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Citation: *The Journal of the Acoustical Society of America* **150**, 3288 (2021); doi: 10.1121/10.0006973

View online: <https://doi.org/10.1121/10.0006973>

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Sound pressure and particle motion components of the snaps produced by two snapping shrimp species (*Alpheus heterochaelis* and *Alpheus angulosus*)

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ABSTRACT:

Snapping shrimps are pervasive generators of underwater sound in temperate and tropical coastal seas across oceans of the world. Shrimp snaps can act as signals to conspecifics and provide acoustic information to other species and even to humans for habitat monitoring. Despite this, there are few controlled measurements of the acoustic parameters of these abundant acoustic stimuli. Here, the characteristics of snaps produced by 35 individuals of two species, *Alpheus heterochaelis* and *Alpheus angulosus*, are examined to evaluate the variability within and between the species. Animals were collected from the wild and the sound pressure and particle acceleration were measured at 0.2, 0.5, and 1 m from individual shrimp in controlled laboratory conditions to address the snap properties at communication-relevant distances. The source and sound exposure levels (at 1 m) were not significantly different between these two species. The frequency spectra were broadband with peak frequencies consistently below 10 kHz. The particle acceleration, the sound component likely detectable by shrimp, was measured across three axes. The directional amplitude variation suggests that the particle motion of snaps could act as a localization cue. The amplitudes of the snap pressure and acceleration decreased with distance, yet the levels remained sufficient for the predicted detection range by nearby conspecifics. © 2021 Acoustical Society of America.

<https://doi.org/10.1121/10.0006973>

(Received 26 May 2021; revised 7 October 2021; accepted 9 October 2021; published online 3 November 2021)

[Editor: Arthur N Popper]

Pages: 3288–3301

I. INTRODUCTION

The ocean is a natural gallery for a diverse array of biological, geophysical, and anthropogenic sounds (Wenz, 1962, 1972; Webb, 1998; Hildebrand, 2009). Many ocean animals have evolved the ability to hear and produce sound as they navigate, communicate, and attract mates (Everest *et al.*, 1948; Au, 1993; Fine *et al.*, 2001). Among these diverse soniferous taxa, snapping shrimps (*Alpheidae*) are ubiquitous sound producers (Johnson *et al.*, 1947) found across many temperate and tropical near-shore waters (Williams, 1984). They comprise a diverse taxon, containing numerous genera and species; two of these genera (*Alpheus* and *Synalpheus*) are capable of producing vigorous snaps (Johnson, 1944; Everest *et al.*, 1948; Kaji *et al.*, 2018).

These snapping sounds have been detected in soundscapes across many coastal habitats, including seagrass, coral and oyster reefs, marsh, mangrove, kelp, and artificial and restored habitats (Bohnenstiehl *et al.*, 2016, Butler *et al.*, 2017; 2019; Lillis and Mooney, 2018; Monczak *et al.*, 2019, Monczak *et al.*, 2020; Mueller *et al.*, 2020). The snap pulse is produced by the rapid closure of the major chela (the larger of the asymmetrical claws), resulting in a high-velocity water jet (creating particle motion) and pressure differential (Versluis *et al.*, 2000). As a result, small bubbles of dissolved gases grow in size and form a larger cavitation bubble, which quickly collapses in the surrounding seawater. A short-duration acoustic pulse forms simultaneously with the bubble collapse, creating a high amplitude snapping sound that is a dominant acoustic feature in coastal soundscapes across multitudes of shrimps.

Snapping shrimp snaps have a diverse array of proposed functions. The most well-known function is as an aggressive behavior employed for communication during intraspecific encounters (Nolan and Salmon, 1970; Schein, 1975). An open major chela can function as an honest signal for competitors to assess body size (Hughes, 2000). If an encounter escalates to snapping behavior, the water jet produced by

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the snapping claw acts as a key mechanosensory stimulus, which is detected by setae on the major chela of the receiver (Herberholz and Schmitz, 1998). This signal operates over short distances (average 9 mm; Herberholz and Schmitz, 1999). It is unknown if shrimps are capable of acoustically detecting the snap from the cavitation bubble implosion, which would presumably allow communication over greater distances. The coordinated group snapping of the sponge-dwelling social shrimp *Synalpheus rathbunae* to defend against intruders (Tóth and Duffy, 2005) suggests the possibility of acoustic communication as animals throughout the sponge synchronize their snapping. Additional proposed functions of the snapping behavior include prey capture, rock-boring, excavation, and communication with commensal organisms (Ritzmann, 1974; Conover and Miller, 1978). With a relatively high impulsive amplitude, the snaps may also function as a physical weapon to defend territory by stunning predators or to kill prey (Schein, 1975, 1977; Schmitz and Herberholz, 1998; Schultz, 1998).

Additionally, the lower frequencies of these broadband snaps may act as acoustic cues for larvae seeking appropriate habitat during settlement (Simpson *et al.*, 2005; Lillis *et al.*, 2013; Lillis *et al.*, 2015) as shrimp snaps occur at higher rates near benthic structures like coral and oyster reefs compared to sand or soft sediments (Spence and Knowlton, 2008). For this same reason, the rate of snaps in the soundscape can be used in environmental monitoring to assess the habitat type and quality (Butler *et al.*, 2017; Monczak *et al.*, 2020). Further, the high amplitude and extremely broadband acoustic spectra of shrimp snaps coupled with high snap rates creates a noise that affects an array of taxa from reef fishes to cetaceans (Wiley, 2015). Given this array of functions and consequences of shrimp snaps, characterizing the acoustic parameters of these sounds is important to understand their functions by shrimps and other taxa and best discern their signature in coastal soundscapes.

