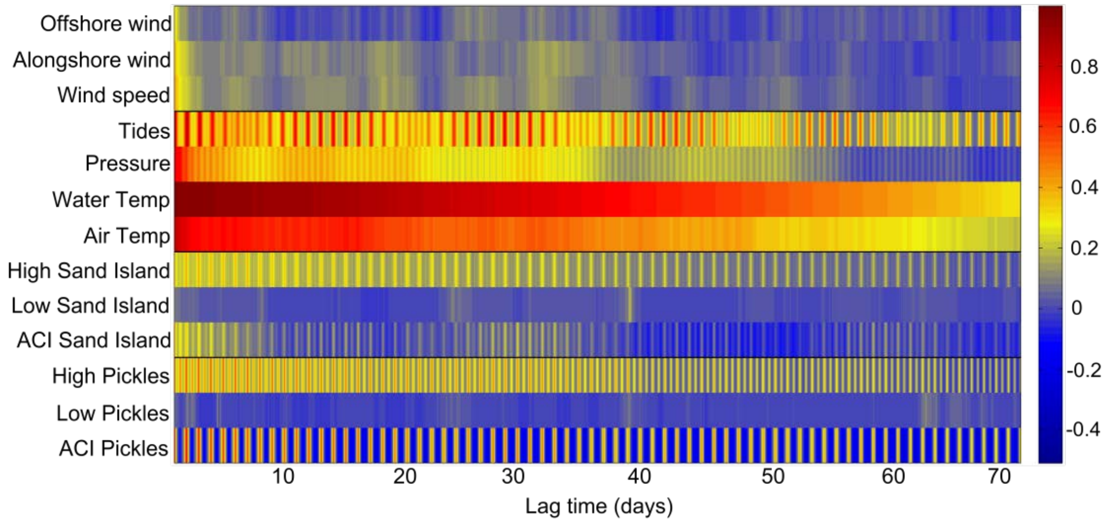


Figure 3.4. Autocorrelation plots for each variable, across lag time in days (color bar represents autocorrelation values). Wind had relatively low autocorrelation values, with lag times of only several days. Strongly periodic signals, such as the tides, ACI, and the high frequency band at each site, appear as vertical bands. Both water temperature and air temperature had high autocorrelation values out to 70 days, which was expected due to the seasonal trends in these data.

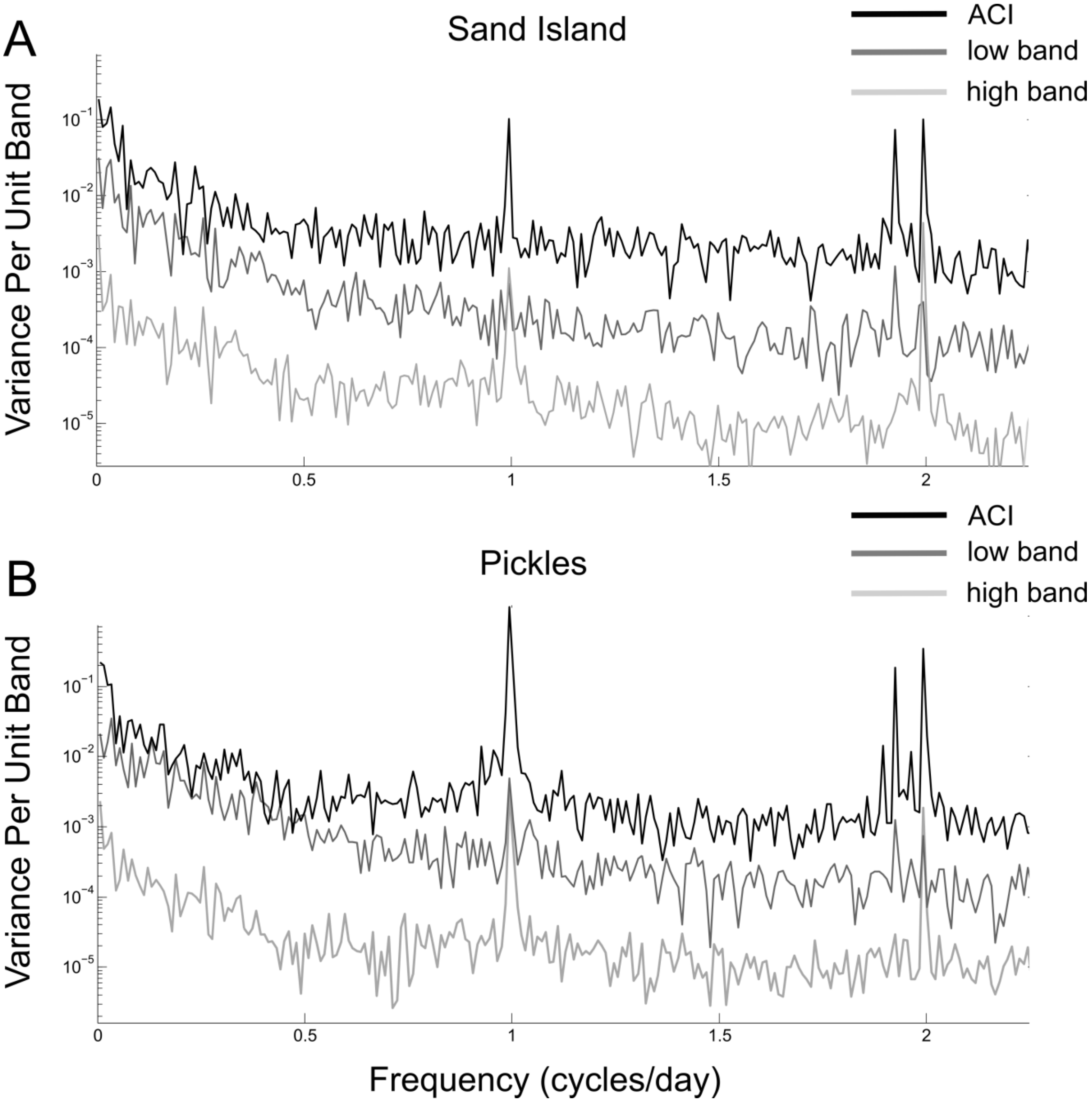


Figure 3.5. Power spectra for Sand Island (A) and Pickles (B) for acoustic complexity (black), the low frequency band (dark grey) and the high frequency band (light grey). Acoustic complexity was highly periodic at both sites at frequencies of once per solar day, twice per solar day, and twice per lunar day. At Sand Island, but not Pickles, the ACI also had peaks at once/synodic and once/sidereal month. The low band at both sites was periodic at frequencies of once/sidereal month, once/solar day, and at once and twice/lunar day. Finally, the high band at both sites had a strongly periodic component at once and twice per solar day. In general, Sand Island had more prominent lunar cycles than Pickles, whereas Pickles had stronger diurnal cycles.

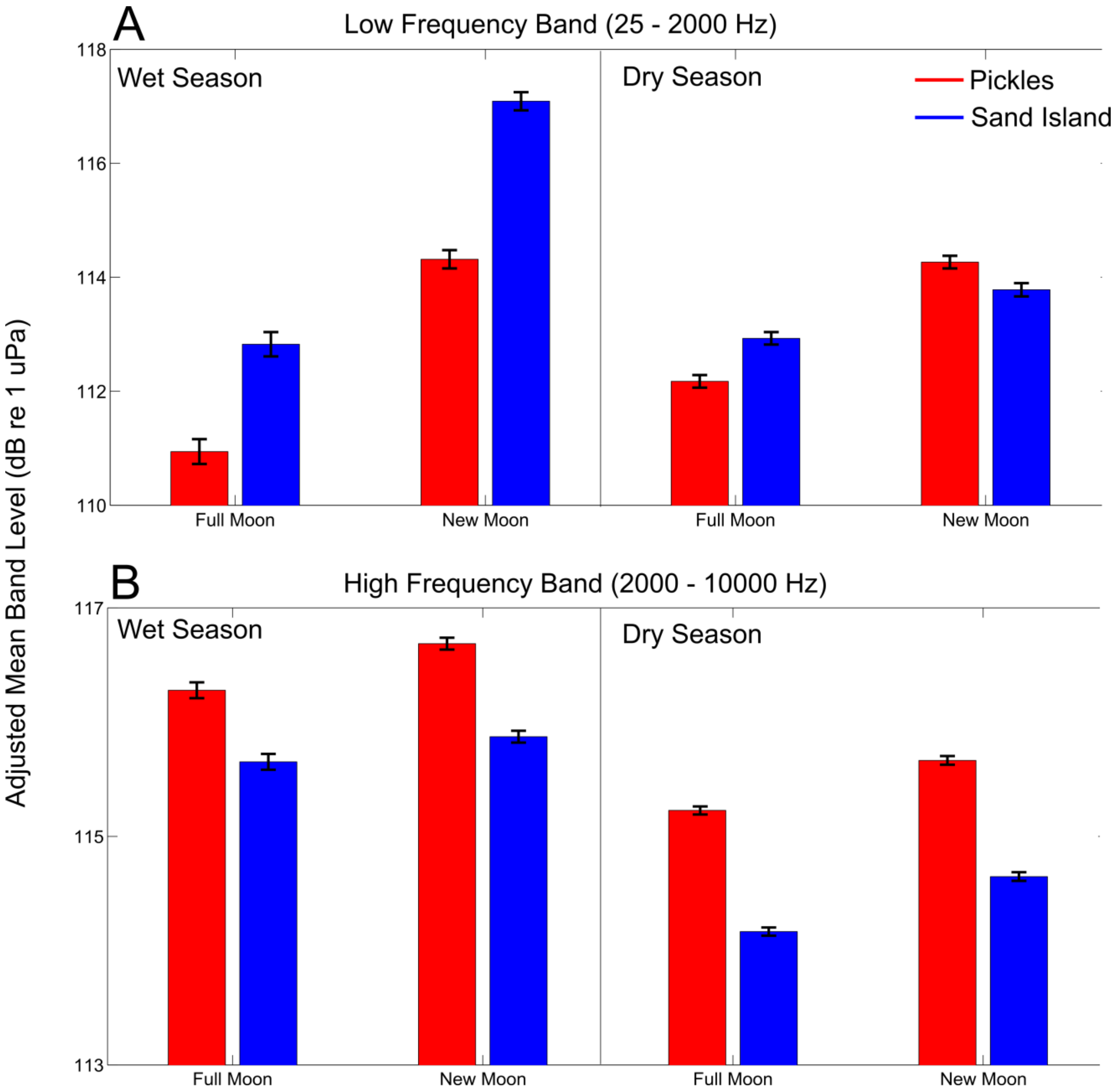


Figure 3.6. Adjusted mean band level (±95% confidence interval) for each site (red: Pickles, blue: Sand Island) at new and full moons during each season, generated from the results of the ANCOVA (all values are significantly different from one another). After accounting for variability due to offshore wind, Pickles had higher amplitudes across all moon phases and seasons in the high frequency band (B). In the low frequency band (A), there was only a slight difference between new and full moons in the dry season, but in the wet season, the differences with lunar phase were pronounced at both sites, and Sand Island had greater amplitudes than Pickles during both lunar phases.

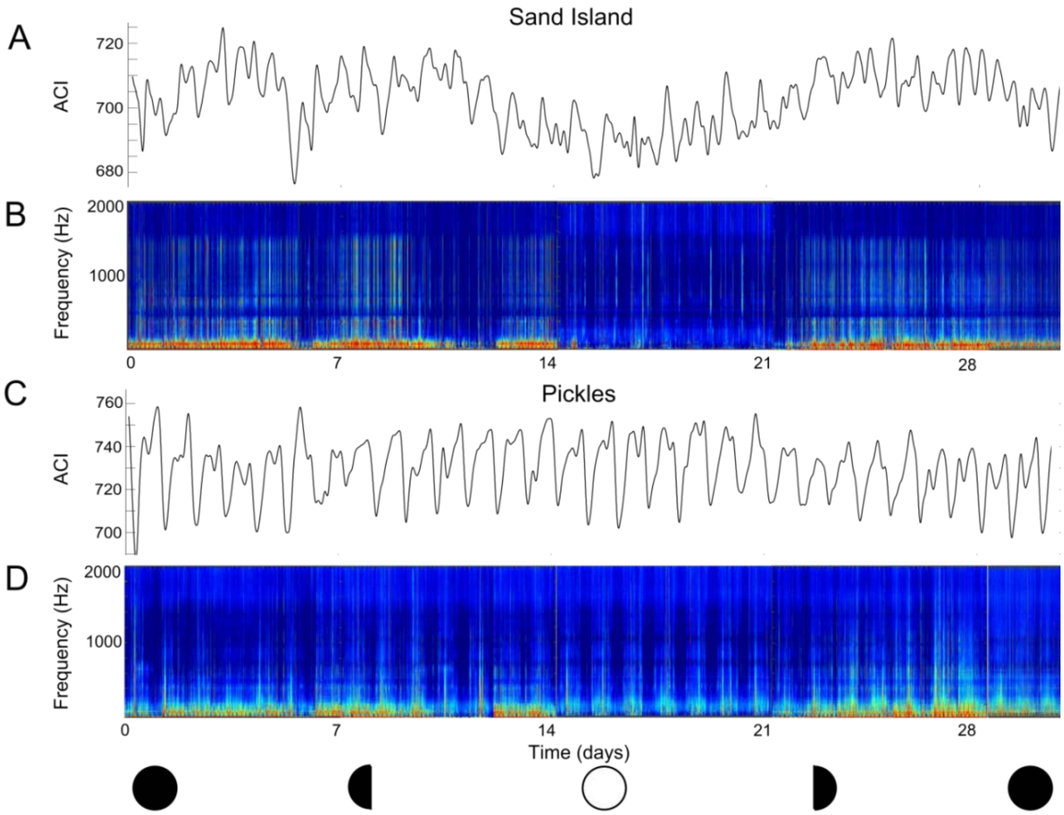


Figure 3.7. A & C: Acoustic complexity for the low band at the two sites during the month of July 2011, smoothed with a 20-pt filter; B & D: Spectrograms from the low at the two reefs. A spectrogram can be read like a musical score, with frequency on the y-axis, time on the x-axis, and bolder colors correspond to louder sounds. Spectrogram parameters: DFT size: 3509, overlap: 50%. The quietest times at both sites occurred during the full moon, and the loudest time occurred during the new moons (B & D). Sand Island had both lunar and diurnal periods in acoustic complexity (A), while Pickles had a highly periodic diurnal signal (C), with more complex times occurring at night. These daily patterns in acoustic complexity at Pickles match the spectrogram (lighter areas depict the presence of more sound sources).

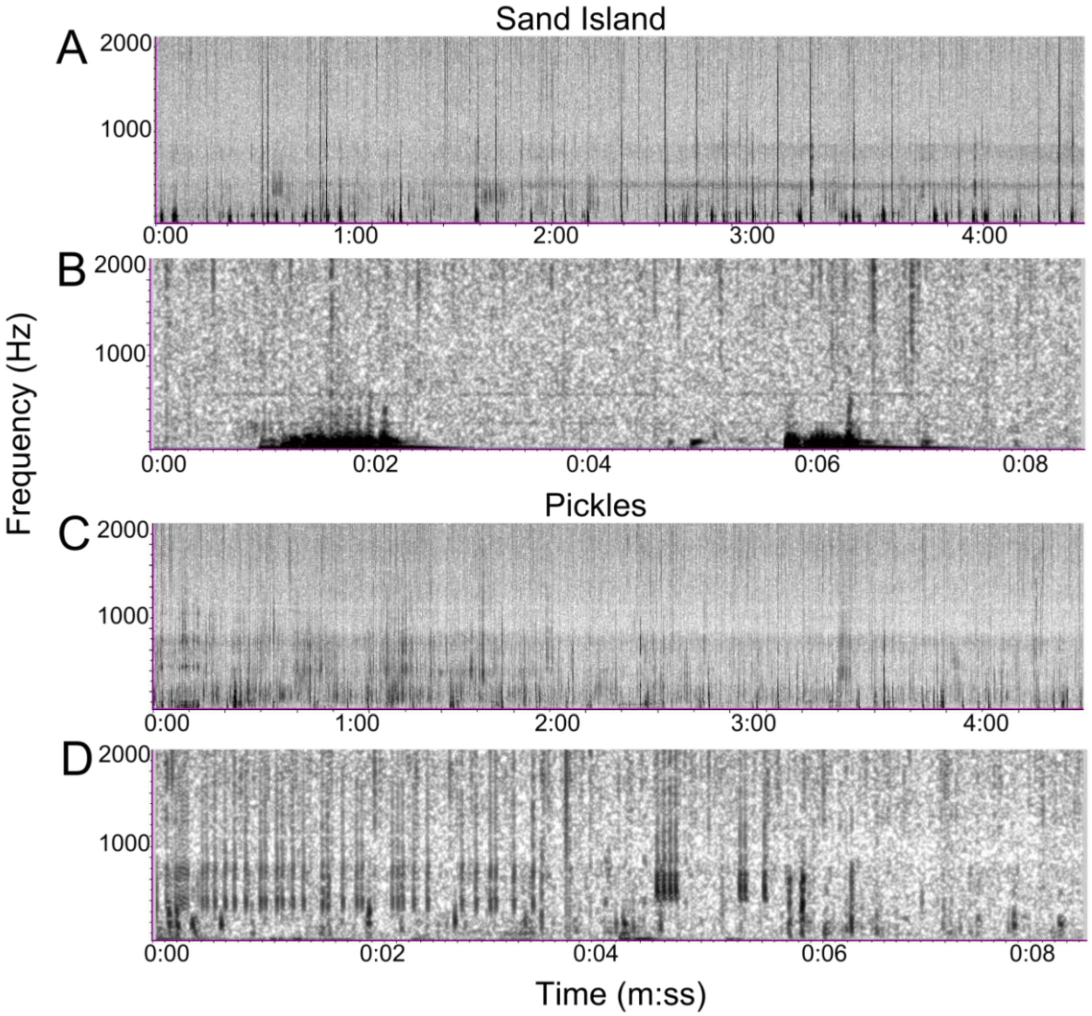


Figure 3.8: Representative short-term spectrograms from Sand Island and Pickles for dusk new-moon periods during the wet season (data from July 1 2011). Spectrogram parameters: A & C: DFT size: 3509, overlap: 50%. B & D: DFT size: 1050, overlap 90%. Sand Island's soundscape was dominated by "growl" and "thump" sounds (dark areas in B), whereas Pickles' soundscape was more complex and had more percussive sound sources (vertical dark marks in D).

CHAPTER 4: UNEXPECTED RESPONSE OF FISH LARVAE TO AMBIENT REEF SOUNDS

Summary

Recent studies have shown that larval reef fishes orient towards high-amplitude playbacks of reef sounds. I further explored the hypothesis that reef sounds guide larval settlement by testing the orientation behavior of larval fishes (*Astropogon stellatus* and *Acanthurus* spp.) in response to sounds played back at natural levels. I deployed an *in situ* behavioral observation platform, coupled with a pair of underwater speakers, within a naturally quiet blue hole. During the day, pre-recorded reef sounds were played back to individual larvae at sound levels equivalent to what the fish would encounter near a real reef, and larval movements were tracked throughout time. Although nearly all of the larvae were significantly directional at the individual-level, little orientation behavior was observed at the group-level. *Acanthurus* larvae did not maintain a significant mean bearing during silence or during sound playbacks. In contrast, *A. stellatus* larvae demonstrated significant cardinal orientation at the group-level during silence, but not while reef sounds were played. These results show that for *A.stellatus,* the sound levels were sufficiently high for them to detect the sounds and to change their orientation behavior. Yet, the lack of a directional response to the sound could be explained by the complicated sound field generated by the speakers, or by the fact that experiments were conducted during the day, while most fish larvae generally settle at night. Further work is needed to disentangle the roles of visual and acoustic cues in larval fish orientation.

Background

The assumption that larval fish are passive drifters has been challenged by research demonstrating that larvae possess considerable sensory and swimming abilities (Montgomery et al. 2001, Leis 2006). While it is likely that fish larvae utilize a suite of environmental cues to navigate towards settlement habitat, evidence for the role of acoustic signals has gained support through field experiments (e.g., Simpson et al. 2005, Montgomery et al. 2006) and hearing tests (Fuiman et al. 2004, Wright et al. 2011). Because coral reefs are particularly noisy habitats (Cato and McCauley 2002) and acoustic pressure can travel great distances in the ocean (Urick 1983), the hypothesis that larval fish could use reef sounds to navigate towards settlement habitat is compelling. The distance at which fish larvae can detect a reef, and thus the importance of acoustic orientation to larval navigation, depends upon the source level and propagation of the sounds, as well as the hearing abilities of the fish (Mann et al. 2007). However, studies testing this hypothesis have either played unrealistically high sound levels in order to obtain sufficient signal-to-noise ratios (Simpson et al. 2005a, 2008, 2010, Mann et al. 2007, Radford et al. 2011a), or did not report received levels (Tolimieri et al. 2000, Leis and Lockett 2005, Simpson et al. 2007). Furthermore, much of the work has focused on groups of larvae – only two studies have tracked individual behavior, using either the diver-follow method (Leis and Lockett 2005) or a choice-chamber design (Holles et al. 2013). While larval fish may travel in groups during their pelagic phase (Victor 1986, Paris and Cowen 2004, Ben-Tzvi et al. 2012, Bernardi et al. 2012), a complete understanding of the role of acoustic signals during their pelagic journey requires the observation of individuals in response to realistic (i.e., “ambient”) sound levels.

The study of larval fish behavior in the field is inherently challenging due to their small size and the inability to attach tracking devices. Furthermore, it is impossible to disentangle the role of acoustic, chemical, and visual cues in the field, unless the work can be conducted in a cue-neutral region, such as pelagic areas far offshore. An ideal location for acoustic playbacks is a relatively quiet area of the ocean, and an ideal tool tracks the behavior of individual larvae while minimizing the "observer effect". I traveled to Dean's Blue Hole (DBH) in the Bahamas, which is a marine blue hole that served as a natural, relatively cue-neutral behavioral arena. Using the Drifting *In Situ* Chamber (DISC, Paris et al. 2013), I observed the response of fish larvae to acoustic cues at amplitudes equivalent to what they would encounter close to a real reef.

Methods

Study Site

To test the use of sound as a directional cue for individual larval reef fish, I deployed the DISC inside of DBH (23°6′23″N, 75°0′31″W), on Long Island, Bahamas. DBH is 202 m deep and 50 m wide at the surface, is sheltered from prevailing winds by a cliff on the northwestern side, and is connected to a shallow bay on the southeastern side (Figure 1A, Wilson 1994). The protection from the wind and deep waters minimized visual cues from surface waves and/or bottom features. Sound levels inside DBH near the time of the experiments were 97 dB re 1 µPa (RMS level over the frequency range of 75-1,000 Hz, Table 4.1), substantially lower than on a coral reef (122.3 dB re 1 µPa over the same frequency range, Staaterman et al. 2014), which allowed me to use more realistic sound levels in these experiments.

Larval Fish Collections

Pre-settlement stage larval fish were collected using light-traps (CARE, EcoOcean, Bellamare, LLC) deployed within DBH as well as *ca*. 200 m from shallow reefs in Clarence Bay, Bahamas (23°6′23″N, 75°0′31″W, Figure 1B). Fish larvae were retrieved from the traps at dawn and kept in covered plastic buckets at ambient temperature until the time of their trial, which was within 24 hours of collection. They were identified to the species-level based on morphology (C. Paris), and any specimens that experienced accidental mortality were preserved for further species identification. All other specimens were released after their trial concluded. A total of 12 *Astrapogon stellatus* specimens (conch-fish; family Apogonidae, caught in DBH) and 11 *Acanthurus* specimens (4 *A. coeruleus* and 7 *A. chirurgus*; surgeonfishes; family Acanthuridae, caught in Clarence Bay) were tested one at a time in these experiments. Results were consistent between the two *Acanthurus* species, so data between species were pooled, and results reported here are for the genus-level.

