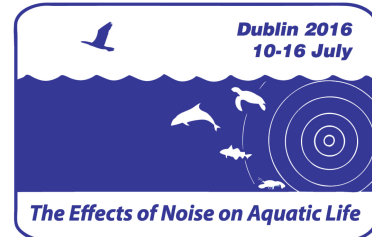




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Loudly heard, little seen, and rarely understood: Spatiotemporal variation and environmental drivers of sound production by snapping shrimp

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Snapping shrimp are abundant soniferous crustaceans that form large aggregations, creating a pervasive crackling in many coastal environments worldwide. The short-duration broadband “snap” generated by their specialized claw is among the loudest bioacoustic sound in the marine environment. Variation in snapping shrimp acoustic activity can substantially alter ambient soundscape characteristics, yet relatively little is known about snapping shrimp sound production patterns, the underlying behavioral ecology or role of environmental factors. Our analyses of acoustic data from tropical and sub-tropical reefs show that snap rates exhibit diurnal rhythms, but that these rhythms vary over small spatial scales (e.g., opposite diurnal patterns between adjacent reefs) and shift over time (e.g., daytime versus nighttime dominance in different seasons). Snapping patterns correlate to abiotic variables such as temperature and light, but the underlying causal mechanisms remain unclear. Ongoing lab experiments to investigate snapping patterns in *Alpheus heterochaelis* find that isolated individuals produce snaps in the absence of external provocation, and that individual snap rate relates to temperature, time of day, and sex. By combining detailed snap analysis of field recordings and manipulative lab experiments, progress is being made towards understanding the sound producing behaviors and environmental factors that drive variation in snapping shrimp-dominated soundscapes.



1. INTRODUCTION

A. SOUNDSCAPE ECOLOGY

Soundscapes are a fundamental element of marine ecosystems. Comprised of the spatially and temporally varying physical and biological sounds that form the ambient acoustic environment, this acoustic medley provides rich sensory information to organisms small and large, and influences a range of ecological processes (Pijanowski et al., 2011). The burgeoning field of soundscape ecology seeks to better understand and apply the study of soundscapes to wider ecological issues, and broadly includes several inter-related research themes (Fig. 1).