Early studies of shrimp (*Alpheus* and *Synalpheus*) snaps focused analyses predominantly on the low-frequency component (below 30 kHz; Dobrin, 1947; Everest *et al.*, 1948; Knowlton and Moulton, 1963). However, snaps are broadband in frequency with energy that can extend up to >200 kHz (Au and Banks, 1998). Individual snaps can have peak-to-peak source levels exceeding 210 dB re 1 μ Pa (Schmitz, 2002; Versluis *et al.*, 2000). Despite the diversity of snapping shrimp species and the prevalence of their sounds in the soundscapes of many coastal habitats, we have quantitative acoustic measurements for only a single tropical species (*Synalpheus paraneomeris*; Au and Banks, 1998). The measurements also typically focus on the pressure component of the snap, despite the likelihood that acoustic particle motion is the relevant acoustic stimulus for detection by shrimps (Budelmann, 1992; Popper *et al.*, 2001; Popper and Hawkins, 2018).

Particle motion, a vector providing amplitude and direction, can be measured using displacement, velocity, or acceleration, and these describe the vibratory component of sound, which is the primary acoustic stimulus for marine

invertebrates and many fishes (Fay, 1984; Kalmijn, 1988; Popper and Schilt, 2008; Fay, 2009; Mooney *et al.*, 2010; Popper and Fay, 2011; Roberts, 2015). Particle motion can be detected when the tissues of the body (which are similar in density to water) are accelerated back-and-forth in the water column by the particle motion stimulus, but a denser sensory component, such as a statolith or otoconia, lags behind in this vibration. This differential movement deflects the auditory hair cells and generates a neurological response. Studies have suggested that crustaceans, such as the common prawn (*Palaemon serratus*), lobster (*Nephrops norvegicus*), and hermit crab (*Pagurus bernhardus*), are sensitive (behaviorally or physiologically) to acoustic stimuli (Goodall *et al.*, 1990; Briffa *et al.*, 2003; Lovell *et al.*, 2005; Roberts *et al.*, 2016). The American lobster (*Homarus americanus*) and crabs (*Carcinus* and *Maja*) may use their sensory hair cells of the statocyst and hairfans to enable particle motion detection (Dijkgraaf, 1956; Cohen, 1960; Jezequel *et al.*, 2021). The American lobster is sensitive to the particle motion component of sound below 2 kHz (Pye and Watson, 2004) with the lowest thresholds between 80 and 120 Hz (Jezequel *et al.*, 2021). A recent study (Dinh and Radford, 2021) conducted on the hearing sensitivity of the snapping shrimp *Alpheus richardsoni* suggested a hearing range of 80–1500 Hz with the greatest sensitivity between 80 and 100 Hz (Dinh and Radford, 2021). Snapping shrimps may be able to detect the particle motion component of the cavitation bubble, allowing for snaps to be used for acoustic signaling between conspecifics beyond the detection of the water jet. This leads to the yet unanswered questions of the amplitude of the particle motion component of snaps and the potential communication ranges of these sounds. Such data would provide a perspective of how shrimps may use snaps as a communication signal.

The objectives of this study were twofold. First, we characterized the source acoustic parameters of the snaps produced by two temperate snapping shrimp species, *Alpheus angulosus* and *Alpheus heterochaelis*, in both particle acceleration and acoustic pressure at three distances relevant to potential communication (≤ 1 m). Second, we compared and characterized the acoustic parameters of snaps recorded in the habitat of the study species to compare to our controlled measurements. Taken together, this study improves our understanding of the interspecific variation of one of the most prevalent biological sounds and for the first time, provides the particle motion measurements necessary to predict if these sounds can function as acoustic signals between conspecifics.

II. MATERIALS AND METHODS

A. Shrimp collection and maintenance

We collected snapping shrimps (*A. angulosus* and *A. heterochaelis*) by hand along the riverbank of the May River estuary, Bluffton, SC, during low tides from March 19 to March 21, 2019. The shrimp inhabited an oyster bed habitat and used oyster shells as cover. After capture, we placed

each individual shrimp into their own 50-ml falcon tube filled with local seawater and transported these tubes in a cooler to local laboratory facilities. We maintained the shrimp by conducting full water changes every 12h until they were transported to the Environmental Systems Laboratory (ESL), Woods Hole Oceanographic Institution, Woods Hole, MA.

At the laboratory, we housed individual shrimp in 1-liter circular, prerinsed, plastic containers with custom mesh openings to allow water flow. The animals were maintained at 20 °C (Lillis *et al.*, 2017) in shallow, flow-through tanks with local seawater. We provided slipper shells and small gravel for shelter. The shrimp were allowed to acclimate to local conditions for six weeks before measurements began.

Our method of shrimp capture was opportunistic, and this led to a disproportionate capture of the two species. We captured over 200 *A. angulosus*, yet only 5 *A. heterochaelis*. As such, we used all of the individuals of *A. heterochaelis* and 20 *A. angulosus* for each set of experiments. These animals were moved to an identical separate tank for housing and the seawater temperature was slowly increased to 27 °C, the approximate conditions found in their habitat during the warmer months when snap rates are highest (Bohnenstiehl *et al.*, 2016). To consider the sex and physical size as potential explanatory factors of individual variation in the acoustic parameters, we made measurements of the body length (from rostrum tip to telson end), body width (maximum torso width), major chela length (from dactylus tip to carpus), major chela width, and wet weight for each individual after the acoustic measurements. We photographed all of the animals used in the measurements for a record and to aid in the sex determination. We used the sexual dimorphism of the major chela to determine the sex (Dardeau, 1984; McClure and Wicksten, 1997; Spence and Knowlton, 2008). As needed, we also used behavioral tests to confirm the sex by pairing the undetermined shrimp with a known male

(Rahman *et al.*, 2004; Mathews, 2002; Hughes *et al.*, 2014). Same sex pairs typically engage in escalated fighting behaviors, whereas a male/female match will show signs of cooperative pairing or minimal fighting compared to same sex matches.