Acoustic Recordings

To examine whether spectral differences affected larval fish orientation, reef sounds were recorded both in the Bahamas and in Florida (Figure 3). The Bahamas recordings were made with a hand-held recorder (Olympus LS-10 PCM recorder, Aquarian Audio H2a hydrophone, 10 Hz-100 kHz, sensitivity: -180.1 dBV/µPa) during the new moon on May 9, 2013 at the reef site where the fish larvae were collected (Clarence Bay, 4 m water depth). The Florida recordings were made with a DSG-Ocean (Loggerhead Instruments; HTI-96 hydrophone, 2 Hz – 30 kHz, sensitivity: -169.7

dBV/µPa) during the new moon of May 3, 2011 at reefs in the upper Florida Keys (25°0'43" N, 80°22'33" W, 7 m water depth). Both recordings were low-pass filtered at 2 kHz, and an additional adaptive filter was applied to compensate for speaker distortion, which was measured during pilot trials. I also measured the ambient noise in DBH at 10 m depth using the DSG-Ocean.

Acoustic Playbacks

The DISC is a free-floating, symmetrical behavioral arena made of clear acrylic, which provides no visual frame of reference (Paris et al. 2008; Figure 4.1C). During experiments, individual larvae were placed within the cylindrical mesh arena (38 cm diameter, 10 cm height) that is transparent to odor, light, and sound, and larvae have a choice of 360º swimming directions. Using a compass and camera system, the DISC autonomously tracks larval movement, while also sensing environmental cues (Paris et al. 2008).

Experiments took place during daylight hours under clear skies. The DISC was tethered to a floating platform at the center of DBH with a small line, and trials were only conducted when the DISC was hanging straight down (during slack tide). A pair of underwater speakers (Clark Synthesis) was mounted to the DISC frame in line with the behavioral arena at a distance of 50 cm (Figure 1). Playbacks were controlled by an audio player (Microtrack II, M-audio) and amplifier (Cerwin-Vega). The sensors on the DISC included an analog compass and GoPro® Hero2 camera which took one photo per second. At the start of each deployment, an individual larva was placed in the arena at the surface by a snorkeler, and the DISC was slowly lowered to its operational depth (8.2 m). After an 8-minute acclimation period, each fish larva experienced three successive “trials” of 5-minutes each: 1) Bahamas sounds (randomized from left or right side), 2) silence, 3) Florida sounds (randomized from left or right side). Part of the motivation to use individual larvae for multiple trials was to observe whether there was a change in behavior in response to the playbacks.

I measured the sound pressure levels received by fish in the behavioral arena by positioning pairs of hydrophones along the two axes (Figure 4.1C, Figure 4.4). Signals from each hydrophone pair were recorded onto custom-designed underwater stereo recorders (Loggerhead Instruments) that recorded each channel simultaneously. Using the pressure gradients between each hydrophone in the pair, I also calculated acoustic particle acceleration in two axes from the Linearized Euler Equation (as in Zeddies et al. 2010, Table 4.1, Figure 4.4). Upon examining these recordings, it became clear that the left speaker produced sounds ~9 dB higher than the right speaker (Table 4.1), probably due to a loose connection of the speaker wires. Therefore, the animals were not subjected to equivalent signals when sounds were played from the left and right, so results from the two sides could not be directly compared. I initially examined the behavioral response to each of the stimulus types separately (i.e. R Bahamas, R Florida, L Bahamas, L Florida) and found no significant differences in the larval response to recording location (Bahamas or Florida), which justified the pooling of data based on amplitude (i.e., which speaker was playing).

Data Analysis

Orientation behavior was examined at the individual-level and at the group-level. First, the position of the larva within the chamber, as well as its swimming speed, was digitized from the 300 camera images for each trial using custom-made software (DISCUS, Irisson et al. 2009). Next, to determine whether the larva was significantly directional (Rayleigh's r-value above critical value) at the individual-level, the position data from each of fish's three trials were subjected to Rayleigh tests (package "Circular" in R, Lund and Agostinelli 2011). A mean angle was calculated for trials in which the fish was significantly directional; these data were then pooled for population-level Rayleigh tests for each treatment (silence, sounds from left, sounds from right). Mean angles were calculated relative to the fixed frame of reference of the DISC (i.e. top, bottom, left, right of the camera's image) and also relative to a cardinal frame of reference after accounting for rotation of the DISC (Paris et al. 2008, Irisson et al. 2009). I expected that the larval fish may not be able to detect the true direction of the sound source, but merely the axis of vibration, due to a 180º ambiguity in their auditory physiology (Zeddies et al. 2011, Popper and Fay 2011). Therefore, for the playback trials, I also tested whether the group-level bearings had significantly bimodal distributions (Batchelet 1981). Finally, I tested whether either the acoustic stimulus or the trial number (first, second, or third portion of the deployment) affected either orientation accuracy (Rayleigh's r) or swimming speed using repeated measures ANOVAs, after first validating assumptions of sphericity.

Results

For *A. stellatus* individuals, in 23/23 of the playback trials, and in 11/12 of the silent trials, there was significant directionality at the individual-level. Relative to a cardinal frame of reference, the fish larvae maintained a group-level bearing, orienting towards the northwest (303º, Figure 4.2A) during silent trials, but not during sound playbacks from either direction (Figure 4.2B-C). Relative to the speaker axis, the fish larvae did not maintain a significant mean bearing during silence (Figure 4.2D) or during sound playbacks (Figure 4.2E-F). The audio stimulus had no effect on r-value ($F_{2,20}$= 0.055, p = 0.946) or swimming speed ($F_{2,20}$ = 0.25, p = 0.782). Likewise, the trial number had no effect on r-value ($F_{2,20}$ = .33, p = 0.721) or swimming speed $F_{2,20}$ = 1.35, p = 0.281).

For 9/9 of the silent trials, and 19/19 of the playback trials, *Acanthurus* larvae demonstrated significant directionality at the individual-level. However, at the group-level, *Acanthurus* larvae did not maintain a significant mean bearing during silence or during sound playbacks, in neither the cardinal nor the DISC frame of reference (Figure 4.2G-L); thus, they did not orient. Audio stimulus type had no effect on r-value ($F_{2,16}$= 2.41, p = 0.121) or swimming speed ($F2_{,16}$ = 1.95, p = 0.175), and the trial number also had no effect on r-value ($F_{2,16}$ = 1.11, p = 0.35) or swimming speed ($F_{2,16}$ = 1.84, p = 0.19).

Discussion

A. stellatus larvae oriented at the group-level during silence (Figure 4.2A), but not during acoustic playbacks (Figure 4.2E-F). The fact that the larvae were not orienting during silent trials within the arena frame of reference (Figure 4.2D) removes the possibility that their behavior was simply an artifact (i.e. they did not have a preference for one section of the behavioral arena). Furthermore, if I had seen a decrease in individual-level directionality during acoustic playbacks, this would imply that the playbacks stressed the fish or created erratic behavior. However, this was not the case. The fish larvae simply maintained different bearings during sound playbacks than they did during silent periods. This result suggests a response to the reef sounds, but not "attraction" to the sounds, as I had anticipated. Their bearing towards the northwest demonstrates true orientation to cues outside the DISC, and a mean bearing in this direction would lead *A. stellatus* alongshore of Long Island (Figure 4.1B).

In contrast, larval *Acanthurus* spp. showed no response to reef sounds; there was no significant group-level orientation during silence or acoustic playbacks, relative to either frame of reference (Figure 4.2G-L). *Acanthurus* larvae have not been used in previous acoustic playback experiments, so there is no basis for comparison with other published studies. Their lack of orientation may be explained by the fact that these larvae have a relatively long pelagic phase (Rocha et al. 2002), and are larger than other fish larvae, so the behavioral arena of the DISC may have been too confining. A molecular study found that *A. chirurgus* has little population structure across areas of the Caribbean, presumably due to their broad habitat preferences, which suggests that larvae may be relatively indiscriminate navigators (Rocha et al. 2002). Finally, settled Acanthuridae form schools (Foster 1985) and are also found in schools during their pelagic stages (Fanning et al. 2006), suggesting that they may rely heavily on group navigation and therefore have limited individual orientation abilities. I was limited by the number and type of larvae that arrived in the light-traps at Long Island, but future experiments of this nature should aim to test a broader range of fish species.

In this study, I attempted to simulate near-field acoustic conditions that fish would experience close to settlement habitat (Staaterman et al. 2014). Because the ambient sound pressure level in DBH was approximately 97 dB re 1 μPa over the frequency range of interest (< 1000 Hz), I deliberately chose to play relatively lower sound levels (*ca.* 114-127 dB re 1 μPa) compared to some of the previous studies (180 dB re 1 μPa, Tolimieri et al. 2000, 2004; 156 dB re 1 μPa, Simpson et al. 2008b) while still maintaining a sufficient signal-to-noise ratio. The sound pressure levels played here, especially from the left speaker (127 dB re 1 μPa, Table 4.1), were within pure-tone pressure detection levels for several species of fish larvae (Wright et al. 2011) and adults (Horodysky et al. 2008, Wysocki et al. 2009, Radford et al. 2012). However, whether *A. stellatus* and *Acanthurus* spp. can detect acoustic pressure in addition to particle acceleration remains unknown (Zeddies et al. 2011, Popper and Fay 2011), and some of the pure-tone particle acceleration thresholds for other species (*ca.* -10 to -60 dB re 1 m/s^2, Wright et al. 2011, Radford et al. 2012) exceed what was generated in the present study (Table 4.1). Therefore, although the speakers were very close to the larvae, it is not clear whether particle acceleration levels were sufficient to elicit a response from these species. Examining the acceleration spectrum generated by the speakers in the axis facing the speakers (Figure 4.4A) compared to the axis that was perpendicular to the speakers (Figure 4.4B) reveals only slight differences. This demonstrates that the acceleration field generated by the speakers was not clearly directional, and thus helps to explain why we did not see a directional response from the fish larvae. These findings demonstrate the complicated nature of acoustic playback experiments in the ocean. Future work in this area should be careful to measure and report the sound field generated by the speakers in order to properly interpret results.

My results contradict findings from some previous larval fish acoustic work, and corroborate others. For example, in nearshore areas, greater numbers of Apogonidae larvae were collected in noisy light-traps than silent traps (Simpson et al. 2004), and more juveniles were observed at noisy patch-reefs than silent ones (Simpson et al. 2007). However, Leis et al (2003) found that this pattern was reversed when light-traps were deployed further offshore (500 m from nearest reef): more Apogonidae larvae were caught in silent traps. These results indicate a location-specific response to acoustic cues for Apogonidae, suggesting that larval fish may utilize multiple cues at once. My results are most similar to those of Leis et al. (2002), who followed individual larvae during the day in the open ocean; they found that pomacentridae larvae maintained a mean bearing during silence, but became non-directional when sounds were played (Leis et al. 2002). Tolimieri et al. (2004) found that groups of pomacentridae larvae placed into choice-chambers moved towards reef sounds during the night, but away from the sounds during the day, when predation risk is highest (Leis et al. 1996). Indeed, Apogonidae larvae in the Bahamas tend to settle at night (Thorrold et al. 1994), and adult *A. stellatus* are nocturnal (Bohlke and Chaplin 1993). These previous studies, along with my own, suggest that fish larvae may have a differential response to reef sounds depending on the location and time of day in which they are encountered. Furthermore, there seems to be an interaction between visual and acoustic signals, which needs to be further examined.

To conclude, I found a group-level response to reef sounds in *A. stellatus* larvae, but not in *Acanthurus* spp. However, the response observed for *A. stellatus* was not an attraction to reef sounds as I had predicted, but rather a disruption of orientation behavior that relied on other (e.g., visual) cues. Future work should aim to disentangle the relative role of visual, acoustic, and time-of-day cues used by coral reef fishes during the settlement process, and how and why the roles of these cues differ among families.

Table 4.1. Received Root-Mean-Square levels at different areas of the behavioral arena. For example, “Pressure A” refers to acoustic pressure measured at hydrophone A (Figure 1C). All sounds have been bandpass filtered at 70 Hz – 1,000 Hz. For details on spectral information see Figures 4.3 and 4.4.

Stimulus type	Ambient sounds (no playback)	L Bahamas	R Bahamas	L Florida	R Florida
Pressure A (dB re 1 μPa)	97.6	127.6	116.5	125.5	106.4
Pressure B (dB re 1 μPa)	97.6	118.9	111.2	117.3	113.0
Acceleration A-B axis (m/s^2)	9.4E-5	.0051	.0014	.0037	8.8E-4
Acceleration A-B axis (dB re 1 m/s^2)	-80.5	-45.9	-56.8	-48.5	-61.2
Pressure C (dB re 1 μPa)	97.6	127.6	111.3	125.5	106.5
Pressure D (dB re 1 μPa)	97.3	121.8	112.2	120.4	108.8
Acceleration C-D axis (m/s^2)	1.1E-4	.0023	6.9E-4	.0023	5.0E-4
Acceleration C-D axis (dB re 1 m/s^2)	-79.1	-52.7	-63.2	-52.6	-66.0
Total acceleration magnitude (m/s^2)	1.5E-4	.0056	.0016	.0044	.001
Total acceleration (dB re 1 m/s^2)	-76.7	-45.0	-56.0	-47.1	-60.0

A. Dean's Blue Hole

B. Long Island, Bahamas

C. Drifting *In Situ* Chamber

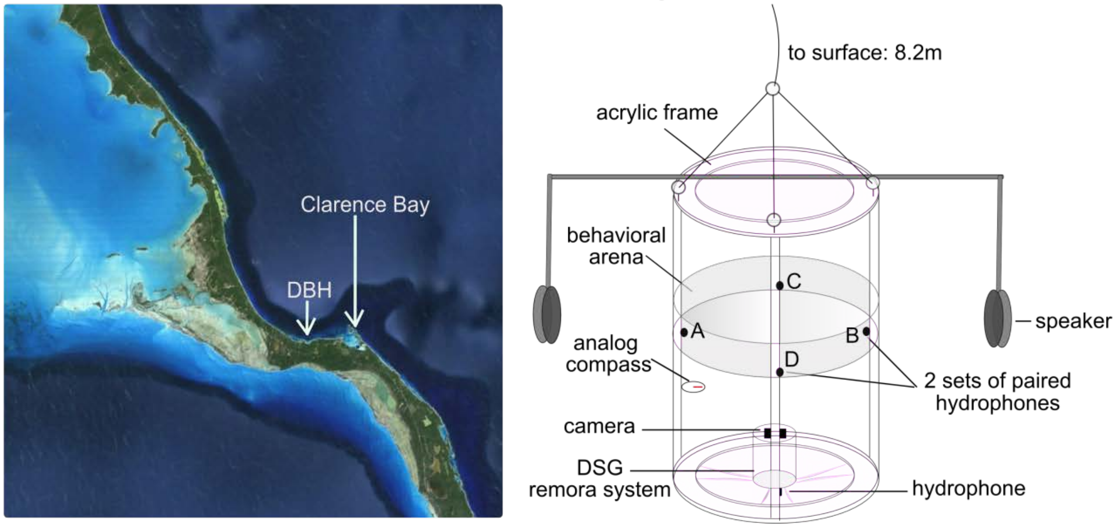


Figure 4.1. Study site and experimental setup. A: Dean’s Blue Hole is a natural blue hole on Long Island, Bahamas, extending 202m deep. Experiments were conducted from the platform in the center of the photo. B: Long Island Bahamas, with the sites of larval collections. C: The Drifting *In Situ* Chamber. A single fish larva was placed inside of the mesh behavioral arena, and sounds were played alternately from the left and right speakers. See Table 1 for received levels at each of the hydrophones during playbacks.

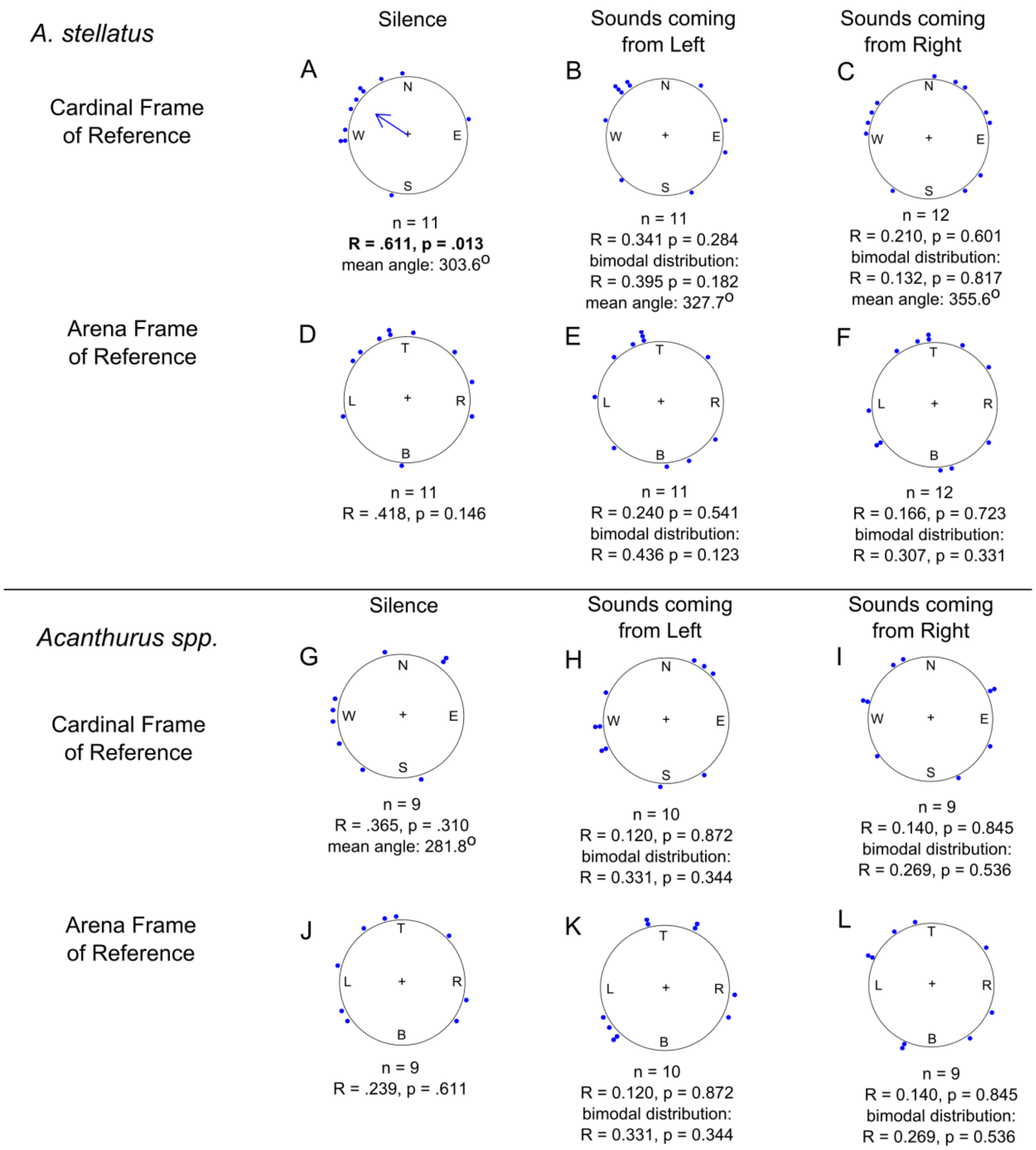


Figure 4.2. Bearings of individual fish larvae (blue dots) during each acoustic treatment. A-C & G-I: bearings are shown relative to a cardinal frame of reference. D-F & J-L: bearings are shown relative to the behavioral arena frame of reference (T, B, L, R denotes Top, Bottom, Left, Right). Significant group-level orientation towards the northwest was observed for *A. stellatus* larvae during silence, but not during acoustic playbacks. There was no significant orientation behavior for *Acanthurus spp* in any of the experiments. Results from playbacks of sounds recorded in the Bahamas and in Florida were pooled based on speaker direction (left or right speaker).

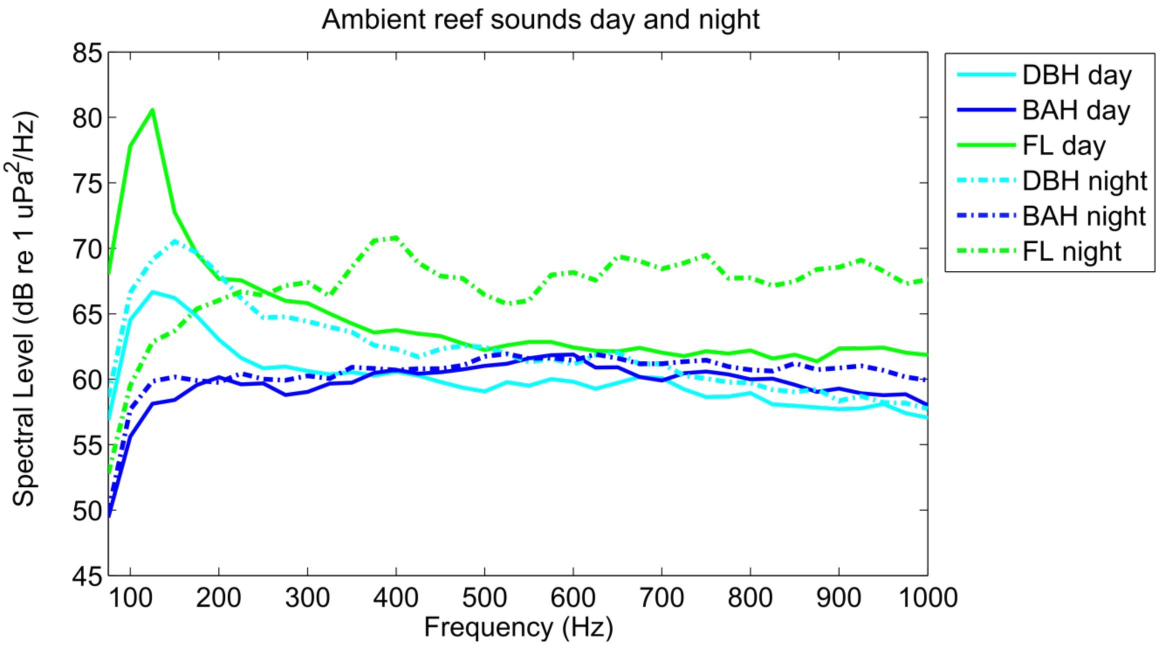


Figure 4.3. Pressure spectra of ambient sounds from Florida, the Bahamas, and Dean’s Blue Hole, recorded during the day and at the night during the first quarter moon. Sounds have been band-pass filtered (75 Hz – 1,000 Hz). Reefs in Florida are shown in green (Sand Island Reef, 25°0’43” N, 80°22’33” W), reefs in the Bahamas (next to light-trap collection site in Clarence Bay, 23°6′23″N 75°0′31″W) in blue, and ambient sounds in DBH in cyan. All three sites exhibited differences across day and night. Ambient sounds in DBH were lower than Florida reefs, but higher than nearby Bahamas reefs in the lowest frequencies, but the reason for this is unknown.