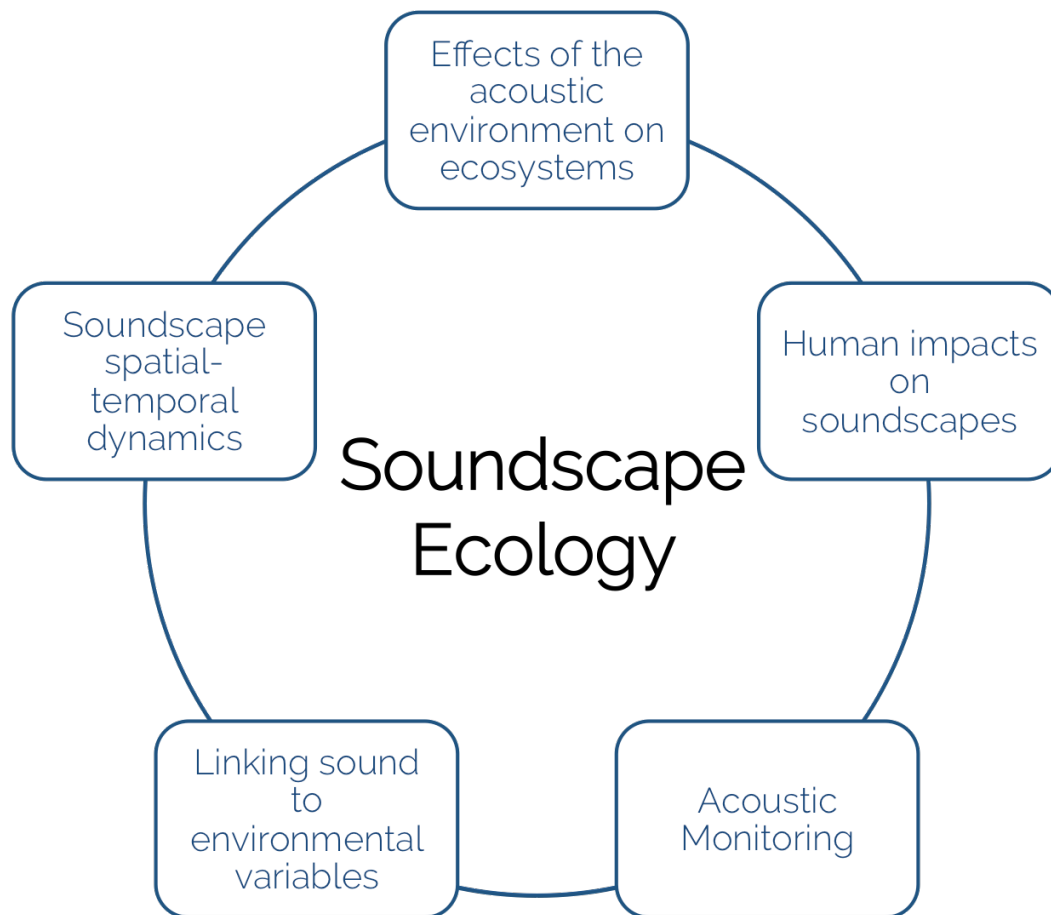


Figure 1. Conceptual diagram of the major inter-related research themes forming the basis of the emerging discipline of soundscape ecology.

To address questions of human impacts on soundscapes and the effect of noise on aquatic life, as well as to utilize acoustic monitoring in these endeavors, we require knowledge of ambient soundscape patterns, the environmental variables driving soundscape dynamics, and the associated ecological and behavioral processes. In many ecosystems, there are certain acoustic sources that dominate the soundscape such that establishing the dynamics of these sounds and their relationship to abiotic and biotic variables is central to the broader research aims of soundscape ecology.

B. SNAPPING SHRIMP AS KEY SOUNDSCAPE ENGINEERS

Snapping shrimp are a widespread family of Caridean shrimp comprising over 600 species and representing a variety of life history strategies and social dynamics (Anker et al., 2006). The loud snaps emanating from structured bottoms in coastal ecosystems are produced by the collapse of a cavitation bubble upon the rapid closure of the large major chela possessed by species of the family Alpheidae (Versluis et al., 2000). Snapping shrimp generally live in large aggregations, resulting in a persistent and distinct crackling noise in areas where they are present.

The role of snapping shrimp acoustic activity as a dominant driver of ambient noise levels in coastal tropical and temperate regions was first recognized by investigators working on underwater recordings collected during WWII (Johnson et al., 1947; Everest, 1948). These early studies revealed that the source of the ubiquitous crackling noises previously ascribed to a variety of phenomena (e.g., shipworms, volcanoes, rolling pebbles) were, in fact, vast numbers of snapping shrimp inhabiting shallow benthic habitats of coastal areas (Johnson et al., 1947). Knowlton and Moulton (1963) suggested that because snapping shrimp are localized to specific substrates, their sound could be used as an indicator of depth, benthic habitat and associated fauna.

Variations in snapping shrimp distributions have been found to account for much of the habitat-dependent differences in soundscapes, in terms of sound levels and frequency content, in a variety of temperate and tropical habitats (Radford et al., 2008; Lillis et al., 2014; Butler et al., 2016). The high levels of sound generated by snapping shrimp colonies can be involved in a range of animal activities, including navigation and habitat selection by settlement-stage larvae (Simpson et al., 2008; Lillis et al., 2015) and perhaps as a cue for migrating cetaceans to avoid rocky shorelines (Allen, 2013). In other instances, the intense broadband crackling noise of snapping shrimp may interfere with useful acoustic signals, an underwater communication problem for humans and marine organisms alike (Knowlton and Moulton, 1963; Au and Banks, 1998; Chitre et al., 2012). Despite their fundamental contribution to the soundscape of many marine habitats, and probable influence on myriad acoustically-mediated ecological processes, the acoustic ecology of snapping shrimp is little studied.

