Sound production patterns of big-clawed snapping shrimp (*Alpheus spp.*) are influenced by time-of-day and social context

Ashlee Lillis,[a)] Jessica N. Perelman,[b)] Apryle Panyi,[c)] and T. Aran Mooney

Biology Department, Woods Hole Oceanographic Institution, MS#50, 266 Woods Hole Road, Woods Hole, Massachusetts 02543, USA

Snapping shrimp are perhaps the most pervasive sources of biological sound in the ocean. The snapping sounds of cryptic shrimp colonies in shallow coastal habitats worldwide create a near-continuous crackling with high spatiotemporal variability, yet the underlying acoustic ecology is not well understood. This study investigated sound production rates and acoustic behavior of snapping shrimp species common in the Western Atlantic Ocean and Gulf of Mexico (*Alpheus heterochaelis* and *Alpheus angulosus*). Snap rates were measured in a controlled laboratory setting under natural light, temperature, and substrate conditions for shrimp held individually, in pairs, and in a ten-shrimp mesocosm, to test hypotheses that acoustic activity varies with time-of-day and social context. Spontaneous snapping was observed for 81 out of 84 solitary shrimp monitored. Time-of-day influenced snap output for individuals and same-sex pairs—higher rates occurred during dusk and night, compared to daylight hours, but this pattern was inconsistent for opposite-sex pairs and a mixed-sex group. These laboratory results provide insight into behavioral rhythms that may influence snapping patterns in natural populations, and underscore the limited understanding of a major sound source in marine environments. © *2017 Acoustical Society of America.*
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I. INTRODUCTION

Sound production is common across a wide range of marine taxa, and the use of sounds has been observed in a variety of behavioral contexts, particularly for mammals and fishes. Comparatively, aquatic invertebrate sound production is less understood, but acoustic signals have been reported during courtship and mating (Salmon, 1967; Popper *et al.*, 2001), defense (Meyer-Rochow and Penrose, 1976; Bouwma and Herrnkind, 2009; Staaterman *et al.*, 2010), and social communication (Berrill, 1976; Silliman *et al.*, 2003; Buscaino *et al.*, 2011). Invertebrate sounds are also produced as a by-product of activities such as swimming and feeding (Radford *et al.*, 2008a; Freeman *et al.*, 2014; Coquereau *et al.*, 2016). Sound production and reception has clear adaptive value for marine organisms (Bradbury and Vehrencamp, 1998), and the combination of bioacoustic signals produced in underwater habitats provides rich sensory information, forming a major component of the ambient acoustic environment, or "soundscape" (Cotter, 2008; Pijanowski *et al.*, 2011). Because soundscapes are implicated in fundamental organismal processes such as reproduction, trophic interactions, and larval recruitment, spatiotemporal patterns in acoustic characteristics likely influence the structure and functioning of marine communities.

The acoustic activity of snapping shrimp (Family Alpheidae) is a major driver of ambient sound levels in coastal seas (Everest, 1948; Johnson *et al.*, 1947; Lillis *et al.*, 2014; Kaplan *et al.*, 2015). These crustaceans are a widespread and highly diverse family of Caridean shrimp, and produce one of the highest amplitude and most common of all biological underwater sounds, termed "snaps" (Johnson *et al.*, 1947; Au and Banks, 1998). The characteristic high intensity acoustic signal of snapping shrimp comes from the collapse of a cavitation bubble upon the rapid closure of their specialized snapping claw (Versluis *et al.*, 2000). Snapping shrimp generally live in large aggregations in structured bottoms of coastal ecosystems (e.g., reef, rubble, rocky shores) (Mathews, 2002b). The snapping of multiple individuals in a colony and multiple colonies in an area results in an audible and ubiquitous crackling sound in locations where they are present (Everest, 1948; Hazlett and Winn, 1962; Lammers *et al.*, 2008). Variation in snapping shrimp sound levels and snap rates have been found to account for much of the habitat-dependent differences in soundscapes, in terms of sound pressure levels and frequency content, within a variety of marine ecosystems (Radford *et al.*, 2010; Lillis *et al.*, 2014; Butler *et al.*, 2016). The high levels and variability of sound generated by snapping shrimp colonies possibly influence a range of sound-dependent animal activities, including navigation and habitat selection by settlement-stage larvae (Simpson *et al.*, 2008; Lillis *et al.*, 2013; Lillis *et al.*, 2016) and perhaps even function as an auditory cue for migrating cetaceans to avoid rocky shorelines (Allen, 2013). In other instances, sounds of snapping shrimp may interfere with other acoustic signals,

[a)]Electronic mail: ashlee@whoi.edu
[b)]Current address: School of Ocean and Earth Science and Technology, University of Hawaii at Manoa, Honolulu, HI 96822, USA.
[c)]Current address: Gulf Coast Research Laboratory, University of Southern Mississippi, Hattiesburg, MS 39406, USA.

an underwater communication problem for humans and marine organisms alike (Au and Banks, 1998; Chitre *et al.*, 2012; Branstetter *et al.*, 2013). Despite their dominant role in the soundscapes of many marine habitats and potential influence on numerous sound-mediated ecological processes, the acoustic behaviors and ecology underlying snapping shrimp sound production patterns are understudied.