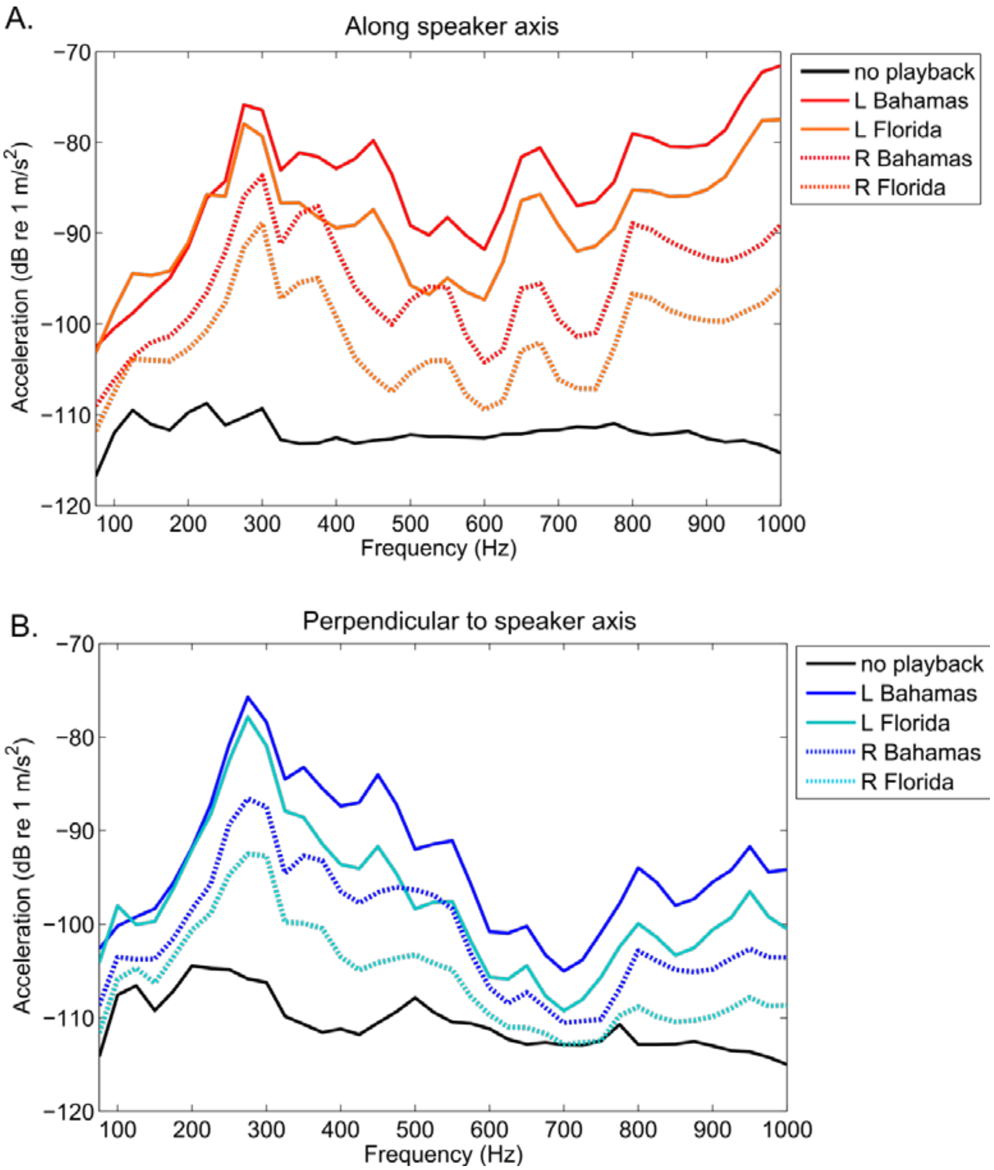


Figure 4.4. A: Received particle acceleration levels along the speaker axis (hydrophones A-B) and B: received particle acceleration in the axis perpendicular to the speakers (hydrophones C-D) during acoustic playbacks and during no playbacks (“silent” trials). For example, “L Bahamas” represents the received acceleration while the sounds recorded in the Bahamas were played from the left speaker. Particle acceleration for each axis was calculated from the Linearized Euler Equation which incorporates the pressure difference between the two hydrophones in the pair (as in Zeddies et al. 2010). Sounds generated by the left speaker consistently produced higher acceleration than sounds generated from the right speaker, regardless of spectral content (Florida vs. Bahamas), hence my choice to pool behavioral responses based on speaker direction. These spectra demonstrate that the acceleration field created by the speakers was not clearly directional; the acceleration received on both axes was almost identical, so it would not be appropriate to expect a directional response from the fish larvae.

CHAPTER 5: PROPAGATION OF ACOUSTIC PRESSURE AND PARTICLE ACCELERATION NEAR A CORAL REEF

Summary

Recent studies have suggested that reef fish larvae may utilize acoustic signals to navigate towards reefs at the end of their pelagic phase. These studies, along with the majority of fish hearing tests, have focused on acoustic pressure as the salient cue, even though most fishes detect particle acceleration – not pressure. To characterize the reef's acoustic field from the perspective of a fish larva, I measured both pressure and particle acceleration with increasing distance from the reef. In addition, I used an acoustic propagation model and verified it with a transmission experiment in the field to understand the structure of the sound wave. Results from the model and transmission experiment were consistent, since both relate to the propagation of an acoustic point-source. However, the reef is not a point source but rather a series of many sources, and the propagation of natural reef sounds did not conform to predictions. Acoustic pressure decreased more rapidly with distance than did particle acceleration. At larger distances, acceleration was greater in the Y- and Z-axes than the X-axis, suggesting that it was not propagation of the reef's acceleration field, but rather local sources, that elevated these measurements. Even at the closest distances, particle acceleration was extremely low – below the detection thresholds of several fish species. Furthermore, acceleration in the direction pointing towards the reef barely exceeded acceleration in the other directions, which means that the signal was not highly directional. The low amplitudes and lack of consistent directionality in the particle acceleration field would make it extremely

difficult for an acceleration-sensitive organism to locate the reef. These findings suggest that acoustic signals alone may not be sufficient to guide larval reef fishes towards shore.

Background

As fish and invertebrate larvae seek settlement habitat at the end of their pelagic phase, it is possible that they could detect and utilize the acoustic signals emanating from coastal habitats (Simpson et al. 2005a, Vermeij et al. 2010, Stanley et al. 2012). Because many soniferous organisms live on coral reefs, their collective utterances create distinct acoustic signatures that could serve as reliable signals, potentially at large distances from the reef (McCauley and Cato 2000). However, the exact distance at which larvae can detect a reef, and thus the importance of acoustic orientation to larval navigation, depends upon the source level and propagation of the sounds, as well as the hearing abilities of the species of interest (Mann et al. 2007). Furthermore, the behavior of acoustic signals in shallow water is one of the most poorly understood aspects of underwater acoustics due to complicated scattering patterns from the surface and seafloor (Urick 1983, Bass and Clark 2002). Thus, although models can approximate acoustic propagation in deep-water conditions, empirical measurements of sound fields are required in shallow waters near coral reefs.

A sound is created by the vibration of an object within its medium. This vibration creates two components of the sound wave: 1) acoustic pressure, which is a scalar (non-directional) quantity, and 2) particle motion, which is directional along a 180º axis and can be measured as displacement, velocity, or acceleration (Kalmijn 1988). Investigators have used ray theory and normal-mode theory to describe the propagation of acoustic pressure with distance, and a parabolic-equation model can be used to predict acoustic propagation at both short and long ranges from the source (Urick 1983, Smith 2001). Traditionally, experiments that aim to quantify propagation of acoustic pressure in the field use a transducer to continuously transmit a signal, and a hydrophone to receive the signal at some distance. But there are multiple, simultaneous paths that the sound wave can follow before reaching the receiver (e.g., the direct path, reverberations off of the surface, and/or bottom), and these arrivals can sometimes overshadow the amplitude of the original signal (Deferrari and Nguyen 1986, DeFerrari et al. 2003). An alternative approach is to transmit an "M-sequence," which combines a continuous sound wave with pseudo-random noise, resulting in a tremendous increase in the received signal-to-noise-ratio after a series of post-processing steps (DeFerrari and Rogers 2008). This approach is useful for elucidating the mode structure of the sound field – the areas of the water column where acoustic rays (lines along which acoustic energy is transported) have constructive or destructive interference (DeFerrari et al. 2003, DeFerrari and Rogers 2008). Ultimately, a combination of predictive modeling and field experiments is required to fully illustrate the propagation of acoustic pressure (Jensen 1981).

The propagation of particle acceleration in shallow water is not well understood. Particle acceleration is highest in the "near-field" region close to the sound source, due to direct displacement of the fluid by the object. As the sound wave moves through the fluid, it generates back-and-forth motions of fluid particles, resulting in additional particle acceleration in the "far-field" region. Theoretically, the transition between the near-field and far-field occurs at a distance of approximately 1 wavelength from the source (Kalmijn 1988, Mann et al. 2007). Thus, the location of the near-field/far-field boundary changes with the wavelength (frequency) of the signal, while the transmission of the signal depends upon the amplitude (source-level) of the signal. Only a few studies have measured particle acceleration in the ocean (Banner 1965, 1970, Siler 1969), and these studies focused on the sound field created by a single point-source, rather than an entire acoustic habitat like a coral reef. Yet an understanding of the propagation of particle acceleration is required to estimate the distance at which fish larvae may detect acoustic signals from the reef.

A few recent studies have measured the propagation of acoustic pressure with distance from a reef (Radford et al. 2011b, Piercy et al. 2014), and playback experiments have reported the acoustic pressure generated by their speakers (Tolimieri et al. 2000, Simpson et al. 2004, Stanley et al. 2012). Yet for the majority of fishes and invertebrates, particle acceleration - not pressure - is the relevant cue (Popper and Fay 2011, Ladich and Fay 2013). A sub-set of fishes that possess connections between the swimbladder and the ear (e.g., a special set of bones called Weberian ossicles, or anterior projections of the swimbladder) can detect acoustic pressure in addition to particle acceleration (Popper and Fay 2011). Although traditional fish audiograms reported sensitivity to pressure (Tavolga 1971, Tavolga et al. 1981), recently there has been a push towards measuring particle acceleration thresholds as well (Lu et al. 1996, 2010, Horodysky et al. 2008, Wysocki et al. 2009, Wright et al. 2011, Radford et al. 2012, Ladich and Fay 2013), which will improve our understanding of acoustic detection in fishes. But the absence of particle acceleration measurements in both playback experiments and in real field conditions remain as critical knowledge gaps that need to be filled in order to truly understand how larval fishes may utilize acoustic signals (Mann et al. 2007).

Here I combine several approaches to examine a coral reef sound field and to discuss its potential relevance as a cue for larval fishes. First, I used a parabolic equation model to simulate an acoustic signal generated by a single point-source. Second, I compare these results to a field experiment in which I transmitted M-sequences. Next, I conducted passive measurements of acoustic pressure and particle acceleration at different distances from a reef. Finally, I interpret the ecological relevance of the results by comparing the measured quantities of particle acceleration to published audiograms for several fish species.

Methods

Study site:

Experiments were conducted near Ball-Buoy Reef (25º19’02” N, 80º11’11”W) in the northern Florida Keys Reef Tract (permit number OMB # 0648-0141). Ball-Buoy reef is a shallow patch reef surrounded by a large sand flat that extends several kilometers towards the southeast, where it eventually gives way to deeper spur-and-groove reefs. This site was chosen because there is little elevation change across the sand flat, and almost no coral or seagrass, which may have created interference due to additional sound sources. I conducted this work during two field trips: October 1-2, 2014, and December 16, 2014, when sea-surface conditions were <4 on the Beaufort scale.

Instruments

Two hydrophone systems were used: 1) a single-channel recorder with a single hydrophone, hereafter called the “soundtrap” (SoundTrap, Ocean Instruments, NZ;

sensitivity: -173.7 dBv/µPa) and 2) a multi-channel recorder with six pressure-sensitive hydrophones, hereafter called the “snowflake” (Loggerhead Instruments, ZoomH6; hydrophone sensitivities: -180.0 dBv/µPa). The hydrophones were mounted on a rigid frame, with the hydrophones in each pair set 15 cm apart (Figure 1). I also used an underwater speaker system for the M-sequence playbacks (speaker: Clark Synthesis, audio player: Microtrack II, M-audio, amplifier: Cerwin-Vega).

Modeling and transmission of a point-source signal:

The Monterey-Miami Parabolic Equation model (Smith 2001, hereafter "MMPE") was used to predict transmission loss and time-of-arrival of individual modes from a point-source in a shallow sand flat. The model was configured to match environmental parameters near Ball Buoy Reef (water depth: 9 m, sediment depth: 15 m, sound speed in water: 1536 m/s, sound speed in wet sand: 2000 m/s, sound speed in limestone (layer below sand): 3500 m/s, Bourbie et al. 1987). The theoretical sound source was 4 m from the surface, centered at 441 Hz with a 110 Hz frequency band, to match conditions from the M-sequence playback. I examined results for the transmission loss and time-of-arrival of the modes at 320 m from the source.

To measure the propagation of a known signal, I used an underwater speaker to project sounds into the water column. The speaker was lowered off the boat to a depth of 4 m from the surface, and the boat was anchored above the reef (the site of the passive recordings). The speaker faced seaward towards the receiver. The receiver was the snowflake, placed at 320 m from the source, on the mid-mount configuration (6.7 m from the surface, 1.8 m from the substrate). M-sequence playbacks occurred during the

October field trip. The file was a 441 Hz signal of 58 seconds duration, at a sample rate of 44.1 kHz and 16 bits. The received signal was downsampled by 25 times to a rate of four times the carrier frequency (441 Hz). Then a series of transformations were applied using custom-made Matlab programs to reveal the arrival times of the signal (Cohn and Lempel 1977). I also measured the source-level of the M-sequence from the soundtrap and compared to the received level on the snowflake.

Passive recordings of reef sounds:

SCUBA divers arranged a transect line on the sand, extending seaward from Ball-Buoy reef to a distance of 100 m. “Point-zero” was located 1m seaward from the edge of the reef framework. The soundtrap was placed directly on the sand at point-zero (facing towards the reef, 330º) and remained there for all of the recordings. I tried two mounting configurations for the snowflake: bottom-mounted (30 cm from substrate) and mounted to a very taught line at 1.8m off the substrate (Figure 5.1). However, due to self-noise on the anchoring system, the mid-mount setup could not be used for ambient recordings and was only used for the M-sequence playback. After the divers placed the snowflake at the proper measurement location and noted the time, they exited the water to preclude bubble noise on the recordings. For measurements > 100 m from the reef, the GPS on the boat was used to measure the distance from the reef, and a hand-held compass was used to position the snowflake along the proper axis (pointing towards the reef at 330º). In October, measurements were made at 1 m, 10 m, 20 m, 40 m, and 80 m from the reef. In December, measurements were made at the same distances as well as 500 m and 1 km from the reef – but the 20 m and 40 m measurements had to be discarded due to boat noise.

Snowflake data processing:

The wav file from each channel was band-pass filtered at 70 Hz-1000 Hz to remove potential interference outside of the frequency range of interest. Due to some extraneous noises from passing boats, I had to truncate each recording to 120 seconds in order to have matching recording durations for each distance. After filtering and truncation, acoustic pressure in Pascals was calculated for each of the six hydrophones.

Next, particle acceleration in each axis was derived using the discretized form of the Euler equation:

$$\frac{p_1 - p_2}{\rho * \ distance\ between\ hydrophones} = particle\ acceleration$$

Where p_1 and p_2 represent the acoustic pressure on each hydrophone (Zeddies et al. 2010) and ρ represents the density of seawater. This equation provided the measured particle acceleration in each axis, as a continuous variable, for each recording location. I then calculated the Root-Mean-Square (RMS) acceleration for each axis as well as total acceleration from the three-dimensional Pythagorean Theorem. These measurements are reported as acceleration in m/s^2 as well as dB re 1 m/s^2 (Table 5.1). Finally, to represent the distribution of the signal across frequencies, I transformed pressure and particle acceleration into the frequency domain (FFT size: 1764 samples, resulting in 25-Hz frequency resolution).

To compare the measured particle acceleration (above) to the acceleration that would be expected in far-field conditions, I used the plane-wave equation: $p = \rho c v$, where p is the pressure at a given frequency (from the pressure spectrum), v is the particle velocity at each frequency, and ρ is the density of seawater. The input p was from the X-axis hydrophone closest to the reef, and once I obtained velocity from the equation, I converted it to acceleration for each frequency using $A = 2\pi f v$. Thus, I was able to compare the measured particle acceleration with the acceleration expected in far-field acoustic conditions.

Results

Modeling and transmission of a point-source signal:

At 320 m from the source, the location of the receiver during the M-sequence playbacks, the model predicted transmission loss of approximately 35 dB re 1 μPa (Figure 5.2). In reality, I measured transmission loss of 29 dB re 1 μPa. The model predicted persistence of the first few modes, and a decrease in amplitude of the higher-order modes with distance (Figure 5.3). The field recordings were consistent with the model's predictions, although the modes were less clearly structured (Figure 5.4).

Passive recordings of reef sounds:

Acoustic pressure

Acoustic pressure measured with the soundtrap at point-zero varied only slightly between recordings (Table 5.1). Although there was a discrepancy between the overall source-level amplitudes measured on the soundtrap and the snowflake (likely due to a calibration issue), the consistency between soundtrap recordings serves as an important reference and allows for a comparison between the snowflake recordings from different distances. The remaining results presented here will focus on data recorded by the snowflakes only.

Acoustic pressure decreased with distance from the source, but not as rapidly as expected from cylindrical spreading, spherical spreading, or the MMPE model (Figure 5.2, 5, 6). At 80 m from the reef, spherical spreading predicts transmission loss of 38 dB (a rate of 0.48 dB/m), and cylindrical spreading predicts 19 dB (a rate of 0.24 dB/m). Empirically, I measured only 6 dB transmission loss in 80m, a rate of .075 dB/m. At 1000 m, spherical spreading predicts 60 dB transmission loss (0.06 dB/m), cylindrical spreading predicts 30 dB (0.03 dB/m), and the MMPE model predicts 40 dB (0.04 dB/m). Yet the empirical measurements reveal only 10 dB loss in 1000 m, equivalent to a rate of 0.01 dB/m. These findings demonstrate that the propagation of pressure is not linear, and the propagation of reef sounds does not agree with models that assume the source of sound is a single point.

Particle acceleration

In general, particle acceleration in all three axes decreased with distance from the source (Figures 5.6 & 5.7). However, there were a few exceptions in frequencies <200 Hz: measurements at 80 m in October, and measurements at 1 km in December. In these instances, the high amplitudes were not explained by any obvious sounds from boats or animal vocalizations, but may have been caused by vibrations from a passing animal or a wave on the surface. Particle acceleration at 1 m vs. 1 km from the reef differed by only 4 dB re 1 m/s^2 – the decline was very gradual (Figure 5.6). There were only small differences in amplitude between the three axes, and these differences were not consistent across frequencies or distances (Figure 5.7).

The predicted values for particle acceleration depended upon the amplitude of the pressure spectrum measured at each distance, and were calculated assuming far-field conditions. Therefore, I expected that the actual acceleration would be greater than the measured acceleration for the closest distances (i.e., in the near-field). This was only the case for frequencies < 200 Hz (Figures 5.8, 5.9, 5.10). Above 200 Hz and near the reef, predicted acceleration exceeded measured acceleration near the reef. Farther from the reef, measured acceleration exceeded predicted acceleration and was fairly uniform across frequencies (Figures 5.8, 5.9, 5.10).

Discussion

Propagation of a point-source signal

Here, I conducted a propagation experiment in the field, and modeled the transmission loss of a point-source signal with parameters that matched field conditions. The results from the MMPE model and empirical study showed high agreement, with only a 6 dB discrepancy in transmission loss. Because the cylindrical and spherical spreading equations do not consider scattering from the surface of bottom boundary, there was a greater discrepancy between these predictions and the empirical recordings. The field recordings demonstrated the mode structure of the water column; at 320 m from the source, several modes were still present, but were not as clear as the model predicted (Figures 5.3 & 5.4). This was not surprising considering the fact that the receiver likely picked up additional sound sources, there were subtle changes in bottom bathymetry, and there may have been additional scattering due to surface waves – factors that the model does not consider. This M-sequence field experiment represents the first of its kind in such shallow conditions, and appears to be a promising method for understanding transmission loss in these environments. Future work should consider a wider range of distances from the reef.

Pressure and particle acceleration emanating from the reef

For a sound wave generated by a point-source, particle acceleration is expected to drop off more rapidly with distance than pressure, and at some transitional point between the near-field and the far-field, the two quantities fall off at an equal rate (Figure 5.11, Kalmijn 1988). Theoretically, acoustic pressure generated by a point-source should initially spread spherically (i.e, 20*log(distance)) and then cylindrically (10*log(distance)) due to the boundaries imposed by shallow water conditions (Urick 1983). The results did not conform to these theoretical predictions. I found that acoustic pressure decreased more gradually than predicted from cylindrical spreading, spherical spreading, or from the MMPE model (Figure 5.2). This can be explained by the fact that the reef itself is not a single point-source, but rather a series of point-sources contributing to the sound field. Previous studies examining the propagation of reef sounds with distance also found a gradual drop-off (Radford et al. 2011b, Piercy et al. 2014). My results corroborated previous findings; despite different source-level amplitudes, the relationships between amplitude and distance were consistent, suggesting similar propagation behavior in these shallow-water environments (Figure 5.12).

Surprisingly, particle acceleration decreased very little with distance from the source (Figure 5.6) and did not follow theoretical predictions (Figure 5.11). Close to the reef, at frequencies between 200-1000 Hz, the predicted levels of particle acceleration - which assumed far-field conditions - exceeded what was measured (Figures 5.8-5.10). This result was surprising, and is difficult to explain. A 200-Hz monopole sound (like a pulsating swimbladder) has a near-field of approximately 7.5 m, while a 200-Hz dipole sound (like an undulating fish body) has a near-field of approximately 1.2 m (Siler 1969). Perhaps, even though the snowflake was placed just at the edge of the reef, sounds >200 Hz originated from other parts of the reef, beyond the near-field boundary. For the lowest frequencies, since the near-field is larger, I expected that measured levels would exceed predicted levels close to the source, which is indeed what I found (Figures 5.8-5.10). Yet I was also surprised to see that RMS acceleration did not drop off rapidly with distance, and at greater distances, acceleration was generally higher than predicted. It is important to point out that the high spikes in acceleration at larger distances were dominant in other axes (e.g. at 80 m in October the Y and Z-axes had high acceleration, Figure 5.7C&E, and at 1km in December the Z-axis had high acceleration, Figure 5.7F), suggesting that the elevated acceleration was due to other sound sources – not the reef itself. In addition, although the overall amplitude of particle acceleration in the direction facing the reef was greater than the other axes, this difference was very small (Figure 5.6), and was not consistent across distances or frequencies (Figures 5.6 & 5.7). This lack of directionality of the reef's acoustic field may be explained by the fact that the reef is not a point-source, or because of complicated scattering on the surface or seafloor. It is also very possible that vibrations from the substrate or other sound sources in the vicinity were detected by the instrument. Taken together, these findings suggest that the particle acceleration field coming from the reef, at least near the substrate, does not follow predictions, nor does it provide a highly directional signal. Although I attempted to measure acceleration at mid-water depths as well, there was just enough movement on the mooring system to render the recordings useless. Future work should focus on a better mooring system that will enable measurements throughout the water column, rather than just near the substrate, to understand how the acceleration field changes with depth.