In recent years, as technology and interest in passive acoustic monitoring of marine communities has grown, it has been proposed that the sounds of snapping shrimp could serve as a measurement of habitat composition or quality (Lammers et al., 2008; Radford et al., 2010), however, consistent relationships between snapping and habitat characteristics have yet to be firmly established. Impetus to examine the influence of environmental variables on sound production by snapping shrimp is growing, given the potential for environmental changes in temperature, dissolved oxygen, and pH to alter soundscapes via their influence on the acoustic activity of these dominant sound producers. Measurements of variation in high frequency band SPL (used as a proxy for snapping shrimp activity) in coastal Japan found correlations with dissolved oxygen levels and temperatures (Watanabe et al., 2002). Shrimp sound production also appears to be influenced by pH levels – an experiment subjecting shrimp to high future CO₂ conditions were recently reported to decrease the snapping rate of an Alpheid (Rossi et al., 2016), suggesting that ocean acidification could potentially result in quieter soundscapes. However, to assess and predict their impact on future soundscapes, the relationships between snapping and water temperature, dissolved oxygen, pH, and other climatological parameters need to be investigated more systematically, and in relevant combinations.

C. OBSERVED SNAPPING PATTERNS AND BEHAVIOURS

Initial reports of snapping shrimp sound patterns showed that snapping is elevated in higher complexity benthic habitat (e.g., cobble vs. mud/sand), presenting slight increases at nighttime with dawn and dusk peaks, but no apparent seasonality (Johnson et al., 1947). However, these reports were based on short-term recordings (often single days) and limited to latitudes with little seasonal variation in water temperature. More recently, studies of temperate rocky reef soundscapes reported seasonal, lunar, and diel variation in the rate of snapping (Radford et al., 2008). Advances in recording capacity and increased efforts to sample coastal soundscapes at high spatiotemporal resolution have provided acoustic datasets that reveal even more complex dynamics in snapping shrimp sound production. Snapping shrimp in coastal Southeastern United States oyster reef habitats showed significant seasonality in snap rates corresponding to water temperature, and shifting diel patterns in both snap rate and mean snap intensity at a single site (Bohnenstiehl et al., 2016). Recent soundscape descriptions from coral reefs also suggest that more complex and highly variable snapping patterns exist than have previously been noted in tropical habitats (Lammers et al., 2006, 2008; Staaterman et al., 2014). For instance, Lammers et al. (2008) found nearby Hawaiian sites to have opposite day-night patterns in the high-frequency band (2-10 kHz) acoustic data, likely reflecting snapping shrimp differences, and a long-term soundscape dataset from the Florida Keys showed shifts from daytime to nighttime increases in this bandwidth depending on time of year (Staaterman et al., 2014).

The limited understanding of snapping shrimp sound production patterns relates to our limited knowledge of the variety of snapping-associated behaviours. The most well-studied role of snapping is as an aggressive behaviour employed during intra- and inter-specific encounters (Nolan and Salmon, 1970; Schein, 1975; Herberholz and Schmitz, 2001), however, other lesser known snapping functions, including prey capture, rock-boring, and excavation, have also been implicated (reviewed in Anker et al., 2006) but never quantified. Given the diversity of life histories, symbioses, and habits, it is not surprising that evidence is mounting for more complex patterns of snapping, and thus a more nuanced impact on soundscapes by snapping shrimp, than was previously considered.

2. SPATIOTEMPORAL VARIATION IN SNAP RATES ON CARIBBEAN CORAL REEFS

A. U.S. VIRGIN ISLANDS

Acoustic datasets collected in 2013 and 2015 at reef sites located within the St. John Virgin Islands National Park were analyzed for snapping shrimp acoustic activity following the snap counting methods of Bohnenstiehl et al. (2016). The available recordings included a 3-month summer 2013 periodic sampling (1-minute every 15 minutes) at 2 nearby reef sites (<500 m apart), Tektite and Yawzi, and a short-term (4-day) continuous dataset collected in November 2015 at the same two sites and one additional reef, Booby Rock, located 1 km from the other sites. The 2013 data were recorded using DSG acoustic recorders (Loggerhead Instruments, calibrated HTI-96 hydrophone, 80 kHz sample rate, 20 dB gain) and 2015 acoustic recordings were collected using SoundTrap acoustic recorders (Ocean Instruments NZ, 96 kHz sample rate).