The most well-known function of the snap is as an aggressive behavior employed by shrimp during intra- and inter-specific encounters (Nolan and Salmon, 1970; Schein, 1975); however, other lesser known snapping functions, including prey capture, rock-boring, excavation, and communication with commensal organisms, have also been anecdotally reported (reviewed in Anker *et al.*, 2006) but not quantified. Early experiments to examine the agonistic encounters associated with snapping have been carried out for several species of *Alpheus* and *Synalpheus*. Visual observations examining the introduction of two shrimp described aggressive snapping, lunging, and pinching, as well as retreating movements by one or both individuals; however, snap rates were not quantified (Nolan and Salmon, 1970). Hazlett and Winn (1962) suggested that the cause for snapping appeared to be territorial behavior (during defense against mantis shrimp and other snapping shrimp), and further studies have documented similarly aggressive behaviors (toward con- and hetero-specifics) associated with snapping in several *Alpheus* spp. (Glynn, 1976; Herberholz and Schmitz, 1998; Hughes *et al.*, 2014). These studies provide detailed short-term observations (minutes to hours) of behaviors, including snapping, in anti-predator and territorial contexts, but variation in shrimp acoustic output under different social and environmental conditions or for longer time periods is not documented.

Recent improvements in underwater sound recording ability and increased efforts to sample habitat soundscapes at greater spatiotemporal resolution have generated datasets that reveal complex dynamics in snapping shrimp sound production. For example, a year-long study of a temperate rocky reef soundscape reported seasonal, lunar, and diel variation in the rate of snapping (Radford *et al.*, 2008b). Soundscape descriptions from coral reefs also indicate seasonality and spatial variability in snapping patterns and diurnal rhythms that had previously been overlooked (Lammers *et al.*, 2006; Lammers *et al.*, 2008; Staaterman *et al.*, 2014; Lillis and Mooney, 2016). Snapping shrimp activity measured in coastal southeastern United States oyster reefs showed significant spatial variability and seasonality in snap rates and sound levels, and shifting diel patterns (Lillis *et al.*, 2014; Bohnenstiehl *et al.*, 2016), that are not satisfactorily explained by current knowledge of the roles and timing of snapping shrimp acoustic signals. These field acoustic data show spatiotemporal complexity in snapping shrimp sound production that likely reflect the intricate social structure, behavior, and diverse life histories of these cryptic animals (e.g., Knowlton, 1980; Duffy, 1998; Duffy *et al.*, 2002; Mathews, 2002a,b; Rahman *et al.*, 2003), and are inconsistent with earlier explanations of crepuscular and nocturnal increases in the use of territorial snapping (Schein, 1977).

In an effort to address some of the factors underlying the variability in acoustic behavior, in the laboratory we examined the snapping patterns of two of the dominant alpheid species in coastal and estuarine reef habitats of the Southeast United States and Gulf of Mexico (*Alpheus heterochaelis* and *Alpheus angulosus*) (Spence and Knowlton, 2008; Hughes *et al.*, 2014). The central aim of this study was to document snapping patterns under controlled conditions in the laboratory to provide new insight into the patterns of variation in snapping shrimp sound production observed in field data. First, experiments were conducted to test the hypothesis that snapping shrimp produce sound spontaneously (i.e., without external provocation), and to quantify the daily patterns in individual sound production as well as its dependence on sex and size. Second, we compared the sound emission rates of shrimp in different social conditions (i.e., alone, in the presence of same and opposite-sex shrimp, and for a multiple shrimp group) to gain insight into variation in snap context as a potential explanation for temporal variation in sound production. Passive acoustic recording technology and automatic snap detection allowed continuous undisturbed observations of animal acoustic activity, enabling quantification of sound production patterns for a high number of subjects and over relatively longer periods than had previously been measured via visual techniques.

II. MATERIALS AND METHODS

Experiments were conducted at the Woods Hole Oceanographic Institution (WHOI) Environmental Systems Laboratory facility between April and August 2016 to examine snapping shrimp sound production and relate snap rates to biological factors (e.g., sex, morphometrics, species) and social condition (solitary, pairs, group). Initial acoustic and video observations of isolated shrimp found that snapping occurred spontaneously, without external provocation or disturbance; therefore, the individual spontaneous snap rate was measured for each subject. Additionally, measurements of snap rates were made for shrimp in different pair combinations (detailed below). A total of 108 wild-caught snapping shrimp were used in the experimental trials, 72 *A. heterochaelis* and 36 *A. angulosus*. All measurements described herein were made for shrimp in constant 20 °C temperature seawater, representative of the mid-range of the population's ambient temperature exposure (approximately 8 °C–29 °C; Bohnenstiehl *et al.*, 2016). While variations in environmental factors (e.g., temperature, light regime, dissolved oxygen) are likely to also affect the snap rates (Watanabe *et al.*, 2002; Bohnenstiehl *et al.*, 2016), the goal of this work was to use controlled laboratory experiments to first provide baseline measurements and comparisons of sound output in relation to social context and individual characteristics. Future work will address the interplay of environmental factors and shrimp bioacoustic activity.

A. Collection and housing of animals

Snapping shrimp were collected by hand in coastal North Carolina, USA, during low tides at oyster bed areas in two locations near Duke Marine Laboratory in Beaufort:

within the North River Estuary and along the shoreline of Pivers Island. Distinctive morphological traits (claw shape and setae) and coloration (antennules and uropod spots) of *A. heterochaelis* individuals clearly fit published species descriptions (Williams, 1984; Spence and Knowlton, 2008), and were easily identified upon collection at the North River site. However, a second smaller *Alpheus* species was found exclusively at the Pivers Island site and did not unmistakably match morphological descriptions, so it was not possible to identify these individuals at the time of live experimentation. These shrimp were later identified as *A. angulosus* based on detailed examination of additional morphological characteristics of preserved specimens (Wicksten and McClure, 1997; McClure, 2002; Heard, 2016). Sex was determined for each *A. heterochaelis* individual based on minor chela morphology (Schein, 1975), and females outnumbered males 2:1 in our sample with 10%–50% of shrimp found in pairs for a given collection date. Because species and sex could not be determined unequivocally at the time of experiments for *A. angulosus*, only the individual snap rates were measured for this species, while individual, pair combination, and group rates were measured for *A. heterochaelis*.