Ecological context

A pressure-sensitive organism could sample the acoustic field near a reef and would detect higher amplitudes as it approached the reef (Figure 5.6). Thus, although pressure is a scalar (non-directional) quantity, by moving around within the vicinity of a reef, the pressure gradient could lead to the source of the sound. However, the hearing abilities of the organism of interest will determine whether this pressure-field is detectable. Hearing in fishes is determined by examining either the behavioral (e.g., Offutt 1968, Popper 1971) or neurological (Ladich 1999, Cordova and Braun 2007) response to played-back sounds, and these techniques can yield very different responses, even for the same species (Figure 5.13A). In the laboratory, pure-tone sounds are presented to the focal organism, but hearing thresholds are typically lower when animals are presented with a wider frequency bandwidth like environmental sounds (Glasberg and Moore 1990). Therefore, to compare the reef soundscape to fish hearing thresholds, I systematically adjusted the published pure-tone thresholds to represent the expected response to a wider frequency band (Figure 5.13B).

A comparison of the reef's pressure spectrum (Figure 5.14A) to adjusted audiograms for larval and juvenile reef fishes (Figure 5.13C) reveals that these reef fish larvae may not be able to "hear" the reef. Only when one adds a buffer to take into account the range of responses measured in different laboratories and with different techniques (Figure 5.13A) is it possible that the larvae of pressure-sensitive fishes could detect the pressure signal from the reef. Furthermore, detection would only be possible during the new moons in the wet season – the time with highest amplitudes (Staaterman et al. 2014a) - and not in the dry season. However, it is important to note that the sounds of the reefs in Florida are relatively low compared to measurements of reefs in other geographical areas (Figure 5.12; McCauley and Cato 2000, Radford et al. 2008, Kennedy et al. 2010, Staaterman et al. 2013, Piercy et al. 2014). Therefore, it is possible that some pressure-sensitive larval fishes could detect the pressure signal of other, higher-amplitude reefs.

An important distinction needs to be made regarding the sensory modality used to detect acoustic signals. While all fishes are sensitive to particle acceleration, only certain species are able to detect acoustic pressure as well (Popper and Fay 2011). When exposing fish to acoustic signals in a laboratory, it is impossible to produce a pressure signal without also producing particle acceleration. Traditionally, authors measured only the pressure signal that the focal fish received, thus overlooking the cue that may be more relevant. Recently, a study by Wright et al. (2011) measured both pressure-sensitivity and acceleration-sensitivity for a suite of larval reef fishes. The acceleration thresholds of these larval fishes (Figure 5.14D) exceed the acceleration levels I measured on the reef (Figure 5.14B). Even when considering a buffer due to differing methods (Figure 5.13A), their detection thresholds still exceed the acceleration levels I measured. Therefore, I can conclude that it is unlikely that acceleration-sensitive reef fish larvae would be able to detect the acceleration signal emanating from this Florida reef.

These findings bring into question the previous work claiming that larval reef fishes could navigate from a great distance using acoustic signals. First, I found that the acceleration signal emanating from the reef is extremely low-amplitude even at close distances from the reef. Second, in order to serve as a directional cue, acceleration in the axis facing the reef would have to consistently exceed the other axes, but this was not the case. Third, Figure 5.14 shows that even after adjusting pure-tone hearing thresholds to accommodate a wider bandwidth, and after considering a buffer due to sampling methods, the acceleration signal from the reef would be too low to be detectable by larval reef fishes. Taken together, these findings suggest that, at least for Florida reefs, acoustic signals alone would not be sufficient to guide an acceleration-sensitive larval fish towards the reef. Further work is needed to examine the acceleration near additional reefs, times of year, and parts of the water column. It is also important to continue laboratory tests of hearing thresholds, and to determine which species are sensitive to pressure vs. particle acceleration, especially in the larval stages.

Table 5.1. Root-Mean-Square (RMS) amplitudes for acceleration and acoustic pressure. All recordings were 120 seconds in length, and were band-pass filtered at 70 Hz -1000 Hz. Pressure is presented in dB re 1 µPa (and µPa in parenthesis); acceleration is presented as dB re 1 m/s^2 (and m/s^2 in parenthesis). The soundtrap remained at point-zero during all of the measurements, while the snowflake was sequentially moved to further distances. For example "soundtrap during 500 m" refers to the amplitude recorded by the soundtrap at point-zero while the snowflake was at 500 m. Note that the soundtrap levels at point-zero did not match up with snowflake levels at point-zero, likely due to a calibration issue. But the important point is that soundtrap levels changed very little across recordings, which means that snowflake measurements at different distances are comparable.

	October					December				
	RMS pressure	RMS accelera-tion (X)	RMS accelera-tion (Y)	RMS accelera-tion (Z)	RMS total accelera-tion	RMS pressure	RMS accelera-tion (X)	RMS accelera-tion (Y)	RMS accelera-tion (Z)	RMS total accelera-tion
Soundtrap during 1m	104.9					104.0				
Snowflake @ 1m	95.2 (5.7E4)	-82.2 (7.8E-5)	-82.4 (7.6E-5)	-83.8 (6.5E-5)	-78.0 (1.3E-4)	95.5 (5.6E4)	-82.8 (7.3E-5)	-83.0 (7.1E-5)	-83.0 (7.0E-5)	-78.2 (1.2E-4)
Soundtrap during 10m	104.7					103.9				
Snowflake @ 10m	94.6 (5.4E4)	-81.8 (8.1E-5)	-82.6 (7.4E-5)	-84.2 (6.2E-5)	-77.9 (1.3E-4)	92.6 (4.3E4)	-83.4 (6.7E-5)	-84.3 (6.1E-5)	-84.6 (5.9E-5)	-79.3 (1.1E-4)
Soundtrap during 20m	104.5									
Snowflake @ 20m	92.3 (4.1E4)	-82.9 (7.2E-5)	-83.2 (6.9E-5)	-85.0 (5.6E-5)	-78.8 (1.1E-4)	Too much boat noise				
Soundtrap during 40m	104.6									
Snowflake @ 40 m	91.0 (3.6E4)	-83.6 (6.6E-5)	-84.0 (6.3E-5)	-85.8 (5.2E-5)	-79.6 (1.0E-4)	Too much boat noise				
Soundtrap during 80m	104.6					104.1				
Snowflake @ 80m	89.7 (3.1E-4)	-83.7 (6.5E-5)	-83.3 (6.8E-5)	-85.0 (5.6E-5)	-79.2 (1.1E-4)	92.6 (4.3E4)	-84.4 (6.1E-5)	-84.8 (5.7E-5)	-84.8 (5.7E-5)	-79.9 (1.0E-4)
Soundtrap during 500m						104.2				
Snowflake @500m	Not measured					87.1 (2.3E4)	-85.2 (5.5E-5)	-85.8 (5.2E-5)	-86.2 (4.9E-5)	-80.9 (9.0E-5)
Soundtrap during 1 km						104.2				
Snowflake @ 1km	Not measured					85.6 (1.91E4)	-85.4 (5.4E-5)	-85.0 (5.19E-5)	-85.7 (5.19E-5)	-80.6 (9.4E-5)

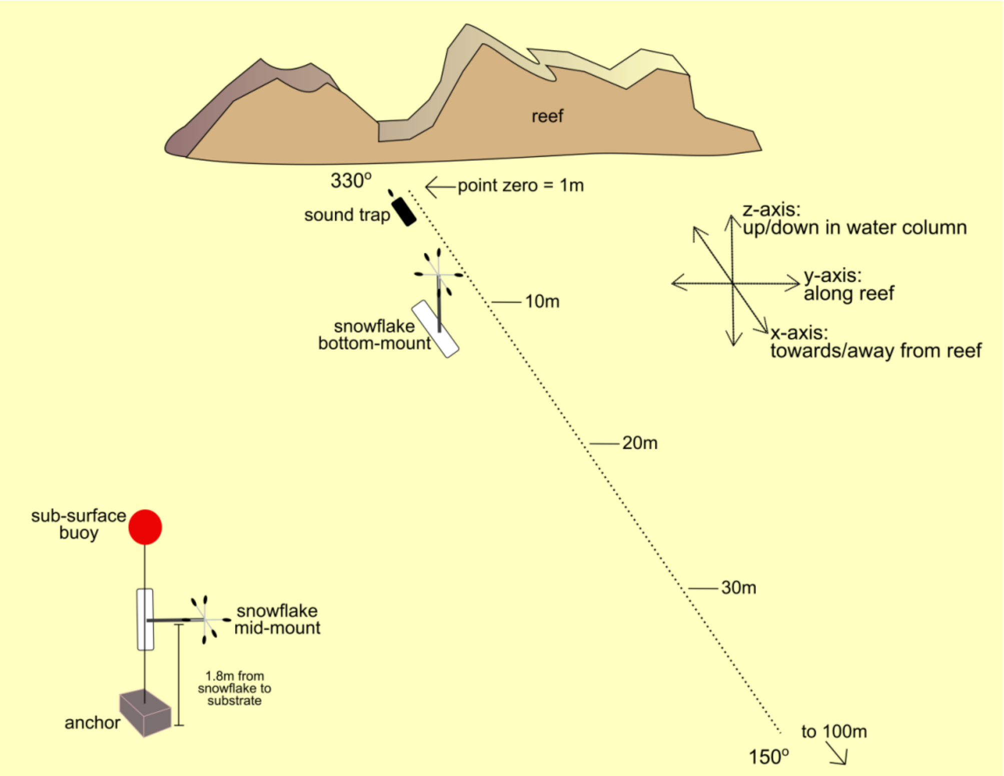


Figure 5.1. Instrument configuration. The soundtrap remained at point-zero for all of the recordings and was used to verify that the source-level sounds of the reef were consistent across the recordings (see Table 5.1). The snowflake was subsequently moved to greater distances, using the bottom-mount setup for all ambient measurements. The orientation of the snowflake was consistent: the x-axis faced towards/away from the reef, the y-axis was aligned with the along-reef axis, and the z-axis was vertical in the water column. The mid-mount snowflake configuration (bottom left) was used only for the M-sequence playbacks.

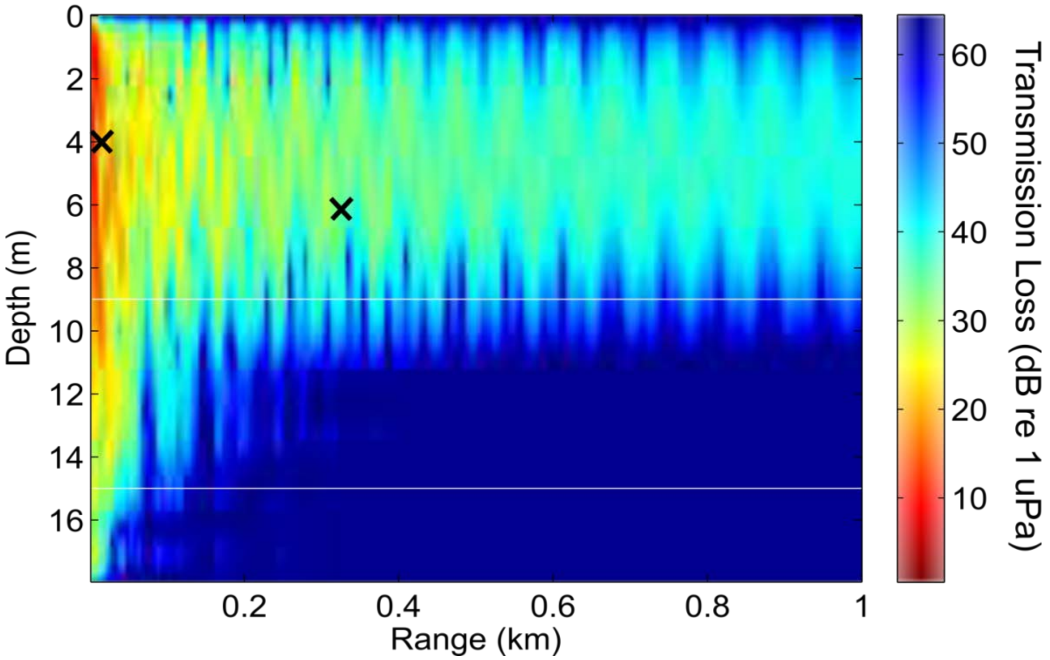


Figure 5.2. Predicted transmission loss with distance from the source, as predicted from the MMPE model. The model was parameterized to match field conditions during the M-sequence playbacks (e.g. the source was 4 m from the surface, the receiver was 320 m from the source and 6.7 m from the surface). X-marks depict source and receiver locations for the M-sequence playbacks. The first horizontal white line represents the boundary between water and sand (9 m), and the second line represents the boundary between sand and limestone (15 m). Close to the source, several modes are visible in the water column, but with increasing distance, these higher-order modes diminish and only the first several modes are visible. The MMPE model predicted approximately 35 dB transmission loss at 320 m from the source.

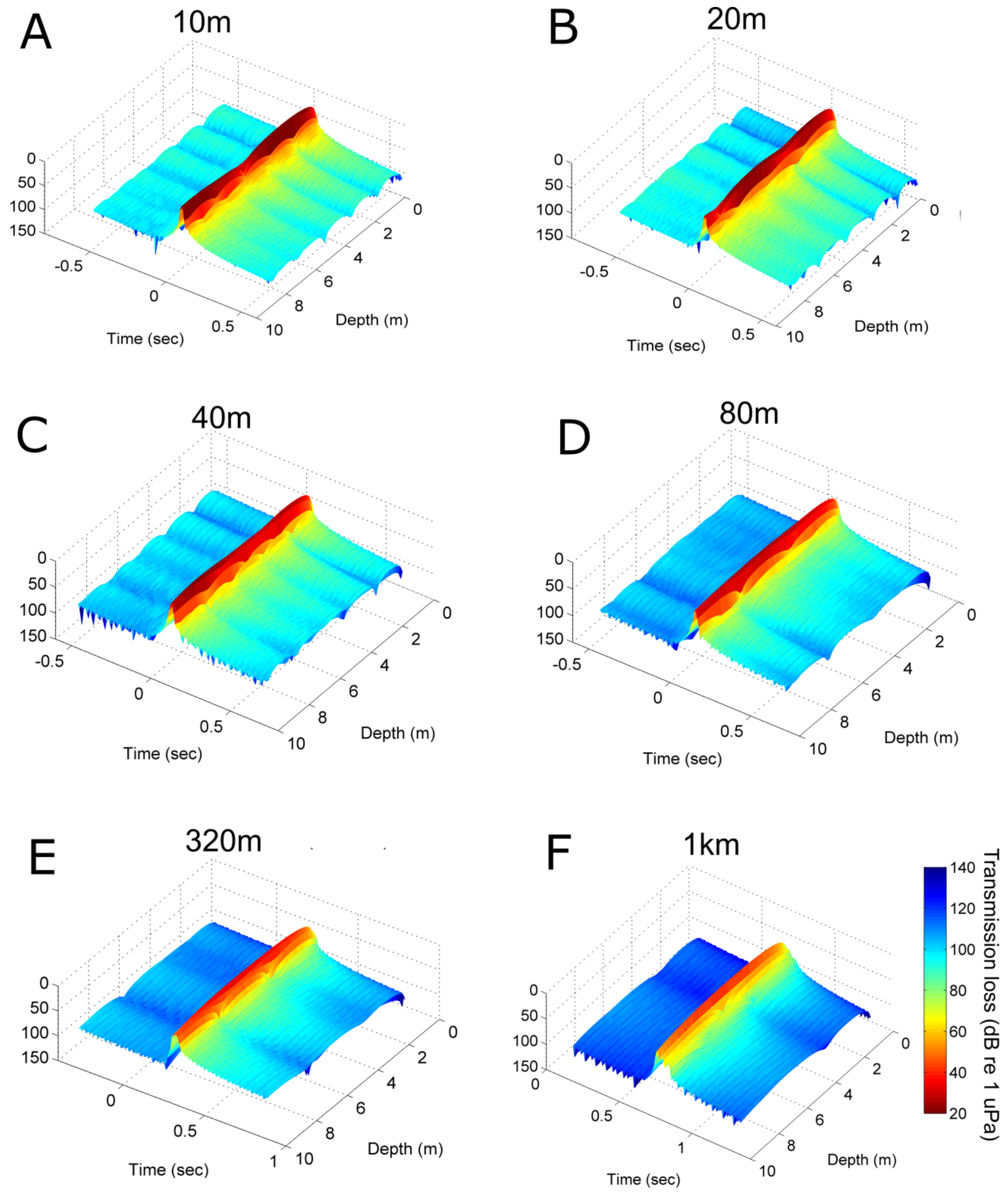


Figure 5.3. Transmission loss (vertical axis, colorbar in F) as a function of arrival time and depth as predicted from the MMPE model. Close to the source (A-D), transmission loss is lowest, and higher-order modes (yellow-green contours) can be seen arriving after the first mode (dark red contour). At greater distances (E-F), only the first few modes are still visible. The higher-order modes take longer to arrive because they have longer travel paths, and diminish with distance because they have more interactions with the surface and bottom.

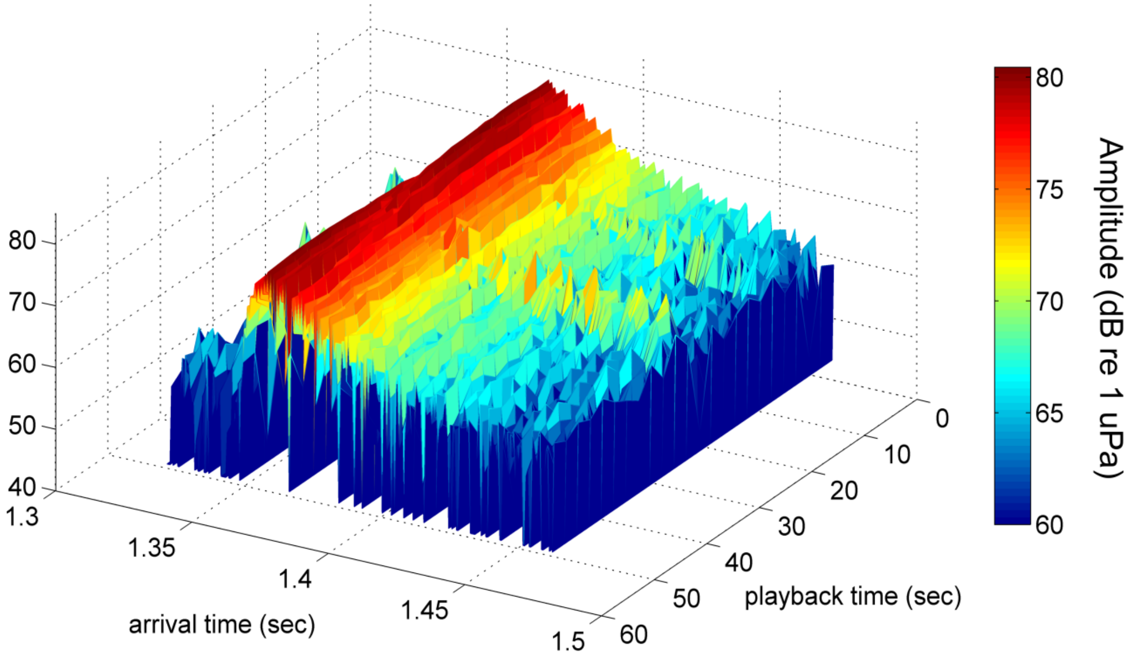


Figure 5.4. Measured amplitude of the acoustic signal received on the hydrophone at 320 m from the source during transmission of the M-sequence. Several modes arrived after the first mode (highest peak, darkest red), but the higher-order modes are not visible. These results are consistent with the predictions from the MMPE model (Figure 5.3), although the structure of the modes is not as clear. This discrepancy was not surprising considering the presence of other sound sources, subtle changes in bathymetry, and waves on the water's surface, which the model does not take into account.

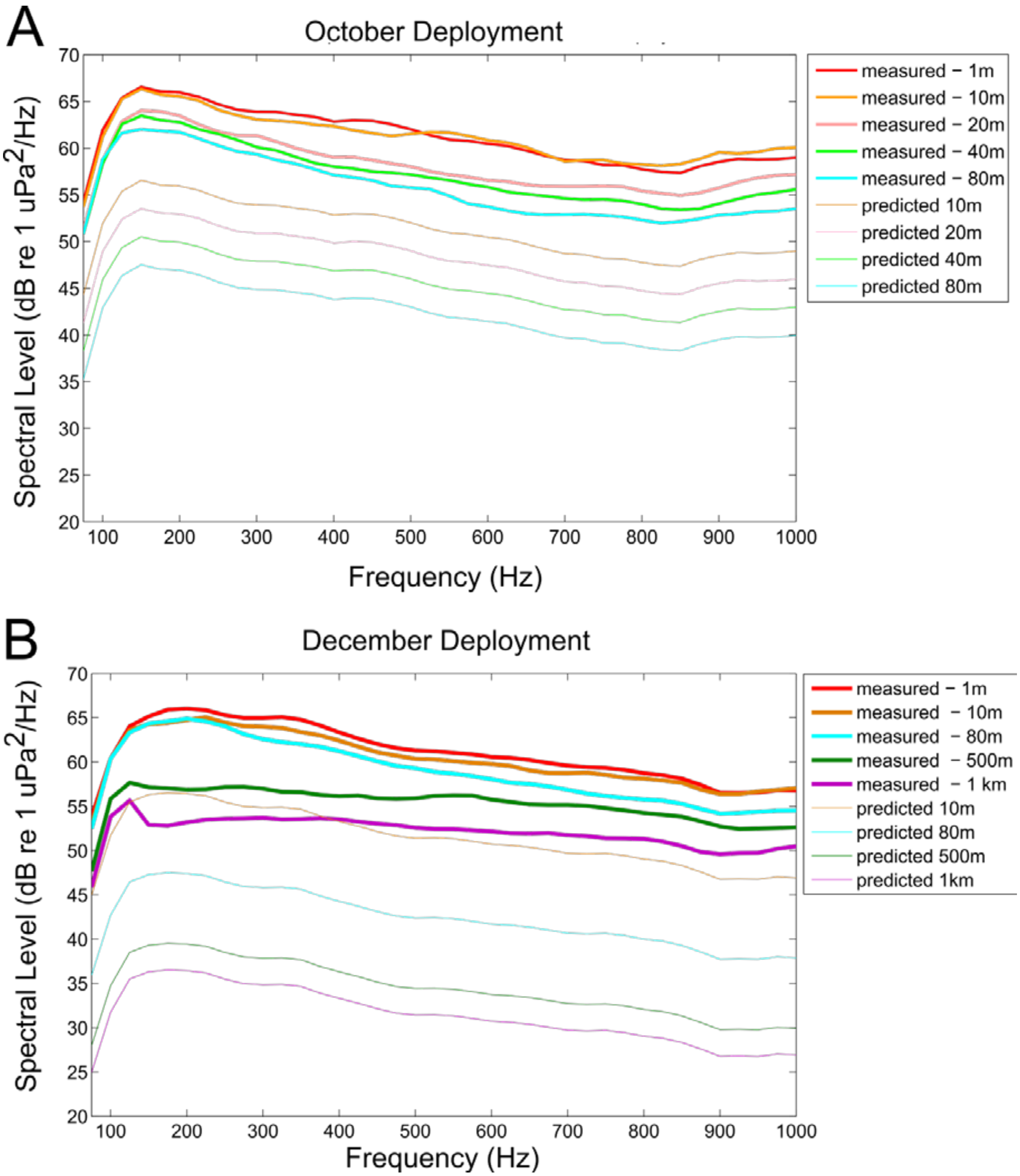


Figure 5.5. Received acoustic pressure with distance from the reef, for the October deployment (A) and December deployment (B). All data refer to pressure measurements on one of the snowflake's X-axis hydrophones. Thin lines represent predicted levels based on cylindrical spreading: 10*log(distance) was subtracted from the source level (measurements at 1 m from the reef) for each frequency. Acoustic pressure decreased with distance, but not to the extent that cylindrical spreading would predict. This is explained by the fact that the reef is not a single point-source, but rather a series of many point-sources.