In contrast to previous assumptions of nighttime increases in snapping across tropical coastal areas (Radford et al., 2014; Nedelec et al., 2015), the U.S. Virgin Island data showed preferential daytime snapping and nighttime decreases in snapping shrimp acoustic activity at Tektite and Yawzi throughout both sampling periods. In summer 2013 there were peaks in snapping at dawn

and dusk; these peaks were more pronounced at the Tektite site, where overall snap rates were lower (Fig. 2). The snap rates were not significantly correlated with water temperatures. During the continuous 4-day period of sampling in 2015, elevated daytime snapping was again evident at the Tektite and Yawzi reefs, however, Tektite did not show the sharp dawn and dusk peaks previously recorded (Fig. 3). Booby Rock reef site showed an opposite pattern of higher rates of snapping at nighttime, no dawn and dusk peaks, but a sharp decrease in snaps at dawn (Fig. 3).

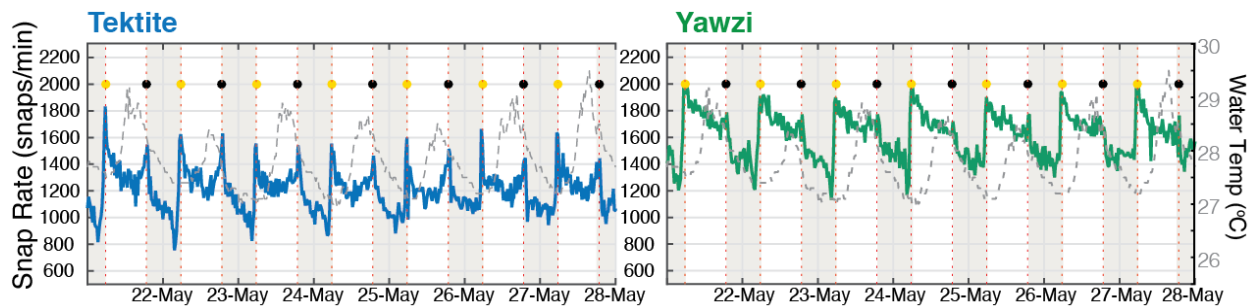


Figure 2. Snap counts for a week in May 2013, showing typical diel variation in snap rate at Tektite and Yawzi reef sites in St. John, U.S. Virgin Islands. Black and yellow points denote sunset and sunrise, respectively. The grey dotted line represents water temperature obtained from NOAA buoy data.