Following transportation (1-day shipping) to the Environmental Systems Laboratory at WHOI, shrimp were housed individually in an outdoor seawater laboratory enclosed by transparent plastic (ambient light-cycle), where they each were provided a 1-liter mesh-sided container with shells and gravel as shelter within a larger shaded flow-through seawater table. Shrimp were fed rations of dried shrimp pellets every three days during the experimental period. This feeding regime was established based on observations that shrimp maintained full guts and consistent food supply within their containers at this rate. Shrimp were acclimated for at least three weeks in laboratory conditions prior to snap rate measurements. All shrimp used for individual snap rate experiments (June 2016) were collected in early May 2016. Pair snap rate experiments were conducted using shrimp from July 2015 and May 2016 collections.

Each shrimp was digitally photographed at the time of experimental use, and body measurements were made using ImageJ open source image-processing software. Total body length (mm) was measured (tip of the rostrum to the end of the telson), and approximate snap claw area (mm^2) was calculated based on the palm length (tip of the dactylus to carpus) and width of the major chela. Neither shrimp missing major chelae nor animals that had recently molted (within two days of the start of the experiment) were used in snap production experiments. Shrimp photographs were also used to later confirm the species identifications and sex determinations made at the time of trials.

B. Experimental setup

Twelve identical 5-liter flow-through plastic experimental tanks were used to monitor snap production of individual or pairs of shrimp over 24-h trials (Fig. 1) under an ambient light cycle. During trial periods there was no other activity or intrusions within the laboratory, and mesh was secured over the top of tanks to avoid airborne disturbances. Each
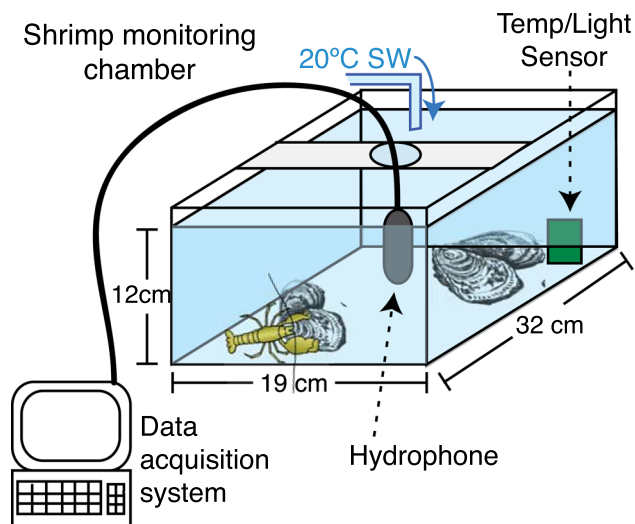

FIG. 1. (Color online) Schematic of experimental tank used to monitor snap production. Twelve identical chambers (each as shown) were used in each trial of individual and pair sound production, each positioned on a foam mat with foam between units. Tanks were provided seawater from a common source and positioned within a shaded seawater table.

tank was placed on an individual closed-cell neoprene foam mat and separated by sound-absorbing open-cell convoluted acoustic foam panels to limit the transfer of sound between experimental units. The 12 replicate tanks were all arranged within a single 2.0×1.0 m seawater table to minimize the effect of any differences in the laboratory environment. Tanks were supplied with 20 °C sand-filtered seawater, exposed to the ambient light cycle, and contained gravel and shells as substrate consistent with the containers in which they had acclimated during non-experimental periods. Each experimental tank was monitored with a HOBO pendant light and temperature sensor (Onset Computer Corporation, Bourne, MA) logging at 1-min intervals, and an HTI-96-min hydrophone (High-Tech Inc., Gulfport, MS; sensitivity: −165 dB re:1 V/µPa, flat frequency response: ∼0.1–30 kHz) recording continuously at a 10 kHz sampling rate, acquiring data in 5-min samples via a data acquisition device (16-bit, NI USB-6343, National Instruments, Austin, TX) connected to a laptop running purpose-written MATLAB acquisition code (MATLAB 8.6, Mathworks, Cambridge, MA).

C. Individual and paired shrimp experiments

1. Shrimp monitoring

The snap rate of a total of 84 single shrimp was measured over seven trials conducted in June 2016 (four trials *A. heterochaelis, n* = 48; three trials *A. angulosus, n* = 36). For each trial, 12 shrimp were randomly selected and each assigned to an individual experimental tank. The recording system was initiated 15 min after introduction of shrimp and continued undisturbed for 24 h. Subsequently, three trials were carried out to measure the sound production for same-sex and opposite-sex pairs of snapping shrimp. In these trials, two individuals were randomly selected to form pairs of female–female (*n* = 11), male–male (*n* = 11), and female–male (*n* = 14), and randomly assigned to experimental tanks.

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Recordings were started immediately upon the simultaneous introduction of the shrimp to the tank, to monitor the 30-min introductory period upon exposure to the conspecific, followed by a 24-h trial as in individual snapping trials.