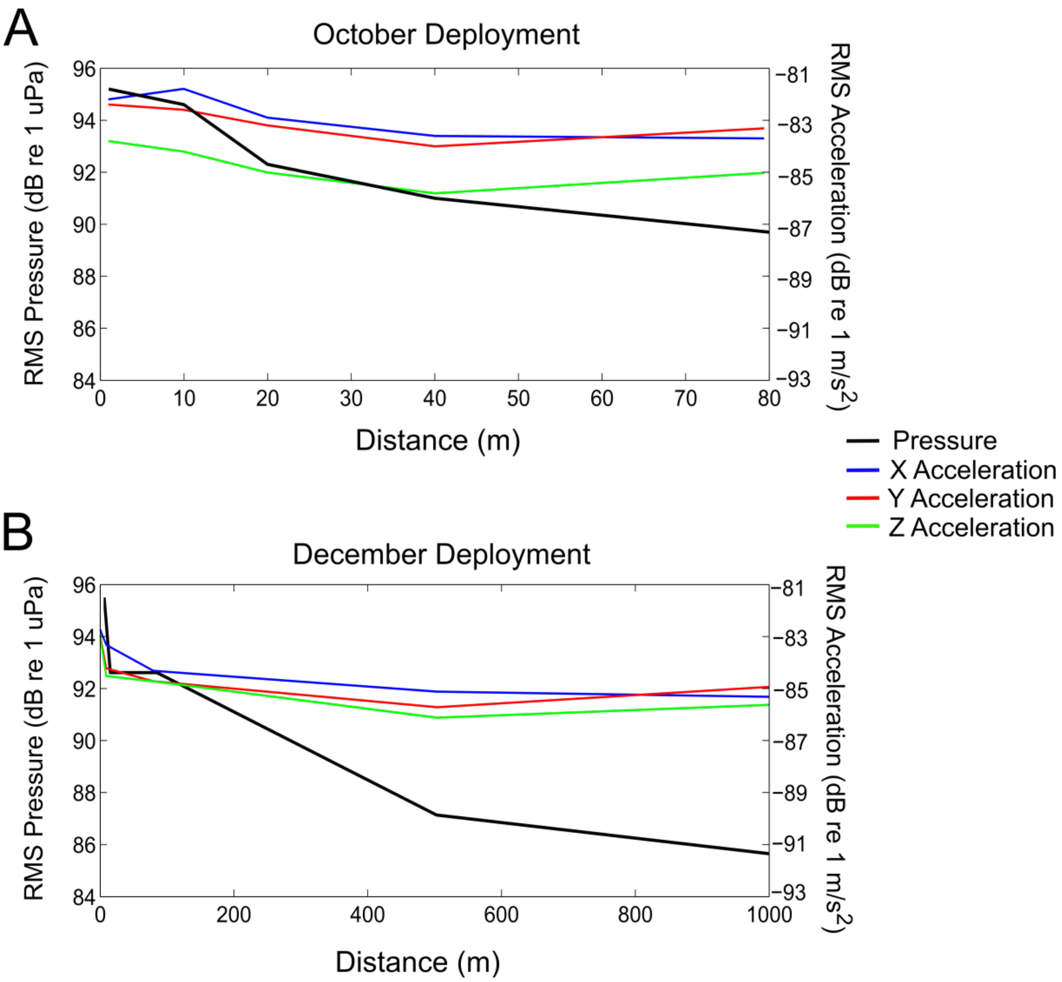


Figure 5.6. Root-Mean-Square (RMS) amplitude of acoustic pressure (left vertical axis) and particle acceleration (right vertical axis) as a function of distance for October (A) and December (B) deployments. All data have been band-pass filtered (70 Hz – 1000 Hz), so the RMS value represents the total amplitude across this frequency band. Pressure dropped off more rapidly with distance than did acceleration, which contradicts theoretical predictions. Acceleration in the X-axis was only slightly higher than in the Y and Z-axes, which means that the sounds emanating from the reef would not provide a clearly directional cue for an acceleration-sensitive organism.

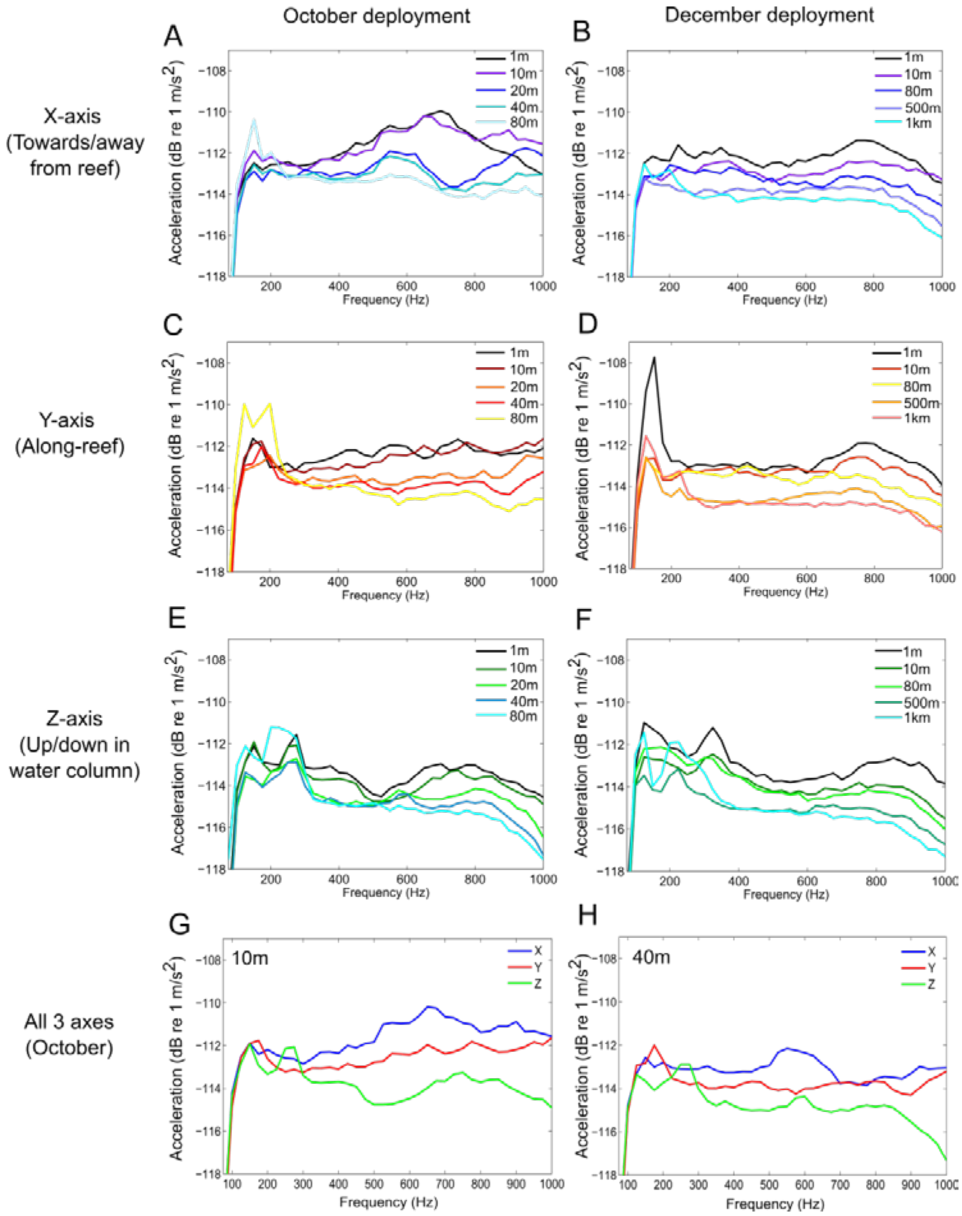


Figure 5.7. Particle acceleration as a function of frequency and distance from the source (A-F). Panels G and H show data from October deployments at 10 m and 40 m distance, to illustrate the patterns across the three axes. While particle acceleration in all three axes generally decreased with distance, these patterns were not consistent across frequencies. For example, in October at 80 m there was an anomaly at < 200 Hz - particularly high acceleration was measured in the Y and Z-axes. At 1 km in December a similar phenomenon occurred – there was higher acceleration at this distance compared to areas closer to the reef. Anomalies at these particular locations, which were not evident at closer distances, suggest local sources of vibration rather than long-distance propagation of the reef's acoustic field. The overall amplitude of acceleration (RMS values) in the X-axis was slightly higher than the other axes (Figure 5.6), but this was not the case for all frequencies (A,B,G,H). These findings demonstrate the complex and unpredictable nature of the particle acceleration field near the reef.

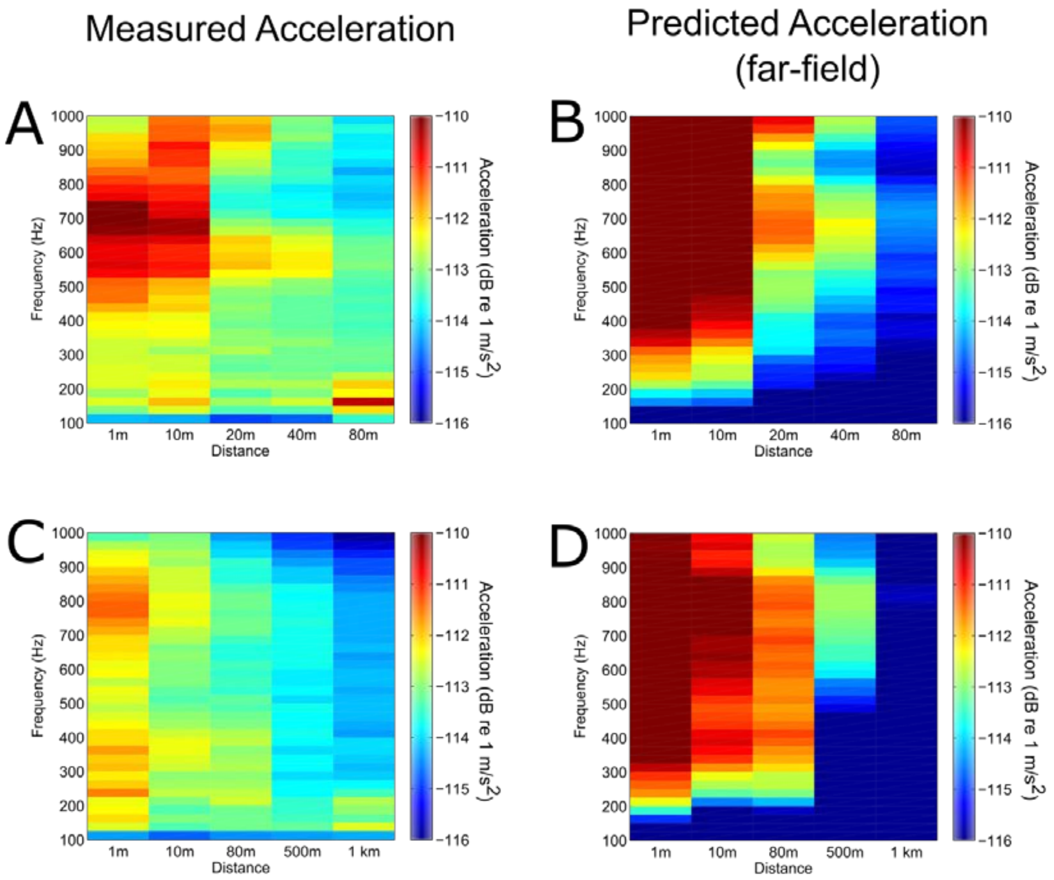


Figure 5.8. Measured and predicted acceleration for the axis facing the reef, from the October deployment (A, B) and December deployment (C, D). Predicted acceleration was derived from the plane-wave equation which used the pressure measured on the X-axis hydrophone closest to the reef, and assumed far-field conditions. Close to the reef, measured acceleration exceeded predicted acceleration in the lowest frequencies, but not in the higher frequencies. At greater distances (500 m, 1 km) measured acceleration was fairly consistent across frequencies and generally exceeded predicted acceleration. This finding implies that there were other local sources of vibration in the sand flat that affected all frequencies.

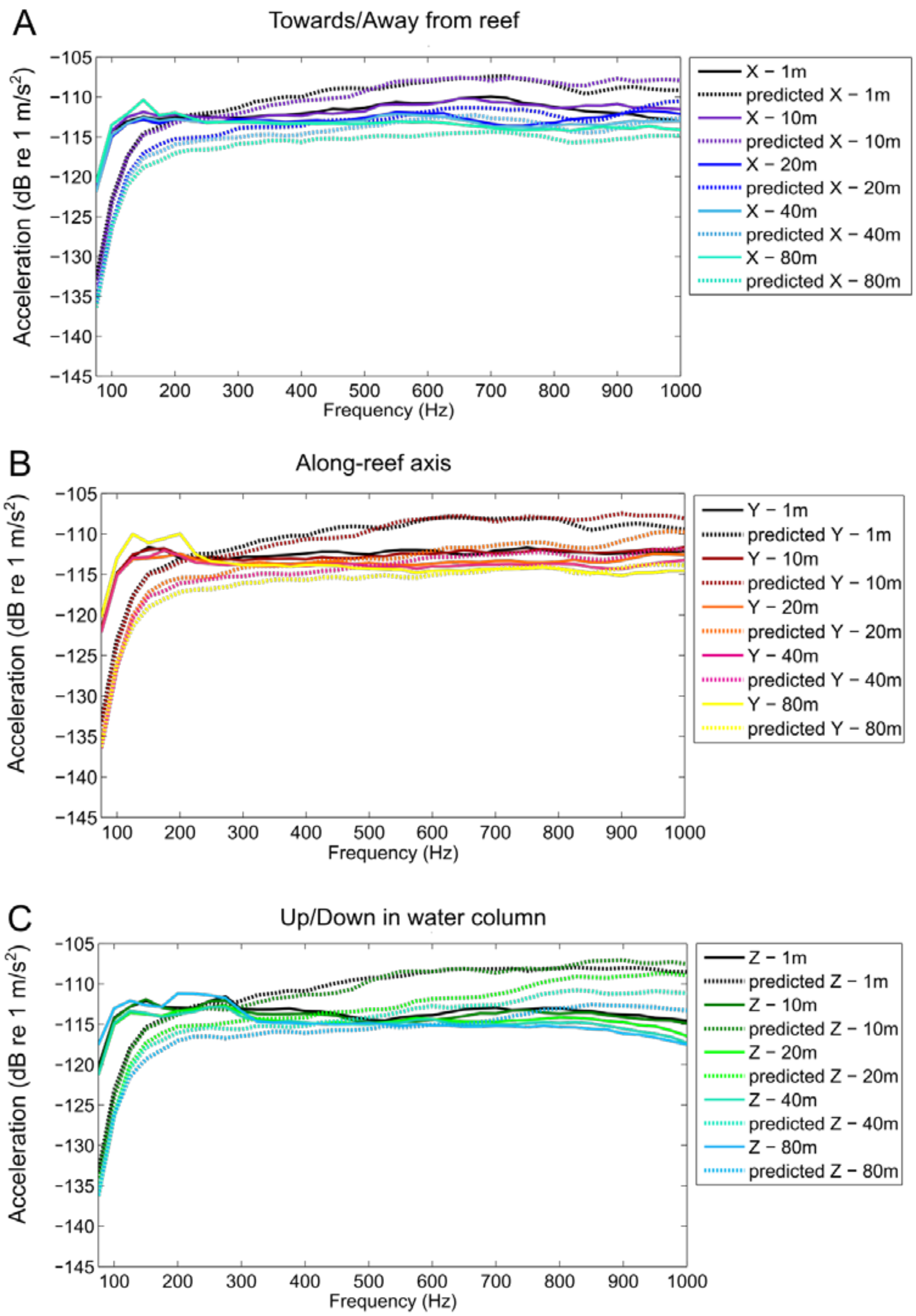


Figure 5.9. Measured (solid lines) and predicted (dashed lines) acceleration from the October deployment. All data have been band-pass filtered at 70 Hz-1000 Hz. Predicted values were generated using the plane-wave equation, assuming far-field conditions. In the lowest frequencies, measured acceleration exceeded predicted acceleration. However, around 200-300 Hz, predicted acceleration began to exceed measured acceleration, suggesting that the snowflake was in the far-field for these frequencies.

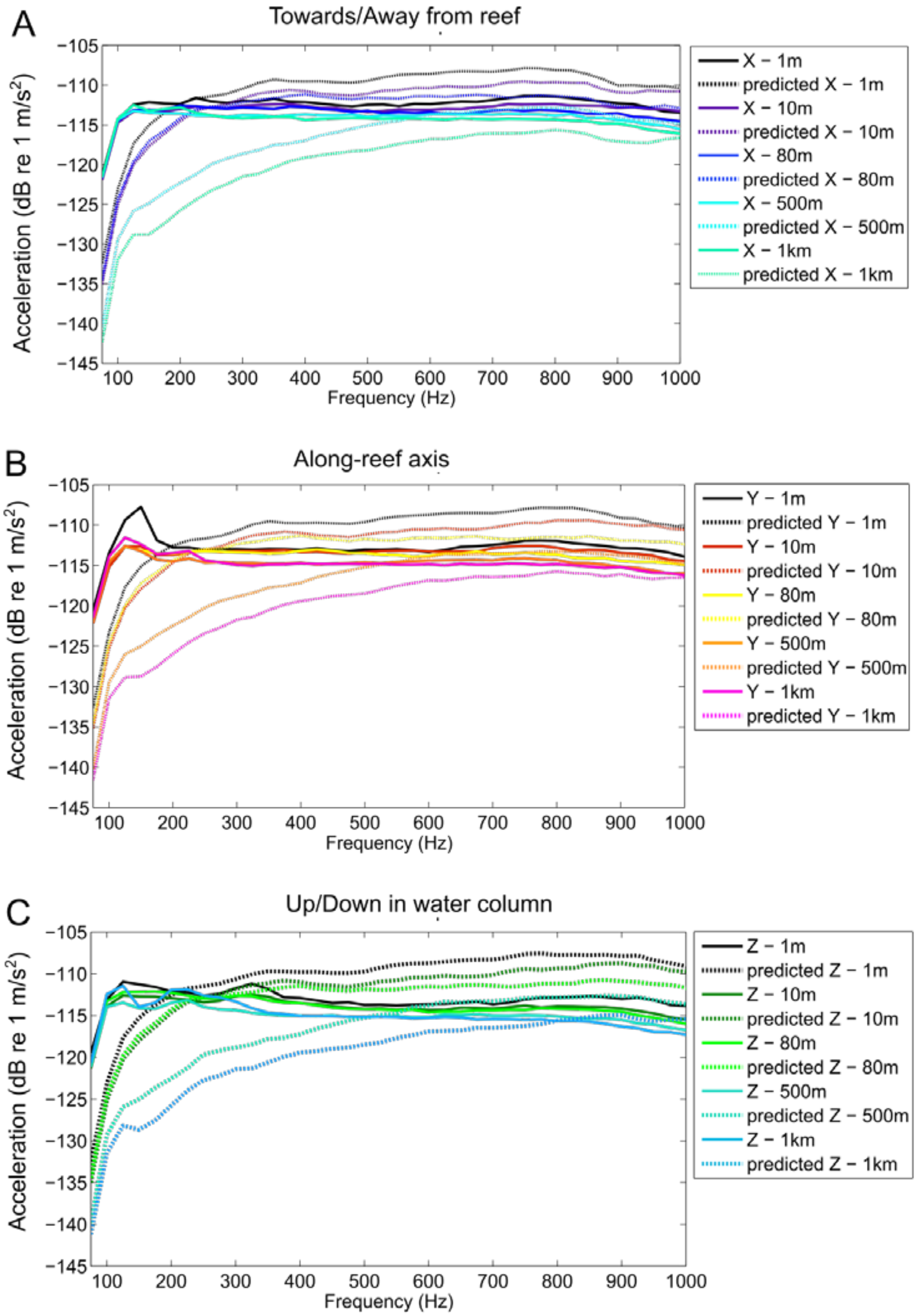


Figure 5.10. Measured (solid lines) and predicted (dashed lines) acceleration for the December Deployment. All data have been band-pass filtered at 70 Hz-1000 Hz. Predicted values were generated using the plane-wave equation, assuming far-field conditions. The greatest differences between measured and predicted acceleration occurred at further distances; predicted acceleration dropped off because of the decrease in pressure, but I was surprised to observe that measured acceleration did not decrease with distance, suggesting additional sources of acceleration near the snowflake during these measurements.

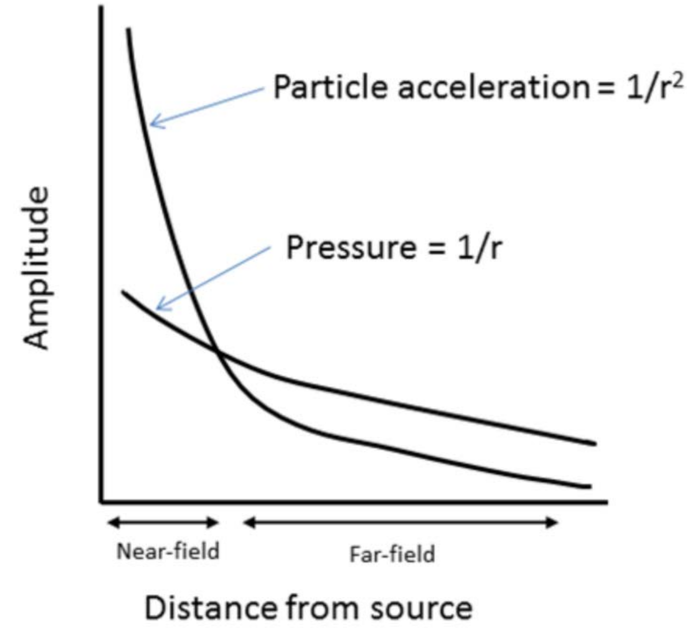


Figure 5.11. Theoretical spreading of particle acceleration and pressure with distance, from a sound generated by a point-source (modified from Schuijf (1975) and Ewing (1989)). Pressure is a scalar quantity that falls off with $1/r$ everywhere in the domain, whereas particle motion is a directional quantity that falls off steeply close to the source (in the "near-field") and falls off with $1/r$ farther from the source (the "far-field, Kalmijn 1988). My results did not conform to these predictions. Particle acceleration and pressure both fell off more gradually than expected, which could be explained by three reasons: 1) the reef is not a point-source but a series of point-sources, 2) there may have been additional sound sources in the sand flat, and 3) the instrument may have been in the far-field for all of the measurements, even close to the reef.