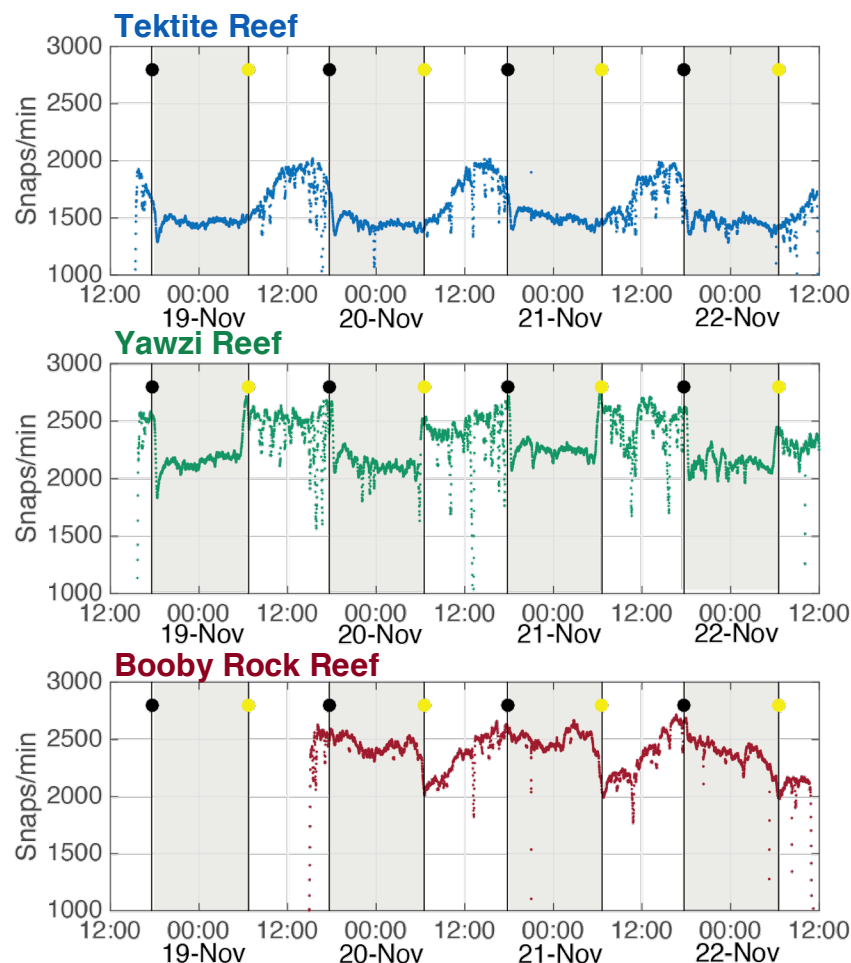


Figure 3. Snap rates during November 2015 at three adjacent coral reef sites in St. John, USVI, showing variability in diel snapping patterns. Shaded areas indicate nighttime, dark and yellow circles denote sunset and sunrise respectively.

B. CURAÇAO

Curaçao, located in the Southern Caribbean, is a 450 km² island fringed by coral reef. In September 2014, eight Curaçao reef sites spaced 1-3 km apart were sampled acoustically for 1-minute every 15 minutes for three weeks using SoundTrap digital acoustic recorders (96 kHz sample rate). Snap counting analyses were again employed to examine spatial and temporal variability in snap rates and snap characteristics (following Bohnenstiehl et al., 2016). These recordings showed variation in overall snap rates among sites, as well as a range of diel patterns (Fig. 4). Several reefs illustrated strong crepuscular snapping activity (Blauwbaai, Sint Michiel, Snake Baai), and other sites produced consistently higher levels of nighttime snapping (Sea Aquarium, Water Factory).