2. Snap detection and data processing

Following the completion of each individual or pair trial, files were digitized and a threshold detector was applied using MATLAB to detect and count snaps in 5-min samples for each tank for the duration of the 24-h trial. The threshold detector was based on the relative amplitudes and short duration corresponding to snaps elicited during method development—owing to their unique production mechanism, snapping shrimp snaps are highly stereotyped and typically saturate the signal in small tanks, making them easily distinguishable from other sounds. Few other high amplitude impulsive sounds were observed in any tank recordings. Following automatic detection, waveforms of all snaps detected were visually examined and any false detections (e.g., caused by mechanical interference of shrimp or rare transient external noise) were removed from the dataset. The total number of snaps and time of snaps was then determined for each individual shrimp or shrimp pair for the duration of the 24-h trial, from which a total snap rate was calculated as the number of snaps per hour (per hour rates were used to allow comparisons of rates from different length segments of the day). For each pair, a snap rate was also calculated for the initial 30-min introductory period. All snap rates are reported as the mean ± standard error (S.E.). Because previous work observed strong diel cycles in snapping in field recordings (Lammers et al., 2008; Bohnenstiehl et al., 2016; Lillis and Mooney, 2016), experimental snap rates (snaps per hour) within different periods of the day (dawn, day, dusk, night) were also assessed for all individuals and pairs. For this analysis, dawn was defined as the period between the beginning of astronomical twilight and sunrise, day was between sunrise and sunset, dusk was between sunset and the end of astronomical twilight, and night was between the end of dusk and beginning of dawn. All local twilight, sunrise, and sunset times were obtained from the U.S. Naval Observatory's Astronomical Applications Department data services (http://aa.usno.navy.mil/data/docs).

3. Statistical analysis

Snap rate datasets for individuals and pairs were first checked to determine if assumptions were met for parametric statistical models (i.e., normal distribution and homoscedasticity of errors). Because individual snap rate data did not meet these criteria, a generalized linear mixed effects model (GLME) assuming a Gamma error distribution (log link) was fit to test for fixed effects of sex (in *Alpheus heterochaelis*) and time of day on individual snap rate of each species, with trial (blocking factor) and subject (repeated measure) as random effects.

Pair snap rates in the 1-h acclimation period were compared to the post-acclimation 24-h trial snap rate using a GLME (Gamma distribution, log link) with trial and subject as random factors. Time-of-day and pair type predictors of snap rates were further examined by fitting a GLME using

the fixed factors of pair type and time-of-day, with trial (blocking factor) and pair (repeated measure) as random effects. As month of trial was not a significant factor for snap rate, it was removed from the final models of pair snap rate. All statistical procedures were carried out using the MATLAB (v.9.1) Statistical and Machine Learning Toolbox.

D. Snapping shrimp mesocosm

To compare snap rates generated by an interacting group of shrimp to the snap rates earlier determined for individuals and pairs, ten snapping shrimp (five female and five male *A. heterochaelis*) were randomly selected and placed in a 75-liter shallow mesocosm tank ($115 \times 48 \times 15$ cm). The tank contained sand and gravel substrate covered with larger cobble and oyster shells to provide plentiful sheltering material for shrimp and was supplied with flow-through $20\,^\circ$C seawater. The shrimp mesocosm was provided ample food (commercial shrimp pellets) during the experimental period. The experiment began on 19 August 2016, with 1-min of acoustic recording collected every 10-min for a three week period, as well as light and temperature measurements using a HOBO data logger as above. Recordings were made at a 48 kHz sample rate using a battery-powered DSG-ST audio recorder (Loggerhead Instruments, Sarasota, FL), equipped with an HTI-96-min hydrophone (High-Tech Inc., Gulfport, MS; sensitivity: -185 dB re:1 V/μPa, flat frequency response: $\sim$0.1–30 kHz) on an extended 3 m cable positioned within the tank. Using purpose-written code in MATLAB (v.9.1), raw DSG files were converted to pressure units (μPa) and a threshold detector was applied to detect and count snaps in all 1-min samples collected. Samples were further divided into dawn, day, dusk, and night periods according to the methods described above for individual and pair trials. Snap rates (in snaps per hour) were calculated in each period for each sample day. To examine the effect of time-of-day on the group snap rates, a Friedman test (for non-parametric repeated measures) was applied with the snap rate measured in dawn, day, dusk, and night of each 24-h sample day treated as a repeated measure.

III. RESULTS

A. Individual snap rates

Snapping shrimp acoustically monitored in isolated tanks, left undisturbed, were found to snap sporadically. This snapping behavior was not linked to any obvious abrupt change in their environment (e.g., light level, external sound) and individuals in the same trial (i.e., exposed to the same ambient environment) did not snap simultaneously. Snapping shrimp showed high inter-individual variability in this solitary sound production—single *A. heterochaelis* generated between 1 and 26 snaps during 24-h monitoring periods. The mean snap rate measured for *A. heterochaelis* individuals was 0.40 snaps/h (S.E. = 0.03, $n = 48$). The snap rate of female shrimp was significantly more variable compared to male shrimp [Fig. 2(a); Bartlett's statistic for unequal variances = 5.3, $p < 0.05$]. No interaction between sex and time-of-day was detected for snap rate, thus this was excluded from the best-fit generalized linear model. Sex had
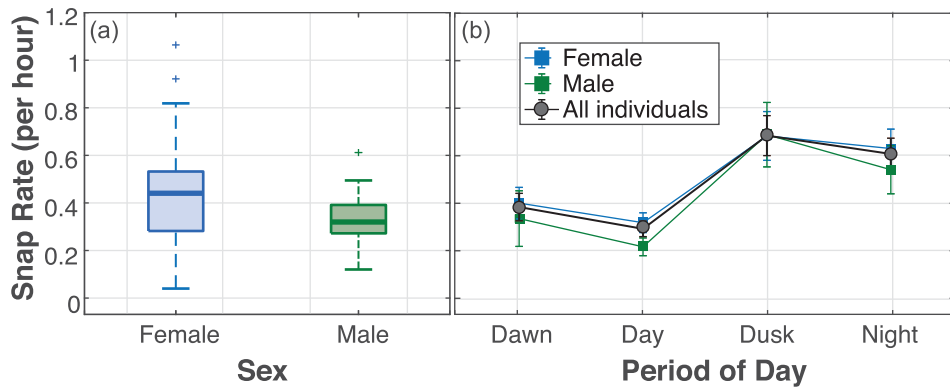
FIG. 2. (Color online) *Alpheus hetero-chaelis* individual snap rate patterns. (a) Snap rate (snaps/h) produced by female and male snapping shrimp during 24-h trials. Box plots show median values (solid horizontal lines), 50th percentile values (box outline), 90th percentile values (whiskers), and outlier values (+ signs). (b) Mean snap rate ($\pm$ S.E.) for dawn, day, dusk, and night periods of 24-h trials for females, males, and pooled data. No significant difference in snap rate or timing was detected between sexes.

no significant effect on snap rate [Fig. 2(a); GLME: $F_{1,187} = 1.41$, $p = 0.24$], but time-of-day was a significant predictor of *A. heterochaelis* snap rates, with dawn and day snap rates lower than dusk and night snap rates [Fig. 2(b); GLME: $F_{3,187} = 9.13$, $p < 0.0001$].