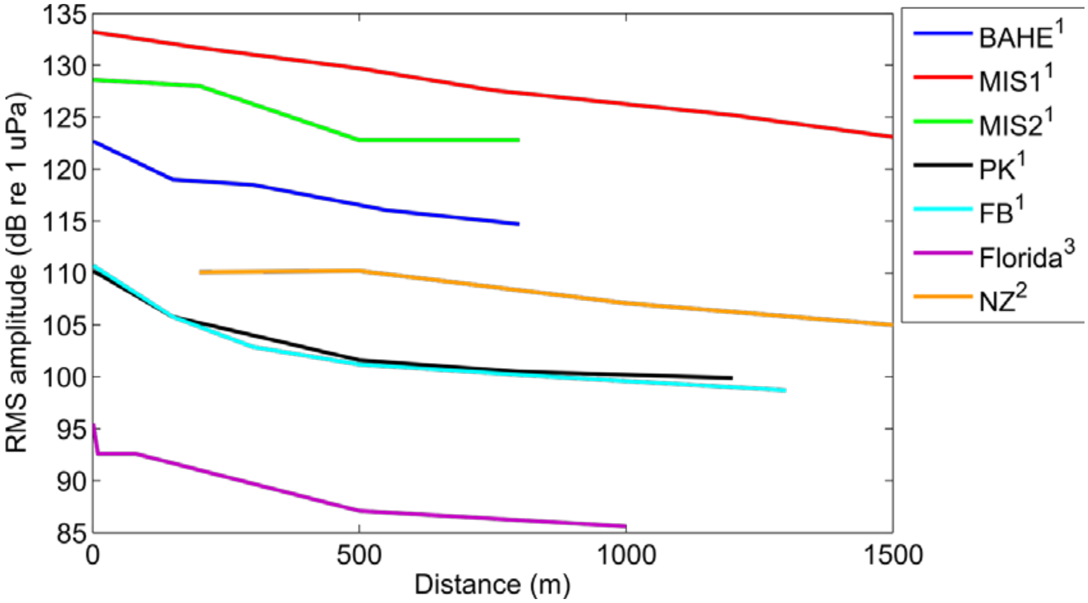


Figure 5.12. Root-Mean-Square (RMS) pressure measured at different distances from several reefs. [1]Data from Piercy et al. (2014), spanning a bandwidth of 100 Hz – 5000 Hz. BAHE, MIS1, and MIS2: reefs in Oman with high coral cover and low fishing density. PK and FB: reefs in Indonesia with moderate coral cover and high diversity of coral and fish. [2]Data from Radford et al. (2011), spanning a bandwidth of 100 Hz – 2500 Hz. NZ: a rocky reef in New Zealand. [3]Data from present study, spanning a bandwidth of 75 Hz - 1000 Hz. Florida: a shallow-water coral reef. The different Y-intercepts result from two factors: the source-level amplitude of the reefs, and the sampling bandwidth. Although these reefs had different source levels, the important trend illustrated here is the similarity of the slopes, which suggests that acoustic pressure propagates in a similar manner from these reefs.

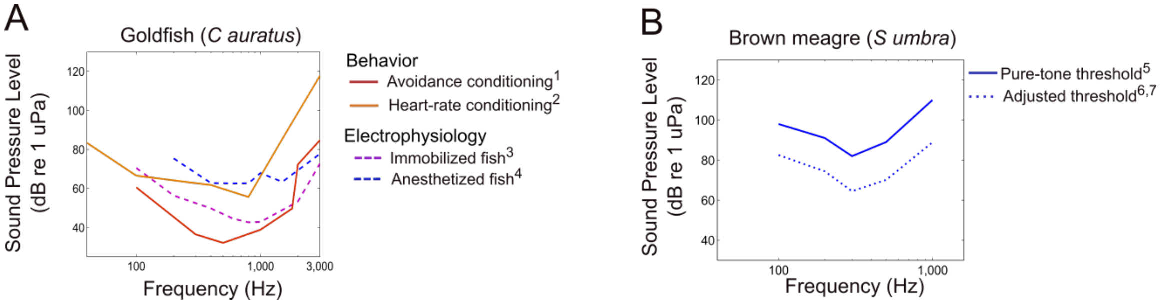


Figure 5.13. A: Pressure-based hearing thresholds for *Carassius auratus*; a very well-studied species in terms of its hearing sensitivity. The audiograms measured with different methods and in different laboratories span a range of nearly 40 dB. B: The pure-tone threshold for *Scianea umbra* and the adjusted threshold. Adjusted thresholds are computed by subtracting 10*log10(CB) from the pure-tone threshold, as in (Glasberg and Moore 1990, Egner and Mann 2005), to account for the fact that wider-bandwidth stimuli are more easily detected than pure-tone stimuli. All audiograms presented in the rest of the thesis are adjusted in this manner. [1](Popper 1971); [2](Offutt 1968); [3](Ladich 1999); [4](Cordova and Braun 2007); [5](Wysocki et al. 2009); [6](Egner and Mann 2005); [7](Glasberg and Moore 1990).

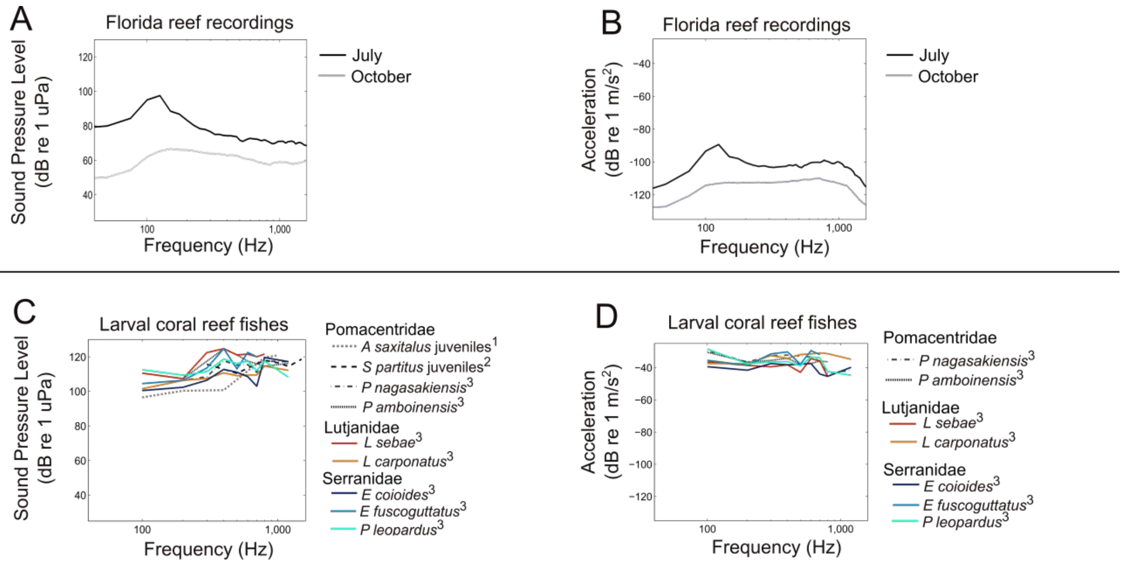


Figure 5.14. Recordings from Florida reefs (top panel) compared to adjusted hearing thresholds (see caption of Figure 5.13) of larval reef fishes (bottom panel). A: Pressure spectra from a Florida reef in July and October. B: Acceleration spectra from October (measured) and July (predicted from plane-wave equation). C: Hearing thresholds in response to acoustic pressure for seven species of settlement-stage fish larvae, plus two species in the juvenile phase. D: Acceleration thresholds for the same seven larval species as in C. The pressure-thresholds (C) generally exceed the pressure-signal from the reef (A), and only overlap when considering a buffer due to sampling methods (Figure 5.13A). Furthermore, the pressure-signal of the reef would only be detectable during new moons in the wet season, and not during the dry season. Acceleration thresholds (D) exceed the ampliudes measured on the reef (B), even after taking into account a sampling buffer (5.13A). This suggests that acceleration-sensitive fish larvae would not be able to detect the acceleration field emanating from the reef. [1](Egner and Mann 2005); [2](Kenyon 1996); [3](Wright et al. 2011) – acceleration derived from pairs of hydrophones, using the Euler equation).

CHAPTER 6: GENERAL CONCLUSIONS

It has been suggested that fish larvae utilize a combination of visual, olfactory, and acoustic cues to find their way to the reef at the end of their pelagic phase (Montgomery et al. 2001, Kingsford et al. 2002, Myrberg and Fuiman 2002, Leis et al. 2011). At least 10 recent experiments have examined the response of reef fish larvae to acoustic cues (Tolimieri et al. 2000, 2004, Leis et al. 2002, Simpson et al. 2004, 2005b, 2005a, 2008, 2010, Leis and Lockett 2005, Holles et al. 2013), yet is still unclear how, where, and when fish larvae are able to detect and orient towards sounds emanating from coral reefs. Using novel methodological approaches, this dissertation aimed to resolve critical knowledge gaps in this field.

This body of work represents a contribution to the field of acoustic ecology and broadens our understanding of the potential role of acoustic cues in the lives of larval fishes. I found that orientation behavior, especially early in ontogeny and from larger distances, would have substantial impacts on the settlement success of fish larvae (Staaterman et al. 2012). This finding suggests that early orientation is critical to the survival of fish larvae, which must be active agents of their own dispersal (Leis 2006). But is it possible that larvae orient in response to acoustic cues? Long-term acoustic recordings of reefs revealed high soundscape variability over daily, lunar, and seasonal time-scales (Staaterman et al. 2014a). The highest amplitudes coincide with the time when most fishes spawn, and their larvae seek settlement habitat. Both acoustic pressure and particle acceleration diminish gradually with distance from the reef, but the amplitude of the particle acceleration signal appears to be lower than the detection thresholds of most larval reef fishes. This finding, together with my behavioral experiment, contradicts previous work demonstrating an “attraction” to reef sounds (e.g., Simpson et al. 2005a).

Coral reef soundscapes from different places and times

The coral reefs in the Northern Florida Keys have lower-amplitude soundscapes than those from the Pacific Ocean (Figure 6.1). Even at the loudest time of year (new moons of the wet season), only the very lowest frequencies exceed amplitudes from Pacific reefs, and these low-frequency sounds are largely attributed to a particularly vocal fish (Staaterman et al. 2014a). Interestingly, the Bahamas reef soundscape is also low in amplitude (Figure 6.1), which may be indicative of a wider trend for Caribbean vs. Pacific reefs. These differences could be attributed to different species guilds, some of which may be more soniferous than others, or due to the overall health and/or biodiversity of the reefs. While reefs in both regions have been overfished, the *Diadema* die-off in the Caribbean had devastating consequences for reef health (Lessios 1988). More work is needed across broad geographic scales to properly explain these results. When comparing reef soundscapes to ambient noise levels expected at different sea states (Wenz 1962), it appears that even on the windiest days, reef sounds in the Pacific still exceed wind-generated noise. In contrast, wind-generated noise has the potential to mask the sounds of Caribbean reefs, potentially limiting the intervals when biological sounds are detectable (Figure 6.1; Wenz 1962, Staaterman et al. 2014a).

One important point to consider is that while the amplitude of the soundscape determines its detectability, the loudest reef may not be the “most attractive” reef. For example, Pickles Reef has lower amplitudes - but higher acoustic complexity - than Sand

Island Reef, indicating that acoustic complexity and amplitude are not necessarily coupled (Staaterman et al. 2014a). Furthermore, each reef seems to have a distinct “acoustic signature.” Sand Island Reef has a spectral peak at <100 Hz, whereas the reef in Panama has a peak around 400 Hz, and one of the reefs in Australia has a peak around 800 Hz (Figure 6.1 and references therein). These spectral peaks are likely due to the sounds of different fishes, which produce sounds with dominant frequencies below 1000 Hz. It is possible that certain organisms listen for distinct spectral peaks, rather than the overall amplitude, in order to move towards areas with conspecifics, or away from areas with predators. Indeed, one previous experiment found differential responses from fish larvae when exposed to parsed-out components of the reef spectrum (Simpson et al. 2008), and another study found that juvenile fishes responded differently to sounds recorded in different habitats (Radford et al. 2011a). This is a very new line of research, and future work is needed to determine which, if any, frequencies are the most “attractive”.

Comparison to previous studies

To put these results into context, I would like to comment on some similarities and differences compared to previous work in this field. The majority of previous studies did not include a spectrum of the played-back sound (i.e. what came out of the speakers). Underwater speakers are notorious for distorting sound quality, so instead authors typically report the received RMS Sound Pressure Level, which sums the amplitude across a particular frequency band (Urick 1983). In some cases, a spectrum of the sound file that was put into the speaker system was reported instead. In Chapter 4, I used the highest-quality speakers on the market (Clark Synthesis), and applied an adaptive filter to compensate for speaker distortion. Yet the spectral quality of the sounds that the speakers produced were quite different from what I had recorded on the reefs (Figure 6.2C). I urge other investigators to use caution in future attempts at underwater playback experiments, and to report the received spectrum (as in Stanley et al. 2011, Lillis et al. 2013), even if it is distorted. The best I can do to compare my work to those of others is to calculate the RMS pressure using matching filter parameters (Figure 6.3). Upon doing so, it is apparent that the playback amplitudes for acoustic pressure used in Chapter 4 fall within the range of what has been recorded on real reefs. Leis and Lockett (2005) used lower amplitudes than I did, and found a mixed response across several pomacentrids, which may indicate that their playback amplitudes were just at the edge of hearing thresholds. Simpson et al. (2005, 2008, 2010) used significantly higher amplitudes, and generally found positive responses to reef sounds. Additionally, Vermeij et al. (2010) placed coral planulae in a choice-chamber while broadcasting high-amplitude sounds and also found an “attraction” to the sounds. These amplitudes were much higher than what fish or planulae larvae would encounter on a real reef, and thus are not very realistic. The fact that I did not see a clear attraction to reef sounds in Chapter 4 when played at ambient levels may be partially explained by the spectral quality (Figure 6.2C), and partially explained by the fact that I used lower amplitudes than those in other studies (Figure 6.3 and references therein).

It is critical to report the acoustic spectrum, rather than just the RMS amplitude across frequencies, because fish hearing tests identify the amplitudes required to elicit responses at particular frequencies. Furthermore, without reporting the spectrum, it is impossible to know the sound field produced by the speakers, and we saw in Chapter 4 (Figure 4.4) that it was not very directional. To determine whether an organism can hear a given signal, one can compare their hearing sensitivity (the laboratory-based audiogram) with the spectrum of the signal (e.g., Figure 5.14; Myrberg 1980, Wysocki and Ladich 2001, Egner and Mann 2005, Lugli and Fine 2007). An important caveat is that results from laboratory-based hearing tests tend vary widely, even for the same species (Figure 5.13A), so a “sampling buffer” can be considered to account for this variability. But generally speaking, at frequencies where the audiogram lies below the signal, the signal should be detectable. For example, I can compare the received pressure spectra from my playback experiment with adjusted hearing thresholds of several fish species (Figure 6.2). Although there is no published audiogram for larval or adult Apogonidae or Acanthuridae, it appears that the sound pressure levels (Figure 6.2C) used in my experiments could have been detectable by other adult reef fishes (Figure 6.2G), but may have been just on the edge of detection for larval reef fishes (Figure 6.E). This example demonstrates the importance of measuring and reporting acoustic spectra during playback experiments in order to understand whether the signal is detectable by a particular species.

Another major shortcoming of previous experiments is the failure to consider particle acceleration as the relevant cue. Hearing tests are now focusing on this stimulus, and there has been discussion about the need to conduct such measurements (Ladich and Fay 2013). To my knowledge, however, this is the first study that measured acceleration during acoustic playback experiments together with the acceleration field near a real reef. Some authors have estimated the acceleration field in order to compare it to fish hearing thresholds (Mann et al. 2007, Radford et al. 2011), but Chapter 5 demonstrates that the actual acceleration does not necessarily match the predicted acceleration. When I compare the field-based measurements (Figure 6.2B) and playback levels (Figure 6.2D) to one another and to acceleration-based audiograms (Figure 6.2F, H, J), it is apparent that the majority of reef fish larvae would be unable to detect the particle acceleration generated by the speakers in Chapter 4, despite the fact that the behavioral chamber was very close to the speakers. Based on the lack of response of Acanthridae larvae in the playback experiment and the high thresholds of other reef fish larvae (Figure 6.2F), it seems possible that Acanthuridae larvae could not detect the signal from the speakers. The non-directional response observed for Apogonidae larvae may be explained by the fact the acceleration field from the speakers was not clearly directional along the speaker-axis (Figure 4.4), or by the fact that the acceleration levels may have been just at the edge of the detection threshold for Apogonidae. It would be difficult to properly interpret the results from Chapter 4 without measuring the output from the speakers. For other experiments using choice-chambers, patch-reefs, or light-traps, investigators should measure and report the acoustic field generated by the speakers.

Hearing sensitivity throughout ontogeny and across habitats

Hearing sensitivity is highly variable throughout ontogeny and among species (Myrberg and Fuiman 2002, Wright et al. 2011, Ladich and Fay 2013). Lu and DeSmidt (Lu and Desmidt 2013) found that zebrafish embryos are sensitive to particle motion at 2 days post-fertilization and hatch with functional ears, and auditory sensitivity continues to improve throughout ontogeny (Figure 6.2; Kenyon 1996, Fuiman et al. 2004, Egner and Mann 2005, Simpson et al. 2005b, Wright et al. 2005, 2011, Sisneros and Bass 2005). For species that do not have specializations for detecting acoustic pressure, hearing sensitivity increases gradually with the proliferation of hair cells (Kenyon 1996, Fuiman et al. 2004, Wright et al. 2011, Lu and Desmidt 2013). For species that are pressure-sensitive, the development of the Weberian apparatus (Higgs 2003) or the auditory bullae (Fuiman 2004) occurs later in the larval period, and leads to a major increase in hearing sensitivity. Indeed, in Figure 6.2 we can see that while some adult reef fishes may be able to detect the pressure-signal of the reef, their less-sensitive larvae probably cannot. Because of this ontogenetic shift, it is critical to continue auditory tests with settlement-stage reef fishes – especially in response to particle acceleration – in order to understand whether soundscapes from other regions and habitats would be detectable and thus could effectively serve as orientation cues.

Ladich (2013) suggests that fishes have a wide range of hearing sensitivities precisely because they inhabit a wide range of habitats and thus encounter a range of ambient noise levels and spectra. His review (Ladich 2013) highlights what was put forth by Myrberg (1980) – the notion that animals living in quieter environments have more sensitive hearing than those living in noisy environments. A comparison of hearing sensitivity in adult coral reef fishes (Figure 6.2G-H) to adult estuarine fishes (Figure 6.2I-J) supports this hypothesis. A classical problem in any auditory system is the ability to extract a signal from noise (Bradbury and Vehrencamp 1998). The relatively high ambient noise in the ocean may explain why acoustic communication for most marine fishes is limited to the near-field (e.g., 15 m for a 100-Hz monopole signal, Lugli and Fine 2007). In a habitat like a coral reef, would it be evolutionarily favorable to have high hearing sensitivity, allowing for the detection of background reef "noise," when relevant "signals" come from nearby mates, predators, or food sources? Indeed, Mann and Lobel (1997) found that courtship sounds produced by reef-dwelling damselfish are only detectable up to 12 m from the source. Thus, it is expected that auditory thresholds for any given species lie just on the cusp of their habitat's background noise (Ladich 2013). Despite wide variability across species, this trend is evident for adult coral reef fishes (Figure 6.2G) and the sounds of the reefs in Florida (Figure 6.2A). Taken together, these findings prompt the question: if adult reef fishes can only detect nearby sound sources, why would we expect their larvae to be capable of acoustic orientation from a great distance?

Can Florida's reef soundscapes serve as an orientation cue for larval fishes?

My findings on reef soundscapes (Chapter 3), their propagation (Chapter 5), and larval orientation in response to an acoustic signal (Chapter 4) suggest that, in order for an organism to orient towards Florida reefs using acoustic cues, certain criteria would have to be satisfied:

- It would only be possible for a pressure-sensitive organism with thresholds at or below 85-95 dB re 1 μPa at 100-200 Hz, because this is the highest peak of the reef soundscape at Sand Island (Figure 6.2A). *Amphiprion clarkii, Epinephelus guttatus,* and *Haemulon scurius* adults (Figure 6.2G) meet these criteria. In order to "orient" towards the reef, these fishes would have to sample the acoustic field, since pressure is a non-directional quantity.

- Detection would also be possible for an acceleration-sensitive organism with thresholds at or below -105 to -90 dB re 1 m/s^2 at 100-200 Hz (such as *Sciaenia ocellatus* adults, Figure 6.2J). However, the acceleration field is not clearly directional, so it would still be difficult for an organism to "find its way" to a reef using acoustic cues alone.
- These criteria are relevant for new moons in the wet season, and the organism must be fairly close to the reef in order to experience these amplitudes. At a quieter time of year or farther from the reef, hearing thresholds would have to be even lower than listed above for detection to be possible.

Given these criteria, and our limited knowledge of auditory thresholds in coral reef fish larvae, it is difficult to draw broad conclusions across all species. However, Ladich and Fay (2013) state that, generally speaking, fishes that lack specializations to detect pressure have thresholds between -90 and -70 dB re 1 m/s^2 for frequencies between 100-1000 Hz. This generalization, plus fact that hearing in larvae is typically less sensitive than that of adults, suggests that the majority of fish larvae probably cannot detect acoustic cues from Florida reefs, let alone orient towards the reef using acoustic cues. It is possible that a combination of environmental signals are used at once, which could decrease the levels required for detection – a research avenue that merits further exploration. Note that these findings may not be consistent across all reefs or all parts of the water column. The louder reefs in the Pacific Ocean (Figure 6.1), for example, may have more overlap with larval (and adult) fish hearing thresholds, and the acceleration field may be more directional than it is in Florida – a question that warrants further investigation. Finally, a provocative question is whether acoustic signals may have played a more major role in historic conditions in Florida. With higher coral and fish diversity, acoustic signals should have higher amplitudes and complexity (Piercy et al. 2014), possibly to a point where the reef soundscape could have served as a reliable orientation cue.

General reflections on this work

Looking back on the process of my dissertation research, there are a few things I would have done differently. Most notably, I would have conducted the propagation experiment (Chapter 5) prior to the behavioral work (Chapter 4) – perhaps concurrently with the acoustic time-series (Chapter 3) – because it would have revealed the very low-amplitude particle acceleration field of the reef in Florida. I also would have liked to make propagation measurements throughout the summer months, as I had originally planned. The propagation work required the snowflake instrument, which was developed separately (through a project funded by NSF-OTIC #1155698 to C. Paris and D. Mann) and was not available until later in 2014. With the knowledge that fish larvae likely cannot detect the reef's particle acceleration field, I may have re-designed the behavioral experiment (Chapter 4) or perhaps focused my efforts on laboratory-based tests of hearing thresholds instead. Detection thresholds, especially in terms of particle acceleration, have only been described for a handful of reef fish larvae (Wright et al. 2011). This is an important piece of the puzzle, and more research is critically needed. It also would have been interesting to increase the spatial coverage of measurements of acoustic pressure and particle acceleration, perhaps creating an "acoustic map" of a focal reef (e.g., Freeman et al. 2014) to better understand how animals living within its vicinity could detect and utilize acoustic signals. This type of information would be relevant not only for larval organisms, but also for adult fishes living on the reef. Finally, I would recommend new parameterization of the biophysical model to simulate “attraction” from the reef at much smaller distances or in response to additional cues. For example, spectral quality or acoustic complexity could be represented by cue strength k, and a combination of the soundscape’s amplitude and the hearing abilities of the species of interest could be represented by the detection distance, β. It would be interesting to simulate potential changes in the “attractiveness” of the reef over time (e.g. historical vs. current conditions, or dry season vs. wet season).

Additional applications

I set out determine the role of coral reef soundscapes in the orientation behavior of larval fish, and I found that acoustic cues alone would not be sufficient for larvae to find the reef. Although the reef soundscapes may not be as important as predicted for larval fishes in Florida, it is possible that other pressure-sensitive organisms rely on these cues to navigate or simply to orient themselves to their surroundings (i.e. “auditory scene analysis,” Bregman 1990). Marine mammals, for example, could use these soundscapes to find their way as they migrate along coastlines.

Soundscapes provide essential information not only for animals, but also for humans that wish to study particular habitats. There is a push in the soundscape ecology community to use acoustic measurements as a proxy for biodiversity and/or species abundance (Sueur et al. 2008, Gasc et al. 2013a, Towsey et al. 2014), but for the most part this work has been limited to terrestrial environments. Measurements of soundscapes can also help investigators understand environmental changes over time, or differences between sites. Finally, given the continued degradation of the marine environment, combined with the rise of anthropogenic noise in our oceans, soundscape data can quantify human-impacts in certain marine areas. Thus, the data collected here can be used for multiple purposes, and can provide critical baseline data in the face of our changing oceans.