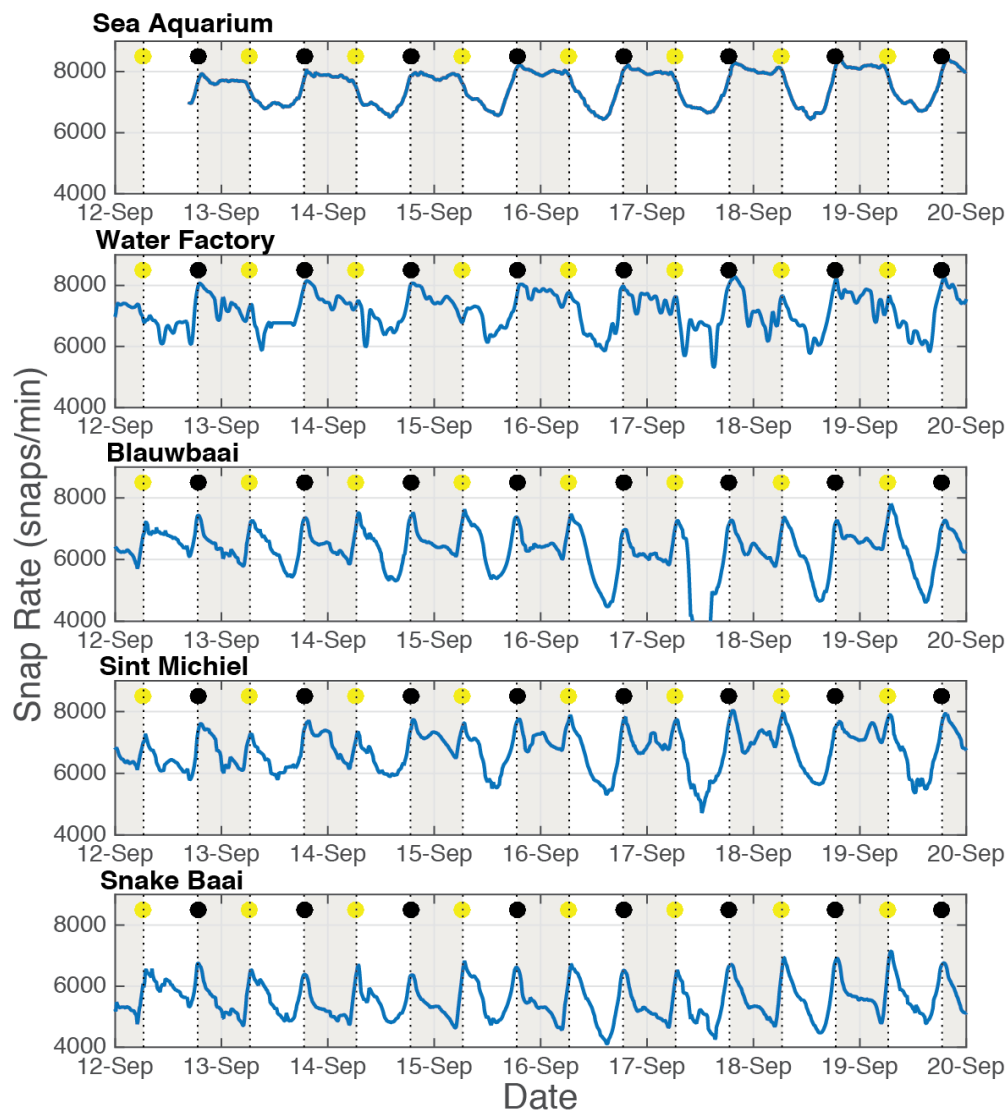


Figure 4. Snap rates during mid-September 2014 at five coral reef sites in Curaçao, showing variability in diel snapping patterns. Shaded areas indicate nighttime, hashed vertical lines with black and yellow circles denote times of sunset and sunrise respectively.

C. SUMMARY

Snapping shrimp patterns observed in Caribbean coral reefs show considerable spatiotemporal variation, particularly in diel periodicity, which do not consistently follow the previously reported patterns of crepuscular activity and elevated nighttime snapping. Moreover, these time-series analyses reveal that the diel periodicity in snapping on coral reefs can differ between closely positioned sites (within hundreds of meters) and shift between sampling times at a single site. The USVI data in particular, recorded in different parts of the year, suggests that there could be seasonal changes in snapping patterns at tropical reefs, despite the limited seasonal water temperature changes, and highlights that characterizations of coral reef soundscapes should consider this potential for variation. For example, many studies have relied on “snapshot” acoustic recordings to represent different coral reefs for comparison and correlation with habitat variables (Kennedy et al., 2010; Piercy et al., 2014; Radford et al., 2014; Nedelec et al., 2015), usually collected at one time point and not simultaneously. It is important to note that we see snap rates change by at least a factor of 2 within minutes, especially at dusk or dawn. Such striking changes are typically overlooked by previous soundscape investigations, where a site or time of day has often been defined from 5-minute recording segments and assumed to be invariable over hours-long time windows. These comparisons between sites or times of day then depend heavily on the shrimp activity in those few minutes, which we now know can be remarkably variable. Thus, the conclusions of snapshot investigations are likely very sensitive to this sampling regime. This problem needs to be addressed before implementing any passive acoustic monitoring or assessment that incorporates snap counting, snap-influenced bandwidths or acoustic metrics of soundscape health and biodiversity.

Longer-term acoustic datasets continue to be recorded at reef sites in the U.S. Virgin Islands, which will allow further examination of spatiotemporal variation in snapping shrimp sound production, particularly over seasonal time-scales. These soundscape analyses will also investigate the relationships between reef characteristics (such as substrate composition and water quality) and snapping behavior. This will provide critical information to assess the role of snapping shrimp in these soundscapes, and their potential use as a monitoring tool. Yet, to best explain and predict the influence of environmental variables on snap production will also require specific experiments to disentangle the underlying mechanisms (i.e., shrimp acoustic ecology).