A. angulosus individuals generated between 0 and 45 snaps during the 24-h monitoring periods (zero snaps were detected for three individuals), and the mean individual snap rate measured for this species was 0.45 snaps/h (S.E. $= 0.07$, $n = 36$). No significant difference in overall snap rate was found between the two alpheid species [Fig. 3(a); $F_{1,266} = 0.12$, $p > 0.05$]; however, *A. angulosus* had more variable snap rates and a greater number of outliers [Fig. 3(a), Bartlett's statistic for unequal variances $= 34.95$, $p < 0.001$]. *A. angulosus* snap rates showed the same daily pattern as *A. heterochaelis* (elevated dusk and night snap rates), with time-of-day as a significant model predictor [Fig. 3(b); GLME: $F_{3,140} = 3.0$, $p < 0.05$]. Individual shrimp size (total length and snap claw area) did not have an effect on snap rates for either species; no significant correlations were detected between snap claw size and snap rate (Fig. 4).

B. Pair snap rates

Snapping shrimp exhibited high levels of snapping immediately upon exposure to another shrimp [Fig. 5(a)]. This initial snapping bout diminished within 30-min of introduction.

Shrimp pairs produced a snap rate of 14.4 ± 1.73 snaps/h during the introductory period, which is significantly higher compared to a mean snap rate of 3.2 ± 0.34 snaps/h in the subsequent 24-h trial (Fig. 5; $F_{1,70} = 53.12$, $p < 0.0001$). Snap rates during the introductory phase did not differ between the pair types [Fig. 5(a)]; however, the 24-h snap rate was affected by pair-type, with same-sex pairs generating overall more snaps compared to opposite-sex pairs [Fig. 5(b); GLME: coefficient $= 0.76$, $t(120) = 1.95$, $p < 0.05$]. This pattern in snap rates varied depending on period of the day—a significant interaction was observed for the predictors of time-of-day and pair type (Fig. 6; $F_{1,120} = 4.97$, $p < 0.001$). Opposite-sex pairings generated significantly lower snap rates compared to same-sex pairs, but only at dusk and night when same-sex snap rates were highest [Fig. 6(a); GLME: dusk coefficient $= -1.2$, $t(120) = -3.61$, $p < 0.001$; night coefficient $= -0.70$, $t(120) = -2.11$, $p < 0.05$]. Time-of-day was a significant predictor for snap rates of both male and female same-sex pairs (but not for opposite-sex pairs), with snap rates significantly higher at dusk and night compared to day [Fig. 6(b); GLME: dusk coefficient $= 0.94$, $t(120) = 3.97$, $p < 0.001$; night coefficient $= 0.77$, $t(120) = 3.23$, $p < 0.01$].

C. Group snap rate time-series

Recordings were collected at a 10% duty cycle in the snapping shrimp mesocosm over 21 days, resulting in a time
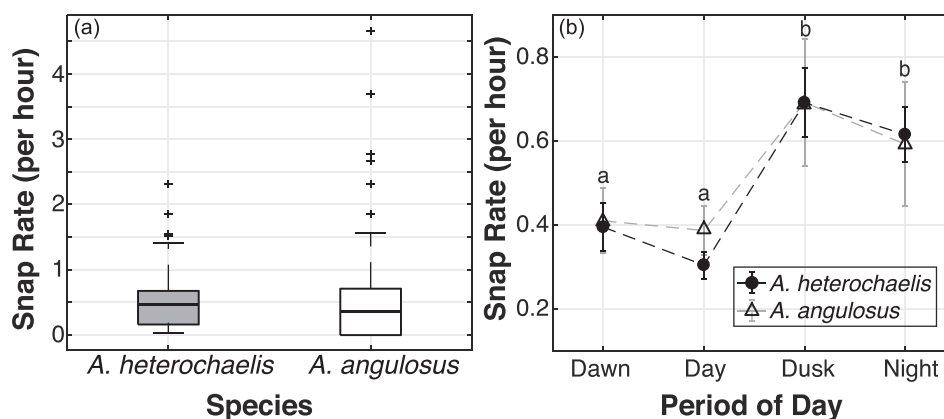