B. Sound pressure measurements

We conducted acoustic measurements of shrimp snaps in a circular tank (diameter, 3.6 m; depth, 2.7 m) filled with local seawater maintained at 27 °C (Fig. 1). For each trial, we carefully moved an individual shrimp to a custom-constructed plastic-meshed rectangular cage (6 cm × 2.5 cm × 2.5 cm; 1 mm thick plastic). The cage was hung in the water column using thin monofilament fishing line, and a weight hung below the cage acted as a ballast for stability. The center of the cage was positioned at 0.65 m depth. We placed three Reson TC-4013 hydrophones (Teledyne Reson, Slangerup, Denmark; sensitivity, -211 ± 3 dB re 1 V/ μ Pa, with a usable frequency range from 1 Hz to 170 kHz) at distances of 0.2, 0.5, and 1 m from the center of the cage to simultaneously record the snaps at these distances (Fig. 1). The hydrophones were at a minimum distance of 1 m from the tank wall, which in pilot testing was determined to sufficiently reduce interference from the wall, bottom, and surface reflections so we could analyze a pure snap from the direct path. The hydrophone outputs were passed through a KH 3382 filter (Krohn-Hite Corporation, Cambridge and Brockton, MA) programmed at 200 Hz–150 kHz bandpass. We used a data acquisition device (16-bit, NI USB-6251, National Instruments, Austin, TX) implemented from a laptop and customized MATLAB acquisition code (MATLAB 8.6, MathWorks, Cambridge, MA) set to record 6 min of continuous data at a sample rate of 300 kHz per channel.

Each animal was allowed 10 min to acclimate before snap induction and recording began. Because the snap rates of individual, isolated shrimp are relatively low (ca. 1/h;

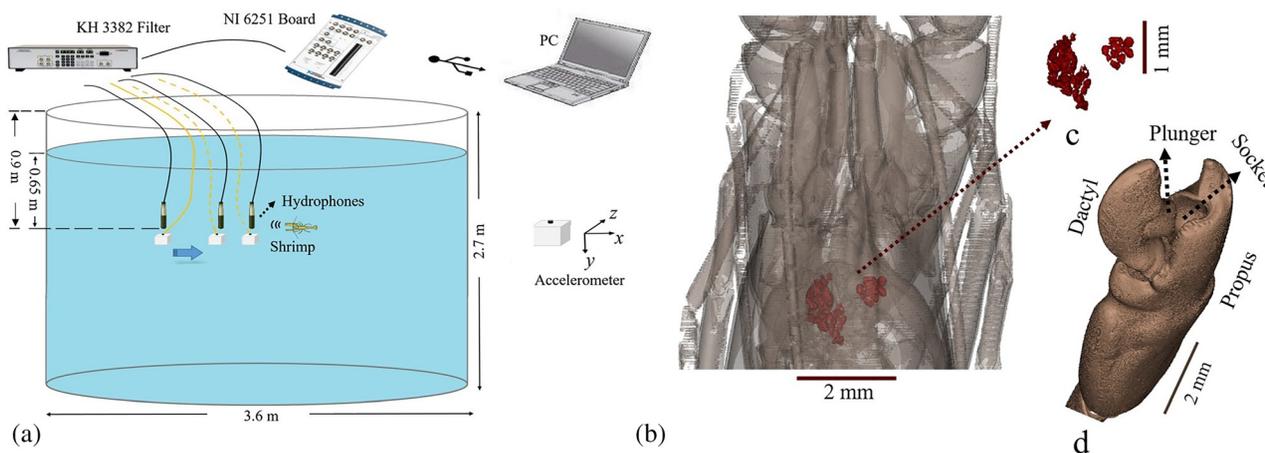


FIG. 1. (Color online) (a) The diagram of the setup used to measure the acoustic characteristics of the snaps from *A. heterochaelis* and *A. angulosus*. Three TC 4013 hydrophones were located at distances of 0.2, 0.5, and 1 m from the location of the snapping shrimp test chamber. The accelerometer measurements differed in that the same distances were measured sequentially (blue arrow indicates the order in which the distances were measured). The sound pressure and acceleration were recorded separately. The acoustic data were transmitted to a bandpass filter and data acquisition board and saved for subsequent analysis. (b) The micro-computed tomography reconstruction of a snapping shrimp head (*Alpheus hoplocheles*; 3.9 cm in body length) performed by the authors, (c) the statolith used for sound reception, and (d) reconstruction of the major chela of the *A. hoplocheles* are shown.

Lillis and Mooney, 2016), we induced snaps by carefully inserting a short piece of monofilament nylon fishing line attached to the end of a wooden dowel into the cage (following Au and Banks, 1998). This agitated the shrimp and caused them to produce snaps at a higher rate than they would without any stimulus. We customized the software to record the impulses that exceeded a set threshold and validated snaps both manually and through customized MATLAB code. For each specimen, we recorded up to three 6-min trials. If a shrimp (*A. angulosus*) produced less than five snaps over the three trials, we replaced it with another randomly selected candidate. In total, we recorded the pressure component of 285 snaps from 20 *A. angulosus* (9 females and 11 males) and 64 snaps from 5 *A. heterochaelis* (1 female and 4 males). The morphological measurements of the 20 individuals of *A. angulosus* were used to consider the influence of the body size on snaps and the variation between males and females.