3. PRELIMINARY LAB EXPERIMENTS

To directly observe sound production patterns by snapping shrimp in relation to controlled biotic and abiotic factors, measurements of snap rates and manipulative experiments were conducted using a species of snapping shrimp dominant in coastal oyster reef habitats of the Southeast United States (*Alpheus heterochaelis*).

A. METHODS

Shrimp were collected by hand in coastal North Carolina in July-August 2015, at oyster beds in the North River estuary near Beaufort. Following transportation to the Environmental Systems Laboratory at Woods Hole Oceanographic Institution, shrimp were housed individually in a shaded outdoor flow-through seawater facility. The shrimp were provided shell and gravel as shelter, maintained in ambient temperature seawater, and fed dried shrimp pellets every 3 days.

Following the initial observation that shrimp snap spontaneously, without the presence of another shrimp or other external provocation, a series of preliminary experimental trials were conducted to examine the shrimp characteristics (e.g., sex, length, claw size) and environmental

variables (e.g., temperature, light) that influence individual snap rates. A series of trials, in which 12 individual or heterosexual pairs of shrimp were placed in separate tanks and recorded continuously, lasted 48-72 h under ambient light cycles in late August and early September. Acoustic recording data were analyzed for the occurrence of snaps using a threshold detector generated in Matlab (The Mathworks, Inc, Boston, MA), with waveforms visually inspected to ensure all signals enumerated matched the characteristics of a shrimp snap (Everest, 1948; Au and Banks, 1998; Bohnenstiehl et al., 2016).

B. RESULTS AND DISCUSSION

Individual snapping shrimp showed high variability in their proclivity for snapping, producing snaps at a rate of less than one snap per day to a maximum of 30 snaps per day in August 2015 trials (N=36). Intriguingly, the spontaneous snapping observed indicates that snapping behavior is used by shrimp for purposes additional to the aggressive and territorial interactions that are commonly reported, which suggests that the signals could serve a broader role in communication. Video observations of snapping behaviors to better understand the possible additional functions of snapping are ongoing.

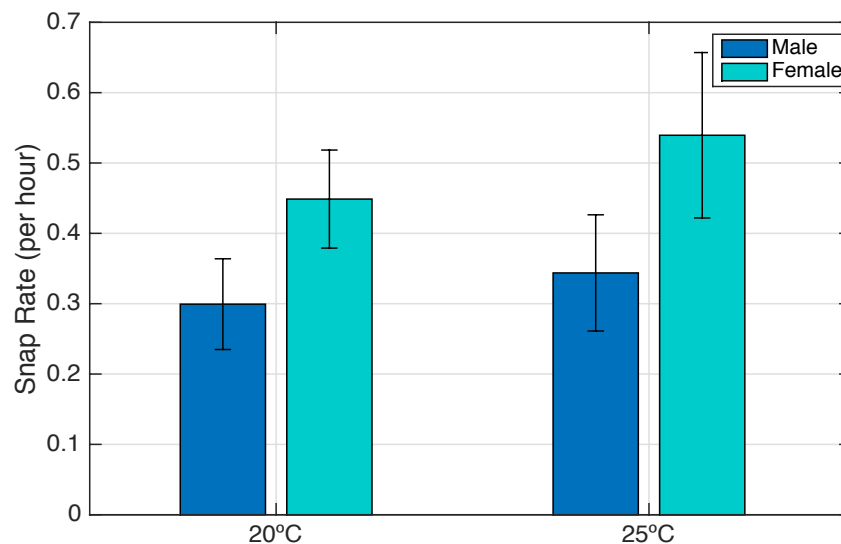


Figure 5. Comparison of mean individual snap rate (± 1 S.E.) produced by male and female snapping shrimp maintained at two water temperature conditions for 72 hour trials.