FIG. 3. Species comparisons of individual snap rate. (a) Snap rates (snaps/h) produced by individual *Alpheus heterochaelis* and *Alpheus angulosus* snapping shrimp during 24-h trials. Box plots show median values (solid horizontal lines), 50th percentile values (box outline), 90th percentile values (whiskers), and outlier values (+ signs). (b) Comparison of snap rates (mean $\pm$ S.E.) at dawn, day, dusk, and night periods between *Alpheus heterochaelis* and *Alpheus angulosus* tested in June 2016 trials. Both species showed significantly higher snap rates during dusk and night periods in these trials compared to dawn and day snap rates (significant differences denoted by different lower-case letters).
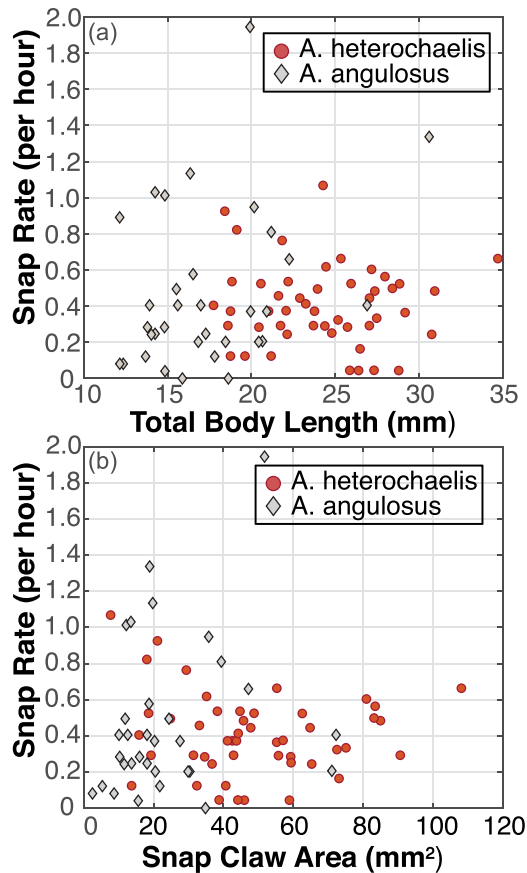
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FIG. 4. (Color online) Scatterplots of individual snap rates with shrimp size metrics. (a) Total body length (mm), and (b) snap claw area (mm²), shown for each *Alpheus* species. *A. angulosus* trended toward higher snap rates with size, but no statistically significant correlations existed at the $p < 0.05$ level.

series of 3003 one-minute samples. The snap rate measured for this group of 10 shrimp was 10.57 ± 0.75 snaps/h. Observed snap rates were highly variable day-to-day during this three-week experiment. Results showed 12 days in which nighttime snap rate was higher than daytime and nine days in which daytime snap rate was higher than nighttime [Fig. 7(a)]; there was no significant effect of time-of-day on snap rates when parsed into dawn, day, dusk, and night,

FIG. 6. (Color online) Time-of-day effects on snap production. (a) Snap rates (mean snaps per hour $\pm$ 1 S.E.) produced by pairs during the different periods of day. Opposite sex pairs produced significantly fewer snaps during dusk and night compared to same-sex pairs. (b) Comparison by type of pair for snap rates within different diel periods. Mean ($\pm$ S.E.) per hour snap rate calculated over 24-h trials within the four periods of the day (dawn, day, dusk, night from left to right within each group of bars). Asterisks indicate significantly lower snap rates during daytime for same-sex pairs. Time-of-day had no effect on opposite-sex pair snap rate.

using each sample day as a repeated measure [Fig. 7(b); Friedman's test, $\chi^2_{3,60} = 3.98$, $p = 0.2641$]. Pooled across the three weeks of data collection, the total number of snaps counted throughout the 24-h cycle did not exhibit a consistent diel pattern [Fig. 7(c)].

D. Summary of findings

The overall snap production by individual snapping shrimp recorded was highly variable, ranging from 1 to 26 snaps for *A. heterochaelis* and 0–45 snaps for *A. angulosus*
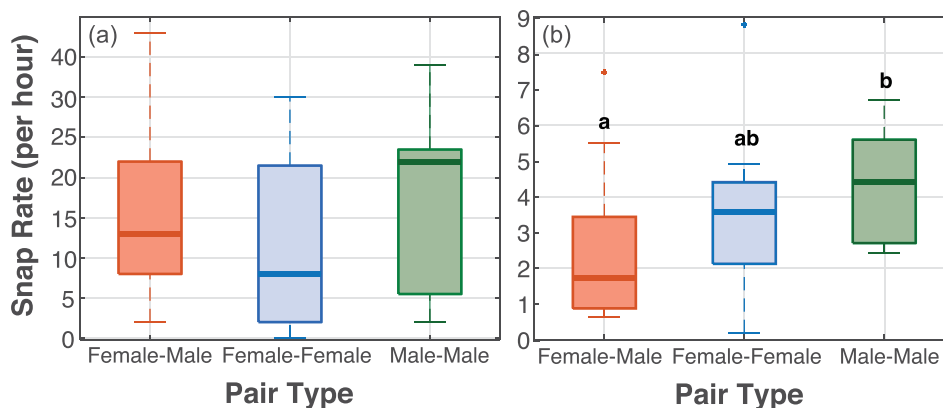