C. Particle motion measurements

We measured the particle motion using the same tank, general configuration, and procedure as described above. However, for these measurements, we replaced the hydrophones with a single customized PCB 480B21 conditioner [frequency range, ($\pm 5\%$) 0.15–100 000 Hz] and W356 B21 accelerometer {PCB Piezotronics, NY; sensitivity, 10 mV/g [1.02 mV/(m/s²)]; flat frequency response, 10 Hz–10 kHz, $\pm 2.2\%$ }. The sampling frequency was 250 kHz, and the cut-off frequency of the low-pass filter was 10 kHz. We measured the particle motion along three axes (x , y , and z directions, thus, three channels) at 0.2, 0.5, and 1 m from the shrimp; however, the limitation of one accelerometer required us to measure the particle motion at these distances sequentially instead of simultaneously. We recorded first at 1 m from each animal, and then moved the accelerometer to 0.5 m and then 0.2 m for another two rounds of measurements. At each distance, we allowed the animals to acclimate before initiating the recordings. We conducted a maximum of three 7.5-min duration trials for each animal at each distance and, again, replaced individuals of *A. angulosus* if they produced less than five snaps across the three trials. We began by using the same 25 shrimp (5 *A. heterochaelis* and 20 *A. angulosus*) from the sound pressure measurements; however, we replaced 10 *A. angulosus* during the course of the particle motion study for a final female to male sex ratio of 8:12. For the particle motion measurements, we recorded a total number of 199 snaps, 175 snaps, and 254 snaps at 0.2, 0.5, and 1 m, respectively, from 20 *A. angulosus* (8 females and 12 males). We recorded 60 snaps, 57 snaps and 85 snaps at 0.2, 0.5, and 1 m, respectively, from *A. heterochaelis* (1 female and 4 males).

D. Data analysis

We used customized the MATLAB scripts (MathWorks, Cambridge, MA) to set a threshold to automatically detect and extract the snaps from the digitized pressure and particle

motion data. This threshold was based on the difference in amplitude between the snaps and background noise in the tank. The snaps were easily distinguishable from the background noise because the tank noise was low relative to the peak amplitude of the snaps. We used the sensitivities of the hydrophone and accelerometer to calculate the pressure and particle acceleration parameters, respectively. We calculated the peak-to-peak sound pressure level (SPL_{pk-pk}) and sound exposure level (SEL) of all of the snaps, and snaps measured at 1 m from the shrimp were used to compare to the estimated peak-to-peak source level in Au and Banks (1998). We calculated the peak and centroid frequencies following the equations and definitions in previous studies (Au, 1993; Au and Banks, 1998; Madsen and Wahlberg, 2007). We calculated the particle acceleration for each axis (x , y , and z) using the sensitivity for each channel and applied the formula $\sqrt{x^2 + y^2 + z^2}$ to compute the total magnitude of acceleration.

We used the Kruskal-Wallis analysis of variance (ANOVA) test (after testing for normality) to determine the significance of the differences between the species in SPL_{pk-pk} , SEL, peak frequency, and centroid frequency for the snaps recorded at each distance. We also used a Mann-Whitney test to compare the snaps recorded at the three distances for both *A. heterochaelis* and *A. angulosus*. All of the statistical analyses were tested using a level of significance of 0.05. To examine whether the same snap was measured simultaneously at three hydrophones, the cross-correlation analysis was applied to estimate the time difference of snaps arriving at 0.2, 0.5, and 1 m.

E. Field recordings

We collected snaps from the field using passive acoustic recorders deployed in the May River estuary (32° 12' 49" N, 80° 52' 23" W), SC (Monczak *et al.*, 2017; Monczak *et al.*, 2019; Monczak *et al.*, 2020) from January 11 to March 1 2019. We deployed Digital SpectroGram (DSG) recorders (Loggerhead Instruments, Sarasota, FL; 20 dB gain; hydrophone sensitivity of -186 dB re 1 V/ μ Pa) at six stations throughout the tidal river estuary, and we programmed these units to record sound for 2 min every 20 min at a sampling rate of 80 kHz. We mounted the recorders in custom-built frames (Mooring Systems Inc., Cataumet, MA), and painted the entire platform with antifouling paint (Type: Trilux 33, AkzoNobel, Amsterdam, Netherlands). We deployed the frames on the bottom with the hydrophones approximately 20 cm above the sediment surface and approximately 10 m from the shore, where the oyster reefs were located. To allow easy deployment and retrieval, a 7-m galvanized chain was attached to the frame, which we then attached to a line and auger along the side of the shore. We serviced the recorders approximately every 90 days for a total of 3 deployments. At the end of each deployment, we downloaded the DSG files and batch converted these files into .wav files using DSG2wav software (Loggerhead Instruments, Sarasota, FL). We used customized MATLAB

scripts (MathWorks, Cambridge, MA) to extract the snaps from the .wav file batches. The snaps generally had a higher amplitude compared to the background noise, and we used a threshold to differentiate the snaps from the background noise for extraction. After converting the data to pressure using the hydrophone sensitivity, the SPL_{pk-pk} , spectrum, and peak frequency of these field snaps were measured using the same method as described above for the laboratory-collected snaps.

III. RESULTS

A. Pressure component of shrimp snaps

A representative snap of *A. angulosus* (Fig. 2) highlights the two portions of each snap—the precursor and a short pulse that is characterized by its rapid onset and high amplitude (similar to Au and Banks, 1998). The cross-correlation analysis showed that the snaps recorded at different distances were significantly co-related ($p < 0.01$). The time differences of arrival for the snaps arriving at the hydrophones at 0.2 and 0.5 m were 0.193 ± 0.041 ms ($n = 349$). The same metric for the snaps arriving at the hydrophones at 0.2 and 1.0 m was 0.535 ± 0.035 ms ($n = 349$). We subsequently aligned the snap peaks recorded at each hydrophone for comparison. The characteristic snap waveform was similar across the three distances (Fig. 2), whereas the amplitude decreased with an increasing distance in both the time and frequency domains (Figs. 2 and 3). The snaps were broadband with the energy extending to over 150 kHz (Fig. 3). The difference in amplitude between the

peak frequency and the lowest amplitude frequency across the recording bandwidth (0.2–150 kHz) was 22.9 dB for *A. heterochaelis* and 24.0 dB for *A. angulosus*. The peak frequencies were consistently below 10 kHz (Fig. 3).