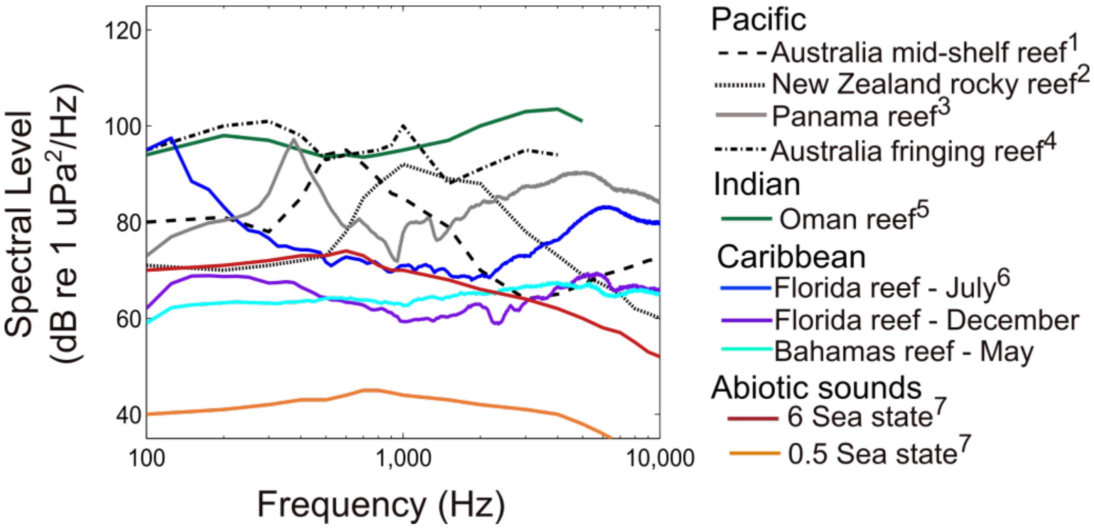
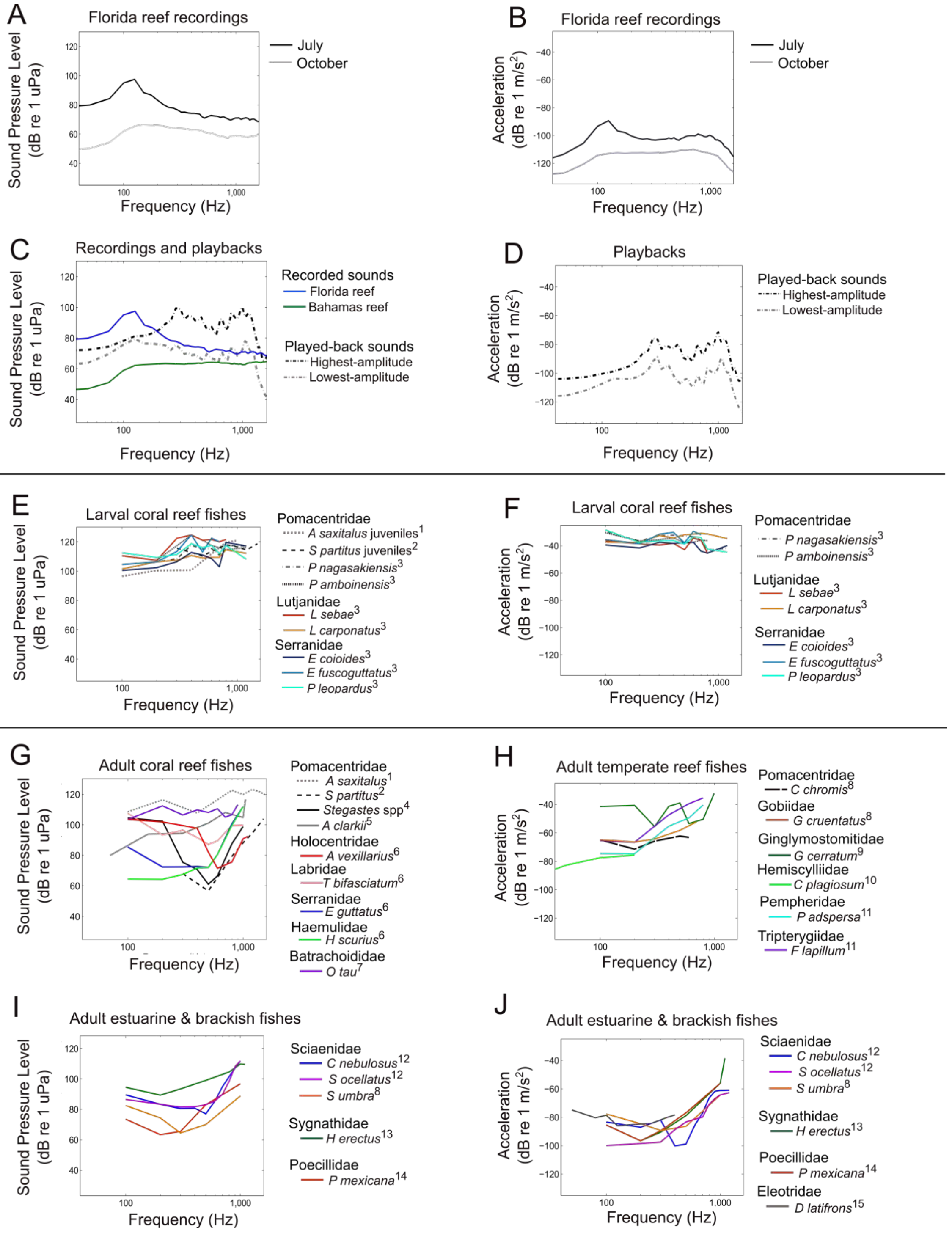


Figure 6.1. Pressure spectra from reef soundscapes recorded in the Caribbean Sea, compared to reefs in the Pacific Ocean, the Indian Ocean, and wind-generated sounds. In general, Caribbean reefs had lower-amplitude soundscapes than Pacific and Indian Ocean reefs, which may be indicative of a larger regional trend, such as differences in species guilds or overall reef health and biodiversity. During calm surface conditions, Caribbean reef sounds exceed wind-generated ocean noise, but on windy days, the sounds of the reefs may be masked. [1]Feather reef in the Great Barrier Reef – Simpson et al. (2008), same spectrum also included in Tolimieri et al. (2004), Simpson et al. (2004); [2]Macroalgae-dominated rocky reef – Stanley et al. (2011); [3]*Pocillopera*-dominated reef in Pacific Panama – from Staaterman et al. 2013; [4]Lizard Island's fringing reef in the Great Barrier Reef – Radford et al. 2011; [5]*Pocillopora*-dominated coral reef in Oman –Piercy et al. 2014; [6]Sand Island Reef in the Northern Florida Keys – from Staaterman et al. 2014 (Chapter 3); [7]Ambient ocean noise based on sea state – From Wenz 1962. Unpublished data include recordings from shallow patch-reefs in Florida (Chapter 5) and in the Bahamas (Chapter 4).

Figure 6.2. Spectra from recordings made on Florida reefs, playbacks from underwater speakers, and hearing thresholds for larval and adult fishes.
A: Pressure spectra from a Florida reef and July and October (Staaterman et al. 2014a).
B: Acceleration spectra from October (measured) and July (predicted from plane-wave equation).
C: Pressure spectra from sound files that were input into underwater speakers (recordings from a Florida reef and a Bahamas reef) compared to the speaker output in the Chapter 4. "Highest amplitude" represents what was recorded closest to the speaker when the playback levels were highest (e.g. hydrophone "A" in Figure 4.1 while sounds were played from the left speaker). "Lowest amplitude" represents what was recorded farthest from the speaker when playback levels were lowest (e.g. hydrophone "A" in Figure 4.1 while sounds were played from the right speaker). Although the amplitude of the sounds fell within the range of what was recorded on real reefs throughout the world (Figure 6.1), here it is apparent that the speakers did not reproduce similarly-shaped spectra to what was recorded on these reefs. Reporting the spectra is necessary to understand the distortion caused by the speakers. This distortion may explain why the fish larvae did not react in a way that we predicted – they did not orient towards or away from the speakers.
D: Acceleration spectra along the speaker axis during the Chapter 4 experiment, for the highest and lowest-amplitude sounds that were played. Again, it is apparent that the acceleration field produced by the speakers was not similar in shape to what was recorded on a real reef (B).
E: Hearing thresholds in response to acoustic pressure for seven species of settlement-stage fish larvae, plus thresholds for two species during the juvenile phase.
F: Acceleration thresholds for the same seven larval species as in E. Both pressure-based and acceleration-based thresholds reveal that coral reef fish larvae likely cannot detect the reef soundscapes recorded in Florida (A & B), and may not have been able to detect the playbacks from the speakers in Chapter 4 (C &D).
G-I: Hearing thresholds for adult fishes living in coral reefs (G), temperate/rocky reefs (H), and brackish/estuarine environments (I-J). Generally speaking, estuarine/brackish fishes have more sensitive hearing than do reef-associated species, likely because they live in quieter environments (Ladich 2013, Ladich and Fay 2013). Hearing thresholds of coral reef fishes (G) lie just at the edge of the background noise in their habitat (A).
[1](Egner and Mann 2005); [2](Kenyon 1996); [3](Wright et al. 2011) – acceleration derived from pairs of hydrophones, using the Euler equation); [4](Myrberg and Spires 1980); [5](Parmentier et al. 2009); [6](Tavolga and Wodinsky 1963); [7](Yan et al. 2000); [9](Casper and Mann 2006) - acceleration measured with pressure-velocity probe; [10](Casper and Mann 2007) – acceleration produced via shaker table and measured with accelerometers; [11](Radford et al. 2012) – acceleration produced via shaker table and measured with accelerometers; [12](Horodysky et al. 2008) – acceleration measured with a pressure-velocity probe; [13](Anderson and Mann 2011) – acceleration measured with a geophone; [14](Schulz-Mirbach et al. 2010) – accleration measured with a pressure-acceleration sensor; [15](Lu et al. 2010) - acceleration produced via shaker table and measured with accelerometers.


A
Florida reef recordings
Sound Pressure Level (dB re 1 uPa)
Frequency (Hz)
July
October
B
Florida reef recordings
Acceleration (dB re 1 m/s²)
Frequency (Hz)
July
October
C
Recordings and playbacks
Sound Pressure Level (dB re 1 uPa)
Frequency (Hz)
Recorded sounds
Florida reef
Bahamas reef
Played-back sounds
Highest-amplitude
Lowest-amplitude
D
Playbacks
Acceleration (dB re 1 m/s²)
Frequency (Hz)
Played-back sounds
Highest-amplitude
Lowest-amplitude
E
Larval coral reef fishes
Sound Pressure Level (dB re 1 uPa)
Frequency (Hz)
Pomacentridae
A saxitalus juveniles¹
S partitus juveniles²
P nagasakiensis³
P amboinensis³
Lutjanidae
L sebae³
L carponatus³
Serranidae
E coioides³
E fuscoguttatus³
P leopardus³
F
Larval coral reef fishes
Acceleration (dB re 1 m/s²)
Frequency (Hz)
Pomacentridae
P nagasakiensis³
P amboinensis³
Lutjanidae
L sebae³
L carponatus³
Serranidae
E coioides³
E fuscoguttatus³
P leopardus³
G
Adult coral reef fishes
Sound Pressure Level (dB re 1 uPa)
Frequency (Hz)
Pomacentridae
A saxitalus¹
S partitus²
Stegastes spp⁴
A clarkii⁵
Holocentridae
A vexillarius⁶
Labridae
T bifasciatum⁶
Serranidae
E guttatus⁶
Haemulidae
H scurius⁶
Batrachoididae
O tau⁷
H
Adult temperate reef fishes
Acceleration (dB re 1 m/s²)
Frequency (Hz)
Pomacentridae
C chromis⁸
Gobiidae
G cruentatus⁸
Ginglymostomitidae
G cerratum⁹
Hemiscylliidae
C plagiosum¹⁰
Pempheridae
P adspersa¹¹
Tripterygiidae
F lapillum¹¹
I
Adult estuarine & brackish fishes
Sound Pressure Level (dB re 1 uPa)
Frequency (Hz)
Sciaenidae
C nebulosus¹²
S ocellatus¹²
S umbra⁸
Sygnathidae
H erectus¹³
Poecillidae
P mexicana¹⁴
J
Adult estuarine & brackish fishes
Acceleration (dB re 1 m/s²)
Frequency (Hz)
Sciaenidae
C nebulosus¹²
S ocellatus¹²
S umbra⁸
Sygnathidae
H erectus¹³
Poecillidae
P mexicana¹⁴
Eleotridae
D latifrons¹⁵
120
100
80
60
40
−40
−60
−80
−100
−120
100
1,000

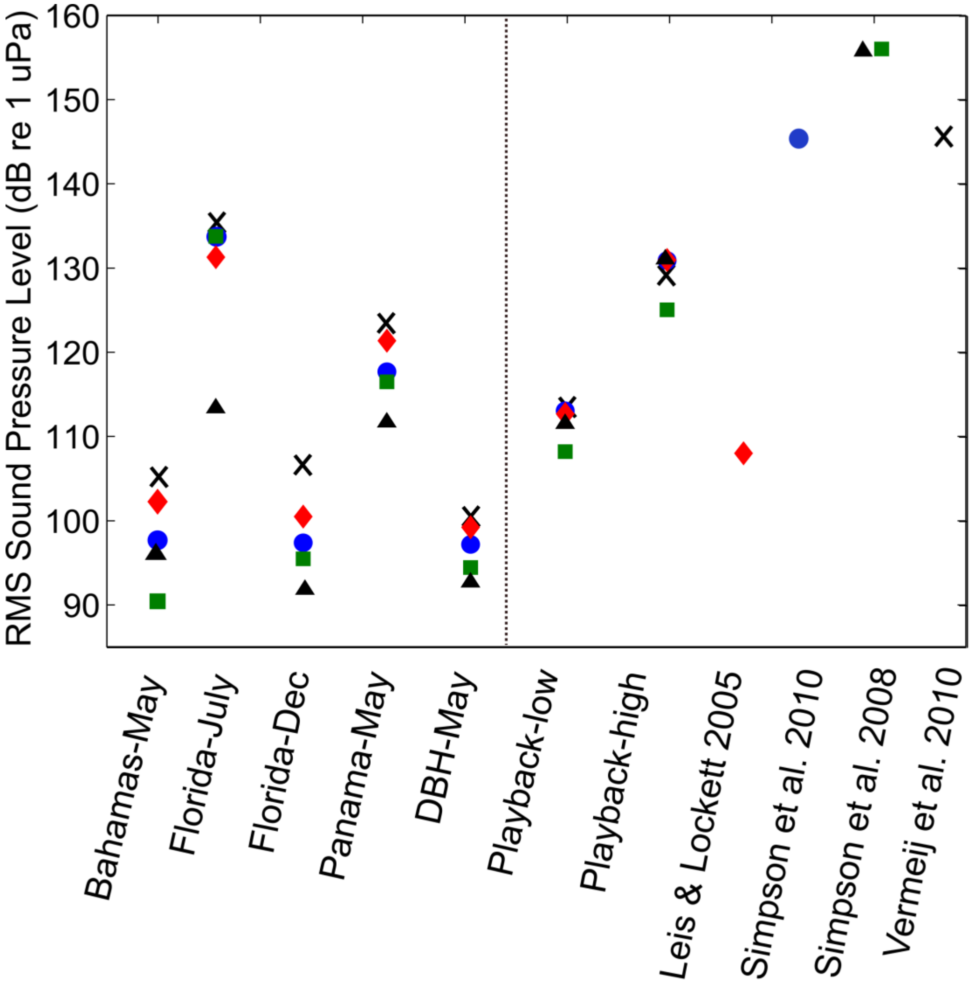


Figure 6.3. Sound pressure levels from recordings of coral reefs made throughout this dissertation (left panel), compared to experimental playback levels (right panel) used during the *in situ* experiment in Chapter 4 ("playback-low" and "playback-high"), as well as four other playback experiments from the literature. Here I have filtered the data to follow the filtering procedures used in the previously published works. For example, red diamonds are comparable, because all data have been bandpass filtered at 80 Hz-4 kHz, following Leis and Lockett (2005). Blue circles: bandpass filter at 0-2 kHz, as in Simpson et al. (2010). Green squares: bandpass filter at 0-570 Hz, as in Simpson et al. (2008). Black triangles: bandpass filter at 570-2000 Hz, as in Simpson et al. (2008). Black crosses: bandpass filter at 10-10000 Hz, as in Vermeij et al (2010). The playback amplitudes used in Chapter 4 fall within the range of what has been recorded on different reefs. In Simpson et al. (2008), the authors used very high-amplitude sounds and caught significantly more Apogonidae larvae in noisy light-traps compared to silent traps, but when I used lower-amplitude sounds in Chapter 4, I did not observe an "attraction" to reef sounds in Apogonidae. Leis and Lockett (2005) used lower-amplitude sounds and found different responses across Pomacentridae species, which suggests that the playback levels were just at the edge of their hearing thresholds.

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APPENDIX

Table A1. Results from an ANCOVA with low band level as the dependent variable, and offshore wind, season, moon phase, and site as independent variables. Interactions are depicted with a *. After accounting for wind, there were significant differences between site, season, and moon phase, and significant interactions between site and season, as well as site and moon phase.

Source	dF	SS	MS	F	p
Offshore	1	91831	91831	4696.1	<0.001
Season	1	5840	5840	298.6	<0.001
Moonphase	2	12838	6419	328.3	<0.001
Site	1	5467	5467	279.5	<0.001
Offshore*season	1	3784	3784	193.5	<0.001
Offshore*moonphase	2	694	347	17.7	<0.001
Offshore*site	1	1638	1638	83.8	<0.001
Offshore*season*moonphase	2	83	41	2.1	0.12
Offshore*season*site	1	270	270	13.8	<0.001
Offshore*moonphase*site	2	314	157	8.03	<0.001
Offshore*season*moonphase *site	2	3	1	0.07	0.94
residuals	19585	382980	20		

Table A2. Results from an ANCOVA with high band level as the dependent variable, and offshore wind, season, moon phase and site as independent variables. Interactions are depicted with a *. After accounting for the wind, there was a significant effect of season, moon phase, and site. However, there were no interactions between site and moon phase or site and season.

Source	**dF**	**SS**	**MS**	**F**	**p**
Offshore	1	435	435	210.8	<0.001
Season	1	8492	8492	4117.9	<0.001
Moonphase	2	486	243	117.7	<0.001
Site	1	4138	4138	2006.7	<0.001
Offshore*season	1	76	76	36.8	<0.001
Offshore*moonphase	2	91	46	22.1	<0.001
Offshore*site	1	98	98	47.6	<0.001
Offshore*season*moonphase	2	15	8	3.71	0.03
Offshore*season*site	1	1	1	0.67	.41
Offshore*moonphase*site	2	7	3	1.6	0.20
Offshore*season*moonphase *site	2	4	2	0.92	0.40
residuals	19763	40757	2		

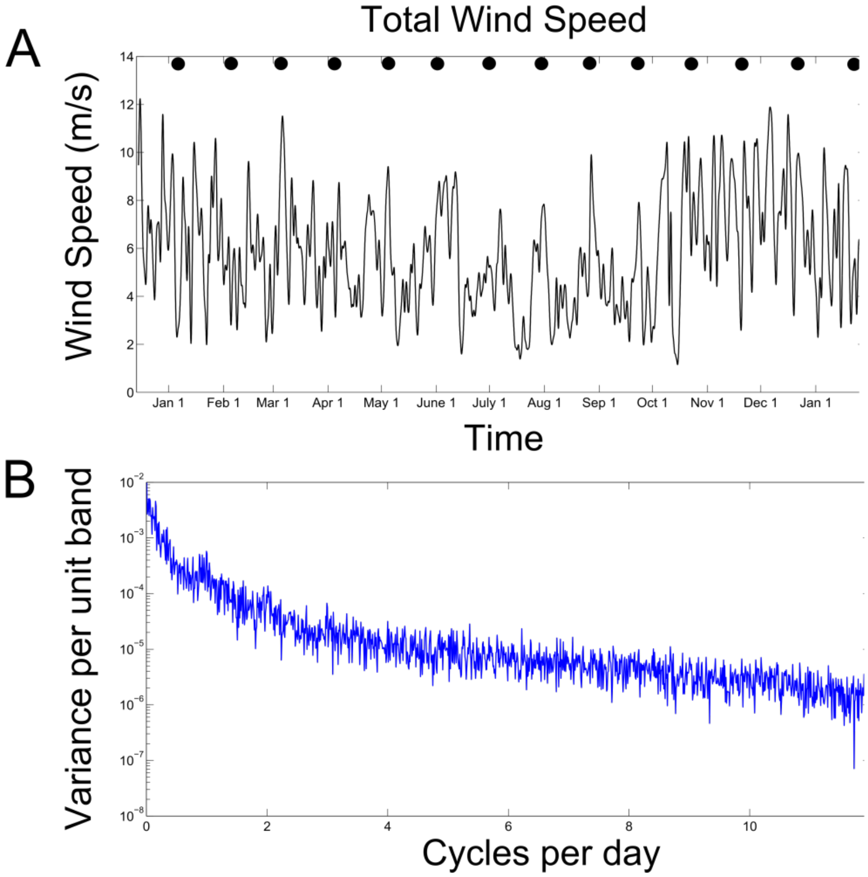


Figure A1. Total wind speed in the time domain (A), smoothed with a 50-pt Hanna filter, and the frequency domain (B). The power spectrum (B) shows a small peak at once/day.

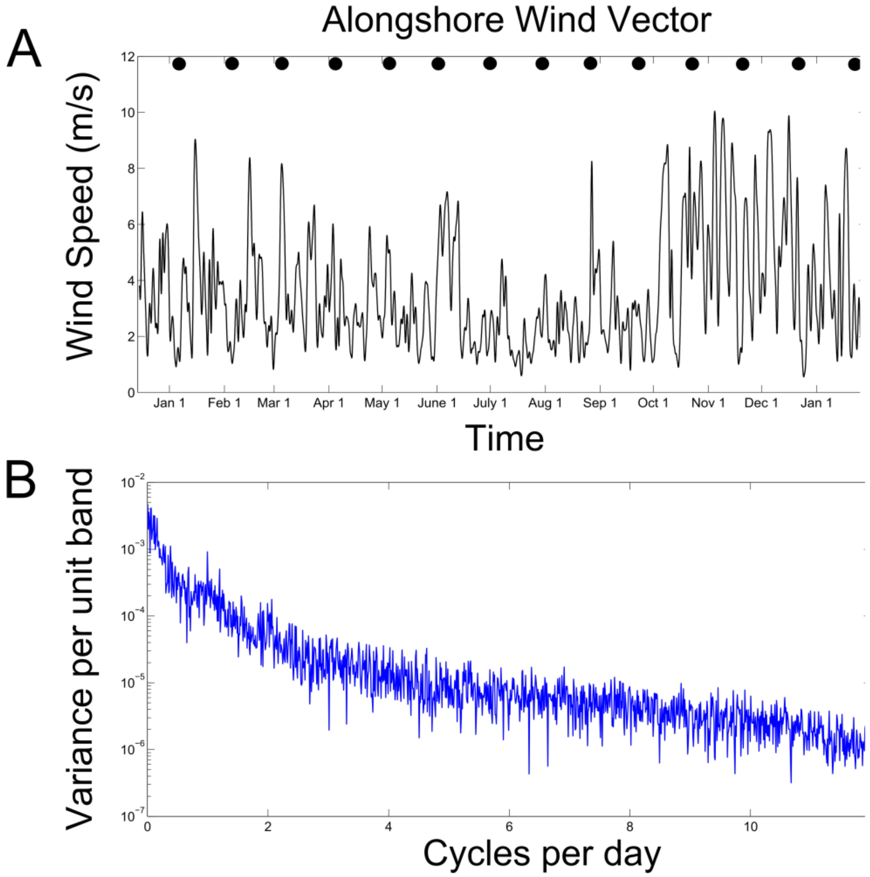


Figure A2. Alongshore wind vector in the time domain (A), smoothed with a 50-pt Hanna filter, and the frequency domain (B). There was a small peak at once/day in the Power Spectrum.