FIG. 5. (Color online) *Alpheus heterochaelis* pair snap rate compared by type of pairing. Observed snap rates for female–male, female–female, and male–male pairs of shrimp during (a) introductory acclimation periods (30-min), and (b) subsequent 24-h long trials. Snap rates were significantly higher in the first 30-min of trials compared to the overall trial snap rates. *Note that the *y*-axes differ in scales. Box plots show median values (solid horizontal lines), 50th percentile values (box outline), 90th percentile values (whiskers), and outlier values (+ signs). Letters in (b) denote significant differences between snap rates for different types of pairings.
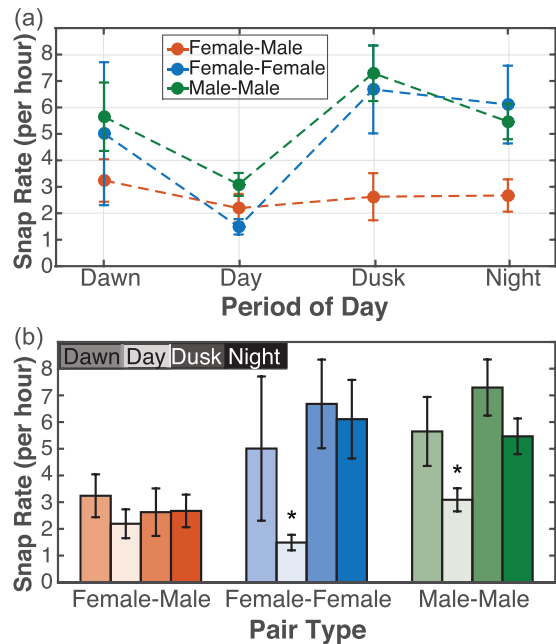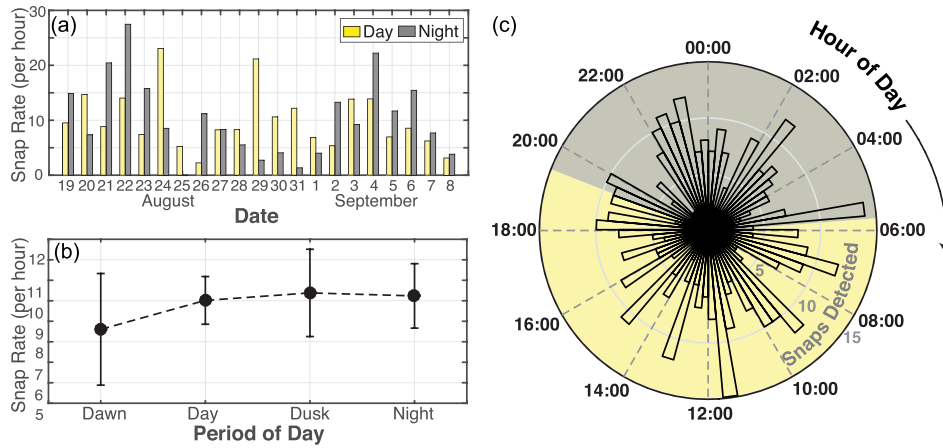
FIG. 7. (Color online) Snapping patterns in a mixed-sex group. (a) *Alpheus heterochaelis* group snap rate patterns by day and night for each day of three week monitoring. (b) Mean snap rates (± 1 S.E.) detected for the mesocosm colony (five males and five females) during each period of the day in August–September 2016 (N = 21 days). (c) Summary of total snaps detected during 21 days within the mesocosm by hour of the day. Angular histogram shows frequency of snaps recorded throughout the daily cycle.

during a 24-h monitoring period, with mean snap rates (±1 S.E.) of 0.40 ± 0.03 and 0.45 ± 0.07 snaps/h, respectively (Table I). Snap rates for solitary shrimp were significantly higher at dusk and night compared to dawn and day periods; shrimp sex and size did not significantly affect these snap rate patterns. Pairs generated between 4 and 211 snaps in a 24-h trial, with mean snap rates approximately seven times higher than measured for individual spontaneous snapping. Snap output increased from opposite-sex pairs to female pairs to male pairs. Day snap rate was significantly lower than at dawn, dusk, and night periods for same-sex pairs but not in opposite-sex pairs or for the mixed-sex group. For a group of ten shrimp measured over 21 days, snap rate was 10.57 ± 0.75 snaps/h. When normalized to a per-shrimp snap rate, this mixed-sex group generated a range of snap rates comparable to opposite-sex pairs, and overall male–male pairs showed the highest snap rates on a per shrimp basis (Table I).

IV. DISCUSSION

Continuous acoustic observations of snapping shrimp in laboratory experiments reveal variability in sound production patterns related to time-of-day and social context, expanding our understanding of factors that can influence acoustic output for this group of animals. The experiments presented here indicate that, in naturalistic conditions in the lab, snapping can occur commonly under isolated conditions in addition to instances of provocation, and that daily patterns of shrimp sound production are shaped by interactions between individual variability and social context. The spontaneous snapping behavior documented here had not previously been described and quantified for *A. heterochaelis* or *A. angulosus*. Production of snaps by lone shrimp implies that the snapping serves functions beyond direct interaction and that solitary snapping could contribute to the complex patterns observed in field recordings. Recently, a similar unprovoked snapping behavior was observed in southern hemisphere snapping shrimp species during a study examining ocean acidification effects (Rossi *et al.*, 2016). That this behavior was frequently detected for two species here, as well as observed in a geographically separated species, suggests that it might be a widespread adaptation in the Alpheidae family and a significant part of snapping shrimp acoustic ecology.

Most previous work on snapping shrimp interactions has focused on the visual, chemical, and hydrodynamic communication aspects of snapping, and some authors have suggested that the sound produced may be a by-product of the visual/hydrodynamic signal (Herberholz and Schmitz, 1998; Schmitz, 2002; Schmitz and Herberholz, 1998). The present results, showing higher snap production during periods without daylight and the occurrence of solitary snapping, without the ability to visually or chemically sense conspecifics,

TABLE I. Summary of results, including the mean (± S.E.) per hour snap rate, normalized per shrimp snap rate, and significant time-of-day effects, observed for shrimp individually, paired, and in a ten-shrimp group. For time-of-day effects, periods with a significant effect and direction are indicated, and "n.s." denotes a non-significant result.

	Individuals		Pairs (*Alpheus heterochaelis*)			Group
	Alpheus heterochaelis	*Alpheus angulosus*	Female–Male	Female–Female	Male–Male	5 Male + 5 Female
Measured mean snap rate (hour^{-1})	0.40 (± 0.03)	0.45 (± 0.07)	2.45 (± 0.55)	3.46 (± 0.69)	4.33 (± 0.49)	10.57 (± 0.75)
Normalized mean snap rate (hour^{-1} shrimp^{-1})	0.40 (± 0.03)	0.45 (± 0.07)	1.23 (± 0.28)	1.73 (± 0.35)	2.17 (± 0.25)	1.06 (± 0.08)
Time of day effect	⇧ dusk and night	⇧ dusk and night	n.s.	⇧ dusk and night	⇧ dusk and night	n.s.