The intraspecific and interspecific variabilities were further addressed (Figs. 4 and 5). The snap amplitudes of *A. heterochaelis* and *A. angulosus* were strikingly similar [Fig. 4(a)] and both decreased linearly with the distance [degree of freedom (df) = 1, $p < 0.01$, $r^2 = 0.95$ for *A. heterochaelis* and df = 1, $p < 0.01$, $r^2 = 0.96$ for *A. angulosus*]. There were no significant differences between the species in the SPL_{pk-pk} measured at each distance ($U = 9655.5$, $p = 0.435$ for 0.2 m; $U = 9794.0$, $p = 0.332$ for 0.5 m; and $U = 9757.5$, $p = 0.357$ for 1.0 m; Mann-Whitney tests). Similarly, the SEL (dB re $1 \mu Pa^2 s$) decreased with the distance [Fig. 4(b)], and there was no significant difference at any distance between these two species ($U = 9018.0$, $p = 0.924$ for 0.2 m; $U = 9035.0$, $p = 0.942$ for 0.5 m; and $U = 9093.0$, $p = 0.995$ for 1.0 m; Mann-Whitney tests). The snap amplitude attenuated by 17.3 ± 2.1 dB ($n = 64$) over the tested range of 0.8 m (from 0.2 to 1 m) for *A. heterochaelis* and 17.2 ± 1.6 dB/m ($n = 285$) for *A. angulosus*.

The peak frequency did not vary significantly with the distance for either species [Fig. 4(c); Kruskal-Wallis ANOVA, $H = 5.849$, df = 2, $p = 0.054$ for *A. angulosus* and $p = 0.845$ for *A. heterochaelis*]. The centroid frequencies of the snaps recorded at the three distances were not significantly different for *A. angulosus* [Fig. 4(d); Kruskal-Wallis ANOVA, $H = 4.396$, df = 2, $p = 0.111$]. However, there was a significant difference with the distance for the centroid

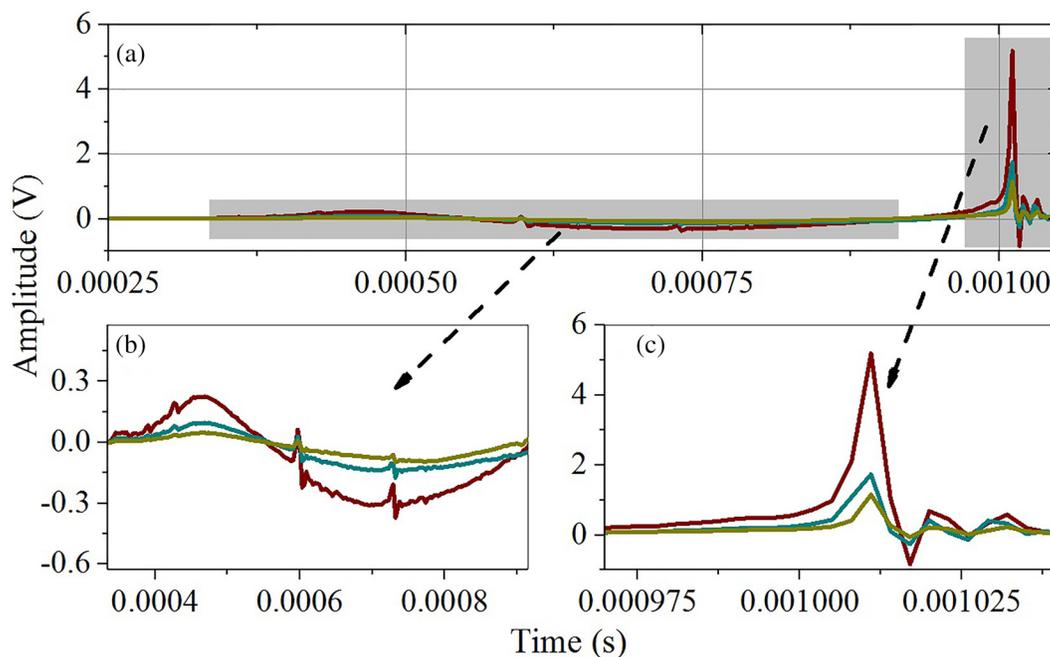


FIG. 2. (Color online) (a) The example waveform of a representative snap from *A. angulosus*. The snap has two distinct components, described as a (b) low amplitude precursor and (c) high amplitude, short-duration pulse. The red, blue, and green lines represent the snaps recorded at 0.2, 0.5, and 1 m, respectively, and were positioned to align the peak amplitudes.

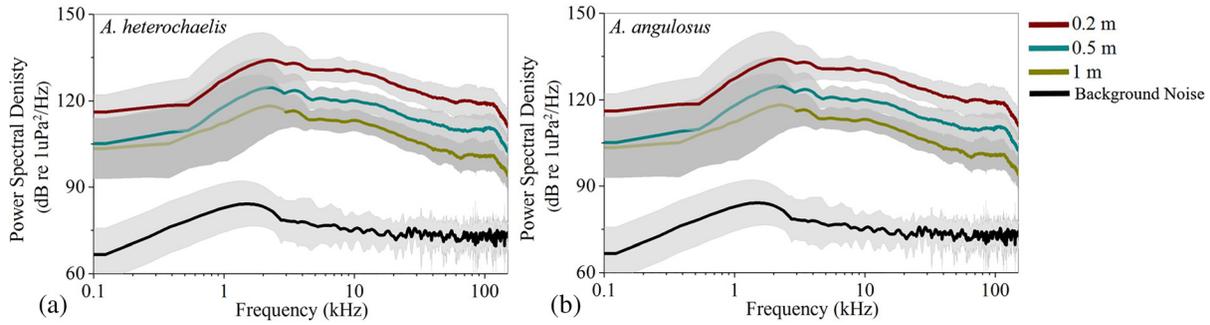


FIG. 3. (Color online) The mean power spectrum and standard deviation (SD) of the snaps recorded at 0.2 (red), 0.5 (blue), and 1 m (green) for (a) *A. heterochaelis* ($n = 64$) and (b) *A. angulosus* ($n = 285$). The background noise in the tank, as recorded at 1 m, is shown in black.

frequency for *A. heterochaelis* [Fig. 4(d); Kruskal-Wallis ANOVA, $H = 11.562$, $df = 2$, $p < 0.01$]. These results suggest that the propagation over the 0.8 m distance primarily affects the amplitude characteristics of the snaps, whereas the frequency characteristics are maintained (Figs. 2–4).