An experiment to compare snap rates between shrimp held at 20° C and 25° C found no significant difference between these two temperatures (Fig. 5, $F_{1,66}=0.997$, n.s.), but female shrimp were found to snap at a significantly higher rate than males ($F_{1,66}=5.995$, $p < .05$), and both males and females snapped significantly more at night versus daylight hours, across both temperatures (Fig. 6, $F_{1,66}=5.828$, $p < 0.05$). Heterosexual pairs snapped, on average, ca. 4 times as much as individuals (Fig. 6), and similarly showed no significant response to the two temperature treatments ($F_{1,20}=0.942$, n.s.), but a tendency for increased nighttime snapping, though statistically insignificant ($F_{1,20}=2.79$, $p=0.11$). The temperature treatments of 20° C and 25° C represent autumn/spring and early summer temperatures, respectively, when diel patterns differ in previously recorded field data for this species (Bohnenstiehl et al., 2016). The nighttime preference under both temperature regimes in lab experiments suggest that the seasonal variation in diel pattern is not necessarily related to temperature; however, further experiments to include a

fuller range of water temperatures, as well as to directly measure the effect of light on snapping patterns, are ongoing. These early experiments also illustrate the need to consider life history and ecological context of the snapping behaviors to disentangle the relative importance of abiotic factors such as light and temperature on driving spatiotemporal snapping patterns.

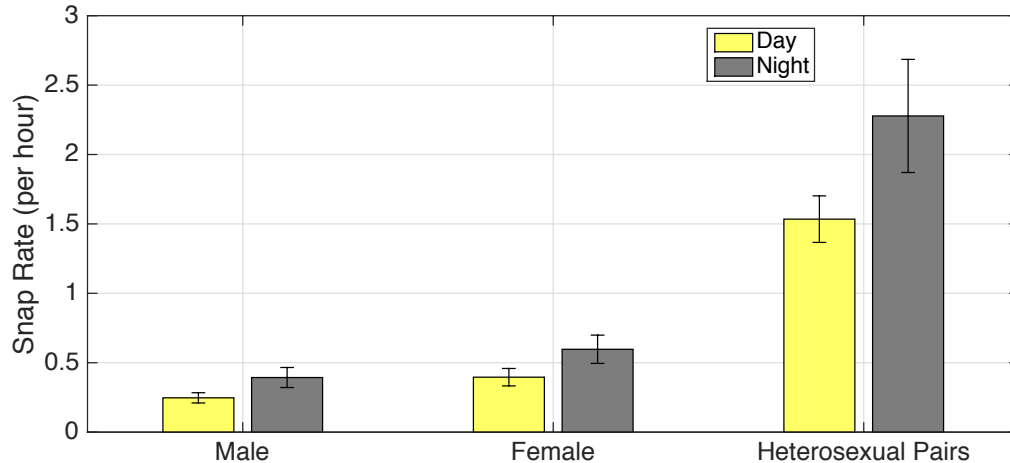


Figure 6. Mean snap rates produced during daytime and nighttime by individual male and female snapping shrimp, compared to male-female pairs.

4. CONCLUSION

The majority of soundscape characterizations have not examined the spatiotemporal variability in snapping shrimp patterns, and this has resulted in the propagation of an oversimplified paradigm of shrimp noise (i.e., crepuscular peaks, elevations at nighttime) in the literature. However, particularly in tropical habitats, where a huge diversity of snapping shrimp species exist, with complex species-specific symbioses, microhabitat, group dynamics, and cooperative strategies, it is perhaps unsurprising to find that their acoustic activity can show substantial small-scale spatial and temporal variability. A reef can be host to dozens of distinct species of snapping shrimp, the majority for which we know little of their acoustic, or even basic, ecology and are thus unable to adequately predict or understand their contribution to the soundscape.

Establishing the acoustic ecology of key soniferous organisms such as snapping shrimp is imperative to assess when and where soundscapes affect ecological processes and how human impacts alter these linkages. Moreover, these studies provide critical information to the effective use of soundscape characteristics for passive acoustic monitoring of marine communities. Without quantifying the variation in snapping patterns from field observations, and understanding the biotic and abiotic influences on this variability via controlled lab measurements, it is not possible to assess the role of snapping shrimp in soundscape-mediated ecological processes or to use their signals as a proxy for environmental change.

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