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suggest that snapping could serve as an acoustic communication signal with conspecifics, competitors, or predators farther away than those in direct visual/tactile contact, for example as a warning signal or sexual advertisement, as is known for other crustaceans (Popper *et al.*, 2001; Staaterman *et al.*, 2010). Additional reasons for solitary snapping could include preventatively maintaining individual spacing or territory (Waser and Wiley, 1979). It would follow from these hypothesized functions that the variability in snap rate among individuals could relate to their reproductive status, molt stage, or physiological state, factors outside of the scope of this study. Future tests of these relationships are needed to better understand the meaning of this signal.

Though a difference in individual snap rate between the sexes was not significant, female snap rates were significantly more variable than males, and a previous experiment, though with a more limited sample size, found females to snap at significantly higher rates than males (Lillis and Mooney, 2016). These results suggest that sexual differences in this spontaneous snap production may exist and could relate to its potential purpose, for instance as a mate advertisement. The possible subtle behavioral differences in the function of male and female individual snapping warrant further examination. Individual snap rate overall did not significantly differ between the two co-occurring species or appear to be strongly influenced by total length or claw size. This is perhaps unsurprising if the unprovoked snap behavior is not necessarily related to aggressive or competitive purposes, where species, size, and sex have been related to shrimp behavior during interactions (Hughes, 1996; Hughes *et al.*, 2014). Complimentary visual observations with snap rate measurements will be needed to better disentangle the behavioral stimuli and role of spontaneous snapping.

The results of our snap rate measurements for pairs confirm that snaps are produced more often in intra-specific interactions compared to individuals and illustrate sex differences in snapping behavior. Variation found in these snap rates and time-of-day patterns between pair-types suggest that social dynamics within shrimp populations might contribute to field soundscape patterns. Pairs of males generated the highest snap rates over 24-h periods, while heterosexual pairs snapped at lower rates, suggesting that same-sex pairs were interacting more aggressively than opposite-sex pairs (Hughes *et al.*, 2014). Previous reports from visual observations of short intra-specific interactions (i.e., <1 h) have found that aggressive snapping and fighting occurs more frequently between same-sex shrimp pairs than between heterosexual pairs (Hazlett and Winn, 1962; Vannini, 1985; Hughes *et al.*, 2014). This trend held over the longer trial length (24 h), but interestingly, no significant difference was found in the initial snap activity (30-min) of different types of pairing. This is in contrast to a study by Hughes *et al.* (2014) that found higher levels of aggression and snapping by paired females compared to males and compared to opposite-sex pairs during only 15-min observations. In our experiments, the acoustic response of pairs of conspecifics measured immediately upon encounter does not reflect the sexes involved in the interaction. However, the differences detected over longer time periods suggest a shift in the sexual behavioral dynamics after initial introductions (e.g., opposite-sex intra-pair aggression decreases more than within same-sex pairs).

Daily activity patterns for alpheid species are not well known; although, early studies of field recordings suggested that shrimp were more acoustically active at dusk and night (Johnson *et al.*, 1947; Knowlton and Moulton, 1963), and laboratory experiments by Nolan and Salmon (1970) found crepuscular increases in snapping for all-male groups. More recent reports of population-wide snapping patterns inferred from passive acoustic monitoring showed crepuscular peaks in snap rates and variable daytime or nighttime elevated snapping (Bohnenstiehl *et al.*, 2016). The daily cycles of snapping measured here for individuals and same-sex pairs under controlled laboratory conditions followed the dusk and night tendency of elevated snapping; however, opposite-sex pairs and our mixed-sex mesocosm did not. Notably, male–female pairs and the mixed-sex mesocosm also exhibited lower overall per shrimp snap rates than same-sex pairs. This may be due to fewer aggressive interactions once opposite-sex animals bond, as these species are known to be socially monogamous and live in heterosexual pairs (Mathews, 2002a; Rahman *et al.*, 2003; Mathews, 2007; Dabbagh *et al.*, 2012; Hughes *et al.*, 2014). These data underscore the deficit in relevant ecological knowledge on snapping shrimp pairing behavior, territory size, home range, population density, and other life history factors in natural populations that may affect sound production. Investigating shrimp snap production under different demographic ratios and environmental pressures, and over longer time periods, will be key to further interpreting the ecological significance of acoustic patterns in the natural environment.

Snapping shrimp comprise over 600 species distributed from tropical to temperate regions, and represent a diversity of life history strategies and social dynamics (Anker *et al.*, 2006). This study describes acoustic behavioral patterns for common alpheids in just one region; the drivers of sound production by snapping shrimp in other habitats remain an open question. By using acoustic sampling to measure activity patterns and acoustic behaviors of visually cryptic species, this work highlights the use of acoustic monitoring and analysis in providing information on patterns in biological activity that are not possible to detect with conventional sampling techniques (Knowlton, 1980). Quantifying sound production in snapping shrimp and the social contexts that influence the acoustic behavior, informs hypotheses to explain the enigmatic field patterns in snapping and provides a framework for further investigating the unknown shrimp biology and ecology that contribute to soundscape variability. Importantly, establishing the conditions that produce particular snap rates and patterns can enhance our ability to predict and understand the soundscape variation due to snapping shrimp (Watanabe *et al.*, 2002; Jung *et al.*, 2012; Bohnenstiehl *et al.*, 2016). Further studies that aim to make more direct links between snapping shrimp, their behaviors, and broader habitat factors are likely to advance passive acoustic monitoring efforts in shallow water benthic habitats.

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