The mean SPL_{pk-pk} for the snaps recorded at 1 m for *A. heterochaelis* was 179.3 ± 7.3 dB re $1 \mu Pa$ ($n = 64$) and ranged from 164.4 to 192.1 dB re $1 \mu Pa$ [Figs. 4(a) and 5(a)]. The mean SPL_{pk-pk} for *A. angulosus* was 180.3 ± 4.2 dB re $1 \mu Pa$ ($n = 285$) and ranged from 164.9 to 187.7 dB re $1 \mu Pa$ [Figs. 4(a) and 5(a)]. The mean SELs at 1 m for *A. heterochaelis* and *A. angulosus* were 128.3 ± 7.7 and 128.7 ± 3.3 dB re $1 \mu Pa^2 s$, respectively [Fig. 4(b)]. Comparing *A. heterochaelis* and *A. angulosus*, the SPL_{pk-pk} , SEL, and peak frequency (Fig. 4) recorded at 1 m were not significantly different ($p > 0.05$), yet there was a significant difference for

the centroid frequency at 1 m [Fig. 4(d); $p = 0.002$; Mann-Whitney test]. As the snaps propagated from 0.2 to 1.0 m, the peak frequency was maintained consistently below 5 kHz [Figs. 4(c) and 5(c)].

Although we observed individual variation in the SPL_{pk-pk} (Fig. 5), this variability did not appear to be a result of the differences in the size of the major chela or sex (Fig. 6). For *A. heterochaelis* ($n = 5$), the body weight, body length, major chela length, body area, and major chela area were 0.79 ± 0.38 g, 30.0 ± 4.7 mm, 13.0 ± 2.8 mm, 183.0 ± 62.7 mm², and 75.0 ± 29.4 mm², respectively. For *A. angulosus* ($n = 20$), these same measurements were 0.29 ± 0.08 g, 21.0 ± 1.6 mm, 9.0 ± 1.3 mm, 86.0 ± 14.7 mm², and 37.0 ± 10.7 mm², respectively. Despite the larger size of *A. heterochaelis*, there was no significant difference in the peak-to-peak source levels between these two species

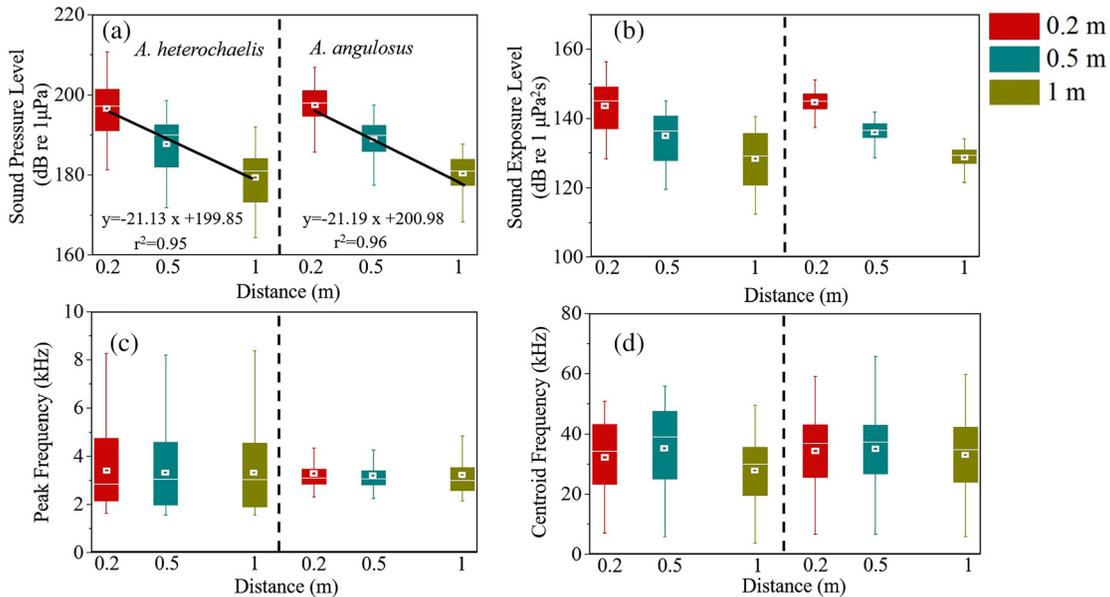


FIG. 4. (Color online) The acoustic parameters of the propagating snaps produced by *A. heterochaelis* and *A. angulosus*. The (a) SPL_{pk-pk} , (b) source exposure level, (c) peak frequency, and (d) centroid frequency for the snaps recorded simultaneously at 0.2, 0.5, and 1 m are shown. The box bottom and top represent the 25% and 75% percentiles, respectively, and the white line and dot within each boxplot represent the median and mean values, respectively. The bottom and top line extensions of the box represent the lower and upper edge values respectively. The attenuation in (a) was estimated using the mean sound pressure level (SPL_{pk-pk}) of the snaps recorded at 0.2, 0.5, and 1.0 m.