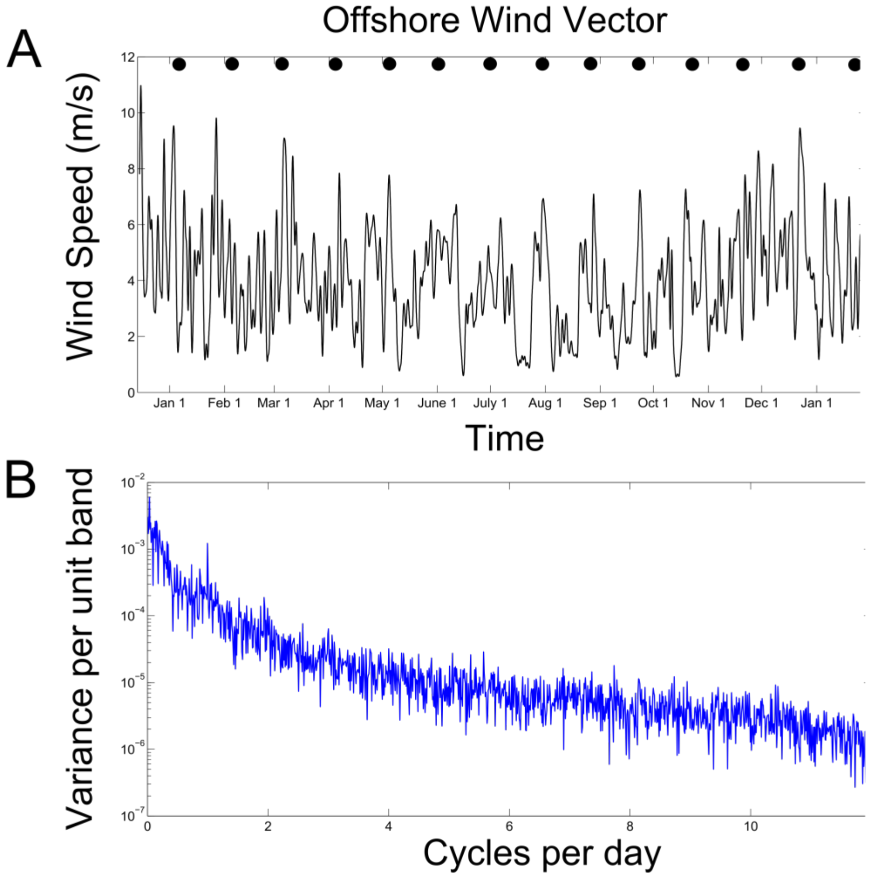


Figure A3. Offshore wind vector in the time domain (A), smoothed with a 50-pt Hanna filter, and the frequency domain (B).Peaks at once/sidereal month (27.32 days) and once/solar day are evident in the Power Spectrum.

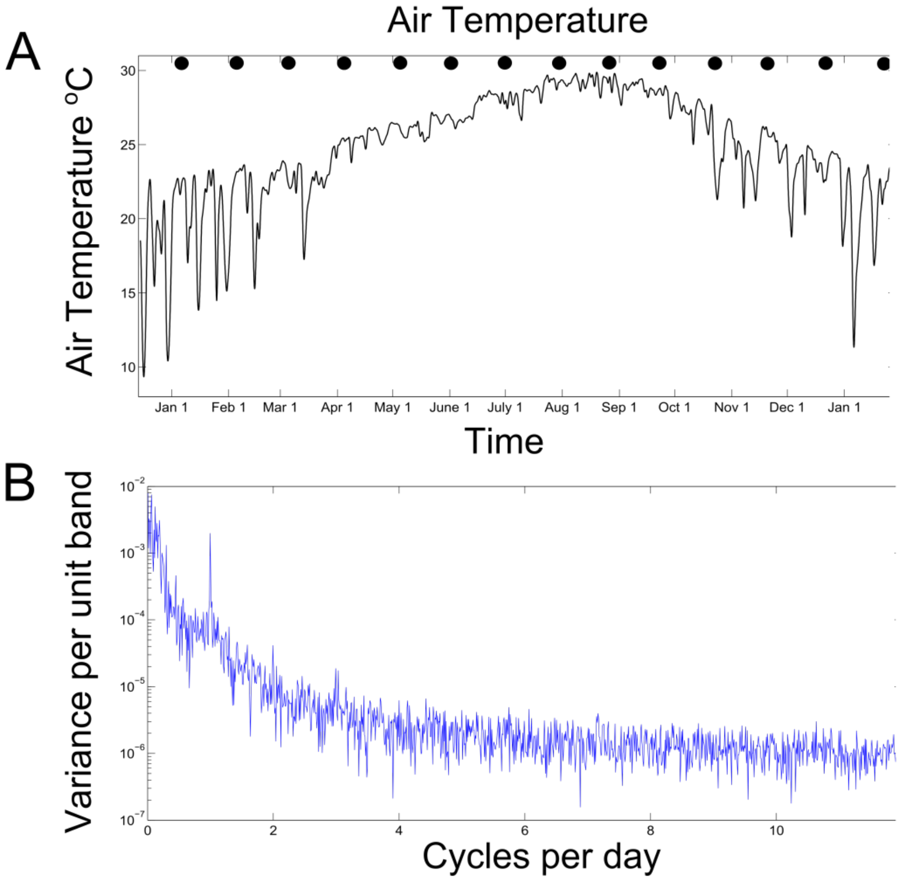


Figure A4. Air temperature in the time domain (A), smoothed with a 50-pt Hanna filter, and frequency domain (B). There was a clear seasonal change in air temperature, as well as a once/day peak as seen in the Power Spectrum.

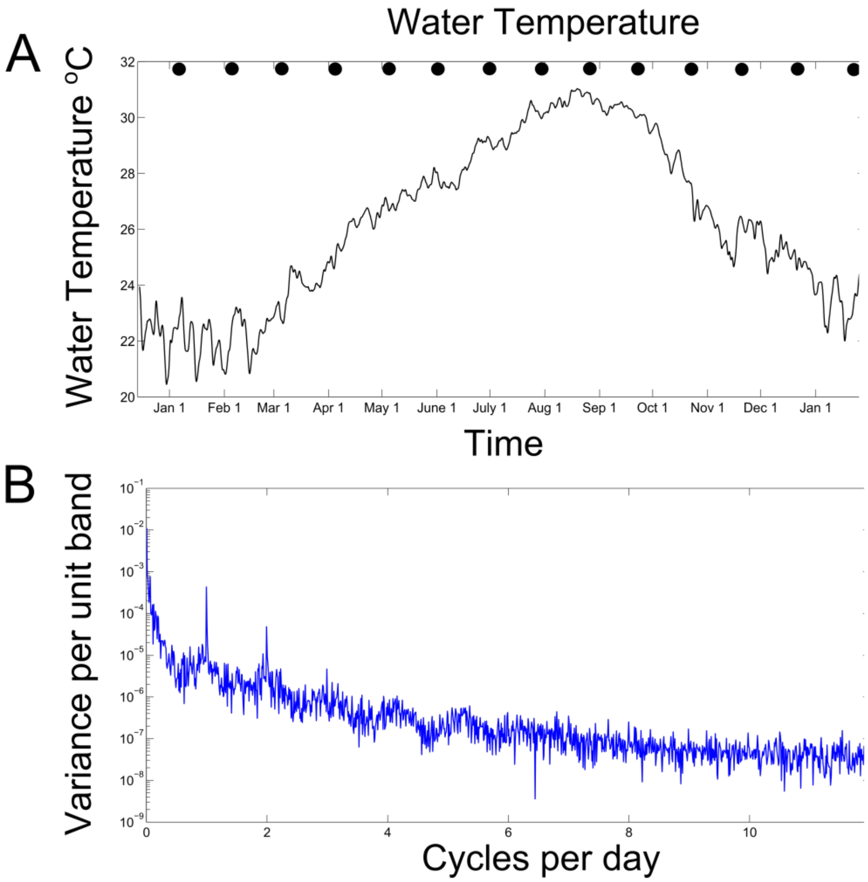


Figure A5. Water temperature in the time domain (A), smoothed with a 50-pt Hanna filter, and the frequency domain (B). In addition to a seasonal trend in the water temperature, there was also a peak at once and twice per lunar day, corresponding to tidal flow.

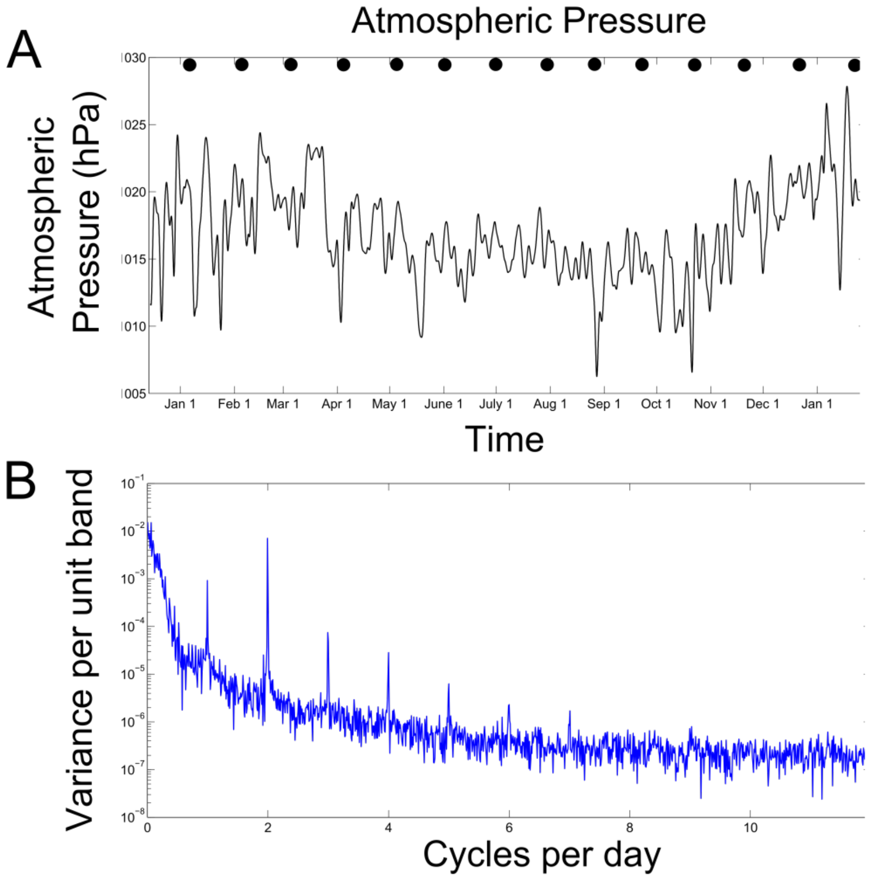


Figure A6. Atmospheric pressure in the time domain (A), smoothed with a 50-pt Hannah filter, and the frequency domain (B). There were large peaks at once and twice per day, with harmonics extending into higher frequencies.

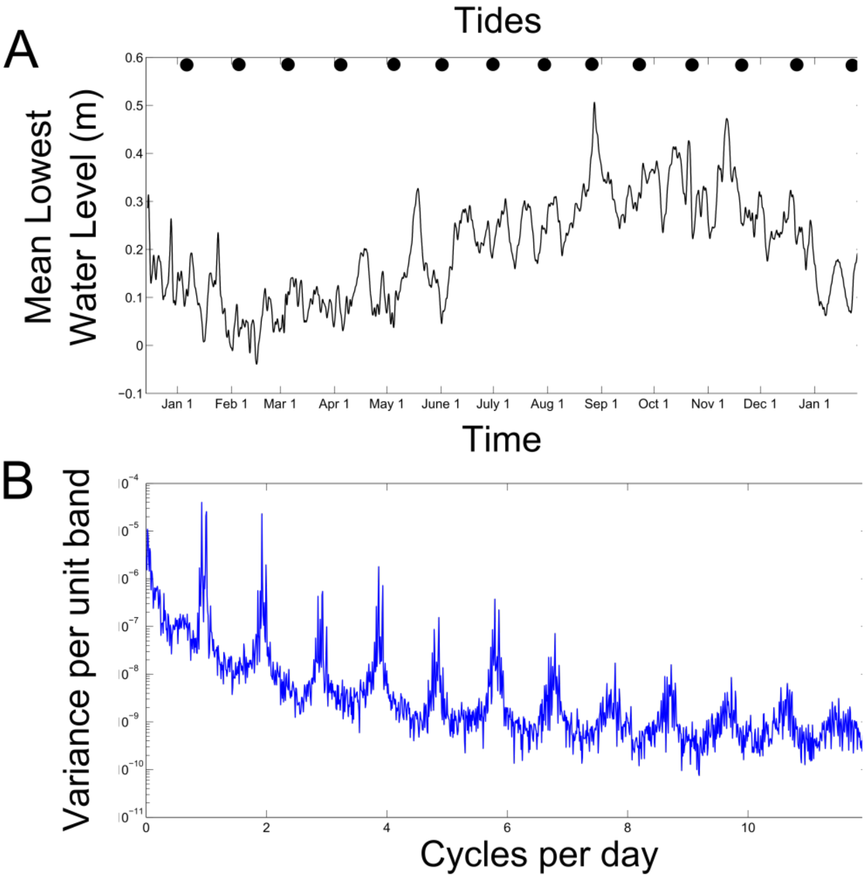


Figure A7. Tides (mean lowest water level, in m) in the time domain (A), smoothed with a 50-pt Hannah filter, and the frequency domain (B). There are many frequency components to tides, which is evident in the Power Spectrum, but the primary peaks occurred at once and twice per lunar day.

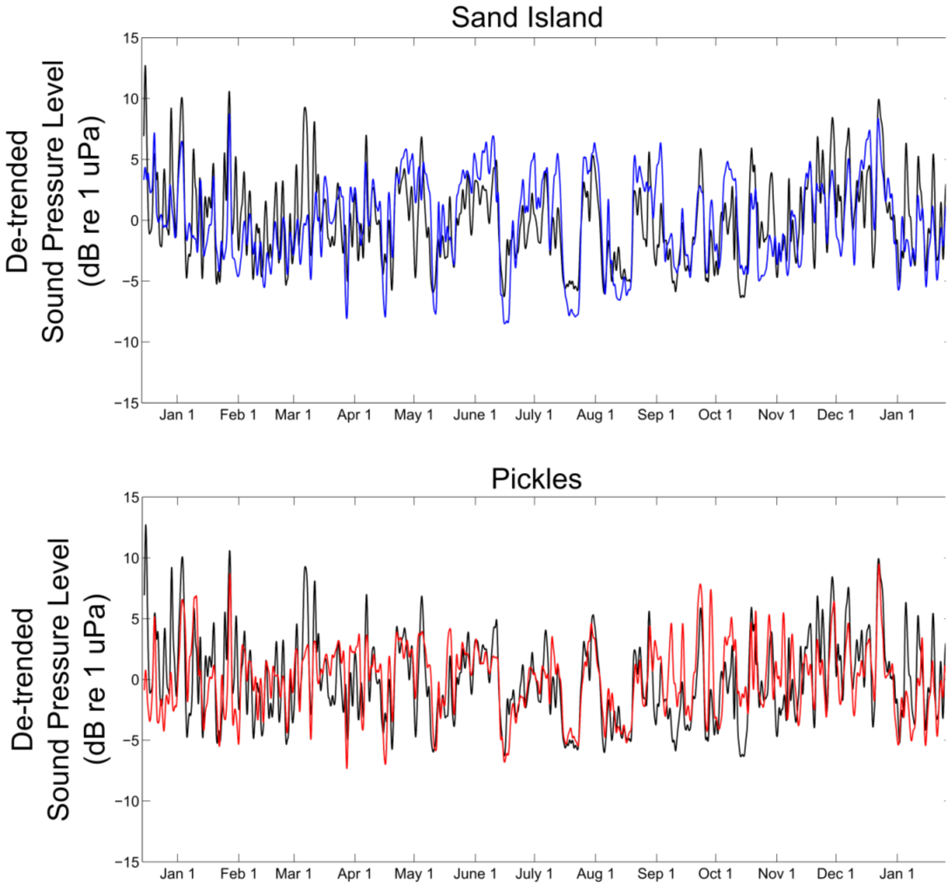


Figure A8. A time series of predicted RMS level (black line), based on measured wind speeds (using relationship in Knudsen 1944), with actual RMS level for Sand Island and Pickles. All data was de-trended before the calculations and plots were made. While both sites had fairly close agreement with predicted sound pressure levels, at Sand Island there was a discrepancy between the predicted and actual values in the wet season, which indicates that there was an additional sound source (i.e., biophony) with a similar period.

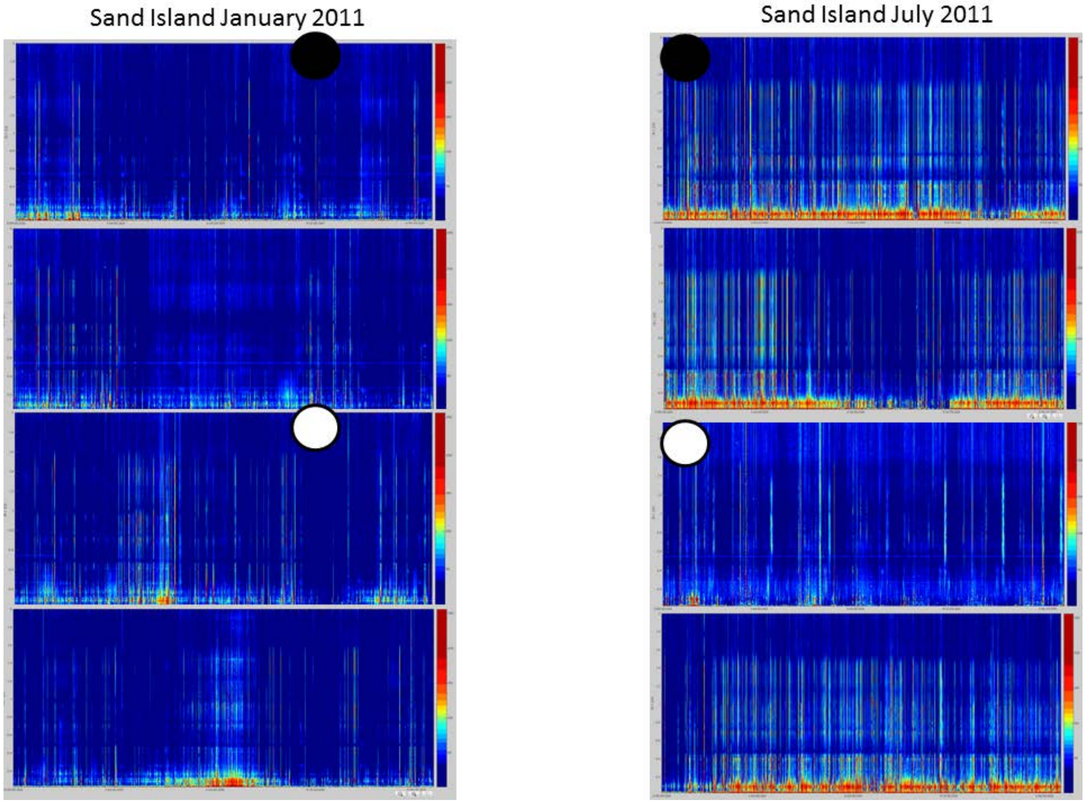
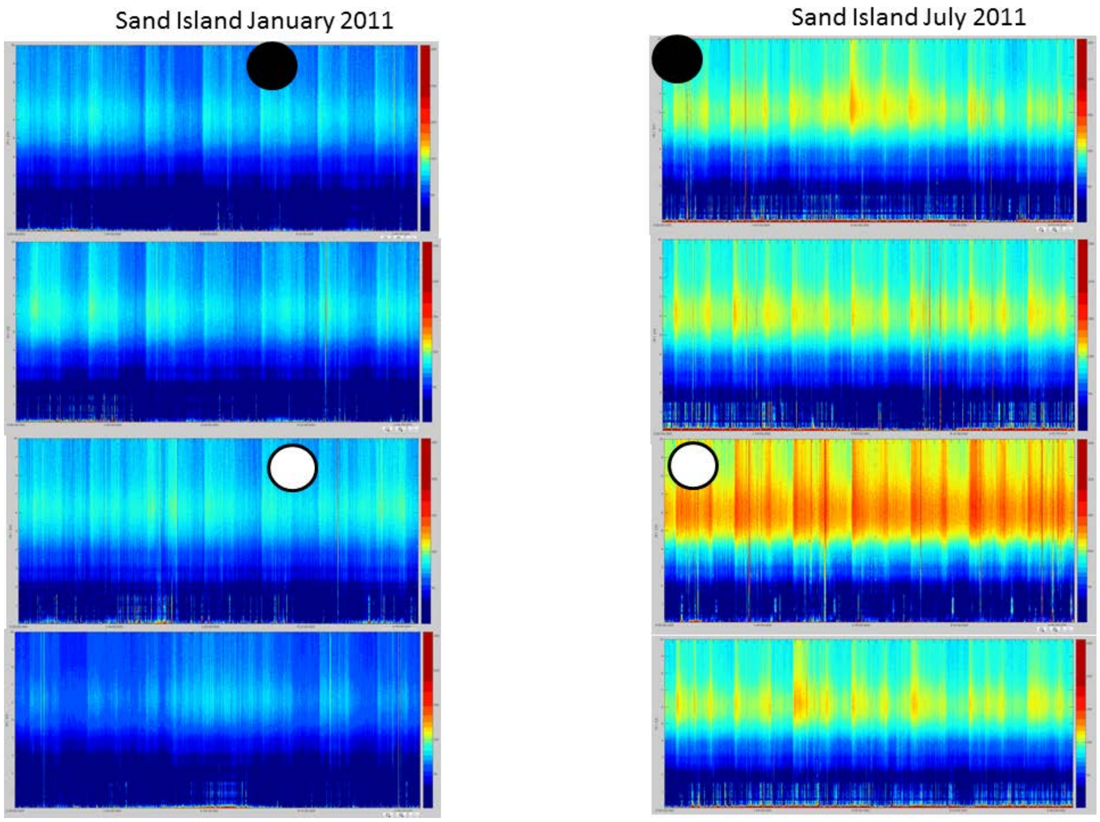


Figure A9. Weekly spectrograms from Sand Island for the low band, 25Hz- 2000Hz, for January and July. Each line represents one week. The vertical axis represents frequency, and the color axis represents relative amplitude. In July the low-frequency fish ‘growl” is more prevalent than it is in January, and it diminishes during full-moon periods.



Sand Island January 2011

Sand Island July 2011

Figure A10. Weekly spectrograms from Sand Island for the entire sampling bandwidth, 25 Hz- 10,000 Hz. The vertical axis represents frequency and the color axis represents relative amplitude. The daily patterns evident in the higher frequencies are snapping shrimp clicks – which peaked during the full moon. Although snapping shrimp sounds were louder during the summer, they were prevalent throughout the winter months as well.