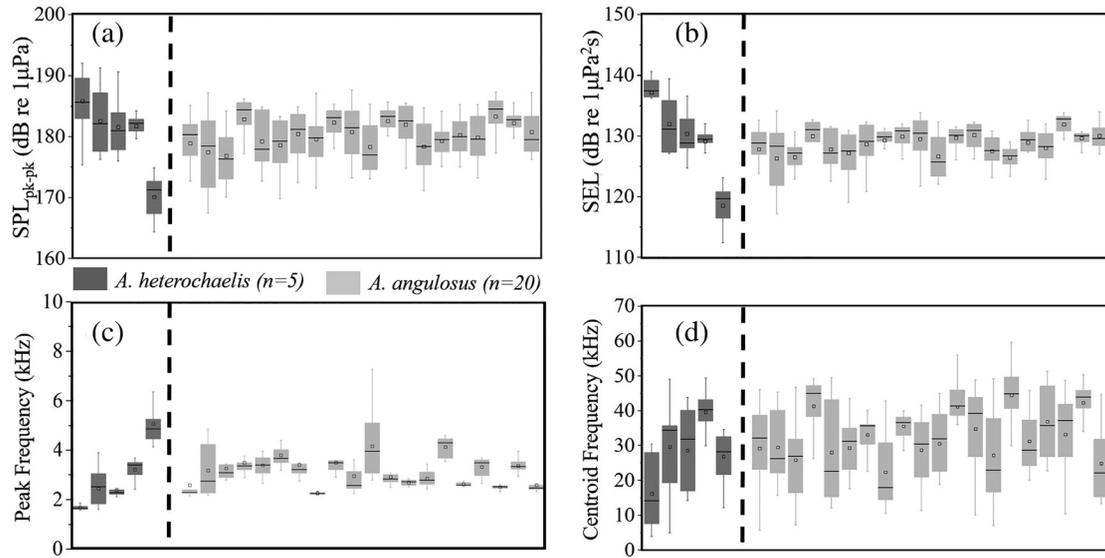


FIG. 5. The individual variation in the snap acoustic characteristics in *A. heterochaelis* and *A. angulosus*. The variation in (a) SPL_{pk-pk} at 1 m, (b) SEL, (c) peak frequency, and (d) centroid frequency of the snaps recorded at 1 m for the 25 specimens in the acoustic pressure measurements are shown. The box bottom and top denote the 25% and 75% percentile of the distribution, respectively, and the median and mean are represented by the line and square, respectively, inside the boxes. The bottom and top line extensions of the box represent the lower and upper edge values, respectively.

($p > 0.05$). Using *A. angulosus* ($n = 20$), we further addressed that there was no significant relationship between the major chela length and SPL_{pk-pk} [Fig. 6(a)] as shown by the linear regression ($df = 18$, $p = 0.94$, $r^2 = 0.003$). Similarly, sexual

dimorphism did not appear to explain the variation in the SPL_{pk-pk} . The males of *A. angulosus* had a greater body weight (0.32 ± 0.09 g, $n = 11$) than females (0.26 ± 0.05 g, $n = 9$), and the major chela length was greater in males

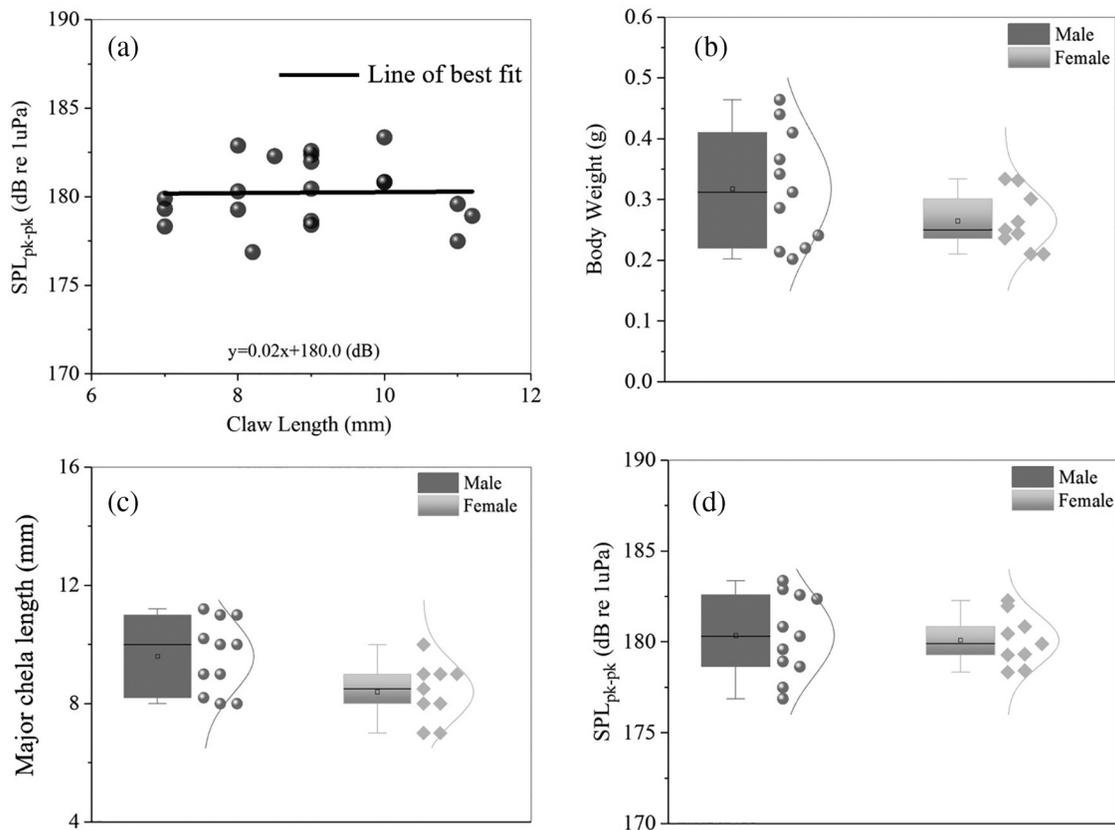


FIG. 6. (a) The estimation of the relationship between the SPL_{pk-pk} (at 1 m) and major chela length ($r^2 = 0.003$, $p = 0.94$) for *A. angulosus*. The comparison of the (b) body weight, (c) major chela length, and (d) SPL_{pk-pk} between male and female *A. angulosus* is shown. The bottom and top line extensions of the box represent the lower and upper edge values, respectively.

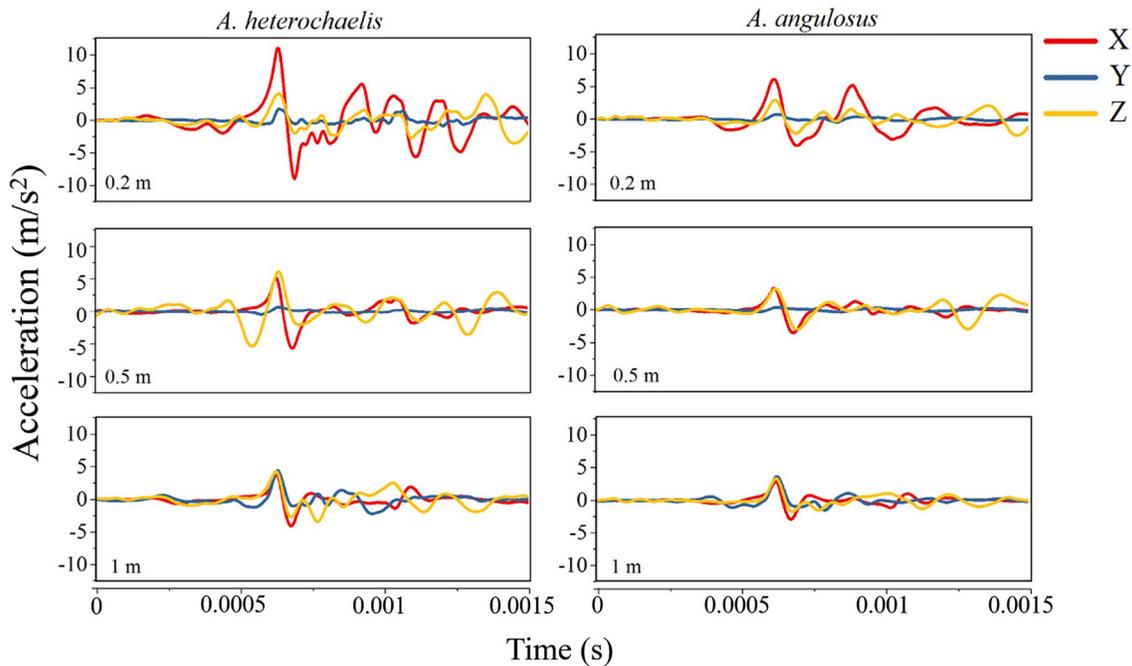


FIG. 7. (Color online) The mean particle acceleration along the x, y, and z axes recorded at 0.2, 0.5, and 1 m for *A. heterochaelis* and *A. angulosus*. The particle motion was measured in the horizontal (x and z axes with x facing the shrimp cage) and vertical planes (y axis).

(9.5 ± 1.2 mm, $n = 11$) compared to females (8.3 ± 1.1 mm, $n = 9$; Fig. 6). After testing for normality ($p = 0.396$; Kolmogorov-Smirnov test) and equal variance ($p = 0.08$), there was no significant difference between the male and female mean SPL_{pk-pk} measured at 1 m ($t = 0.30$, $p = 0.767$; student's *T*-test) despite the differences in the morphology.

B. Particle acceleration characteristics of shrimp snaps

The acceleration in all directions (x, y, and z axes) showed relatively low oscillations before and after the peak (Fig. 7). The mean acceleration of all of the snaps recorded at each distance showed that the particle acceleration in the horizontal x axis, which represented the axis toward and away from the shrimp cage, decreased with the distance (from 0.2 to 1 m) for both species (Fig. 7). The acceleration in the second horizontal direction (z axis) was lower than

that measured along the x axis at 0.2 m, but the magnitude along these two horizontal axes were comparable at 0.5 and 1.0 m. For both species, the acceleration was the lowest in the vertical (y axis) direction at 0.2 and 0.5 m, yet at 1 m it was approximately the same magnitude as the accelerations in the horizontal x and z axes.

The total acceleration decreased with the distance (Fig. 8) as observed in the propagation of the sound pressure. Breaking this down into the three planes measured by the accelerometer, the snaps showed a directional component. For example, for *A. heterochaelis* along the x axis (in line with the medial plane of the animal), there was almost a 15 dB decrease in the acceleration from 0.2 to 1 m (Fig. 9). The variability was smaller along the y axis. Along the vertical z axis, the power spectral density was slightly greater at 0.2 and 0.5 m (approximately 5 dB re 1 m/s²) compared to that measured at 1 m.

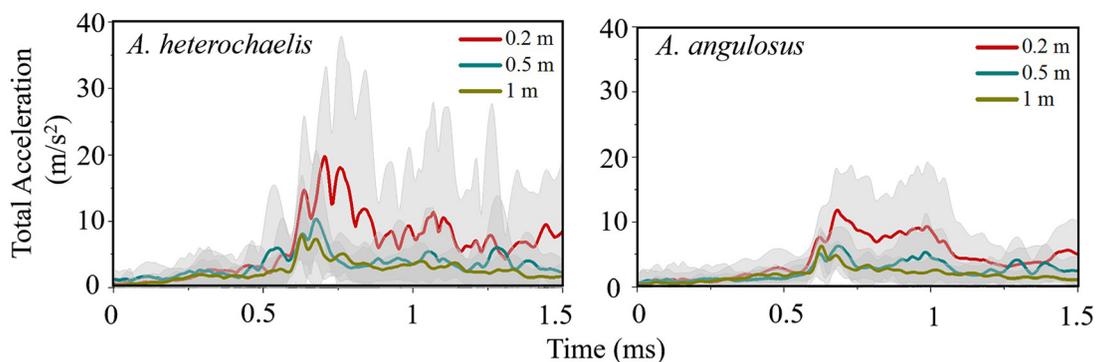


FIG. 8. (Color online) The meantotal acceleration and SD (gray shading) of the snaps recorded at 0.2, 0.5, and 1 m for *A. heterochaelis* and *A. angulosus*.

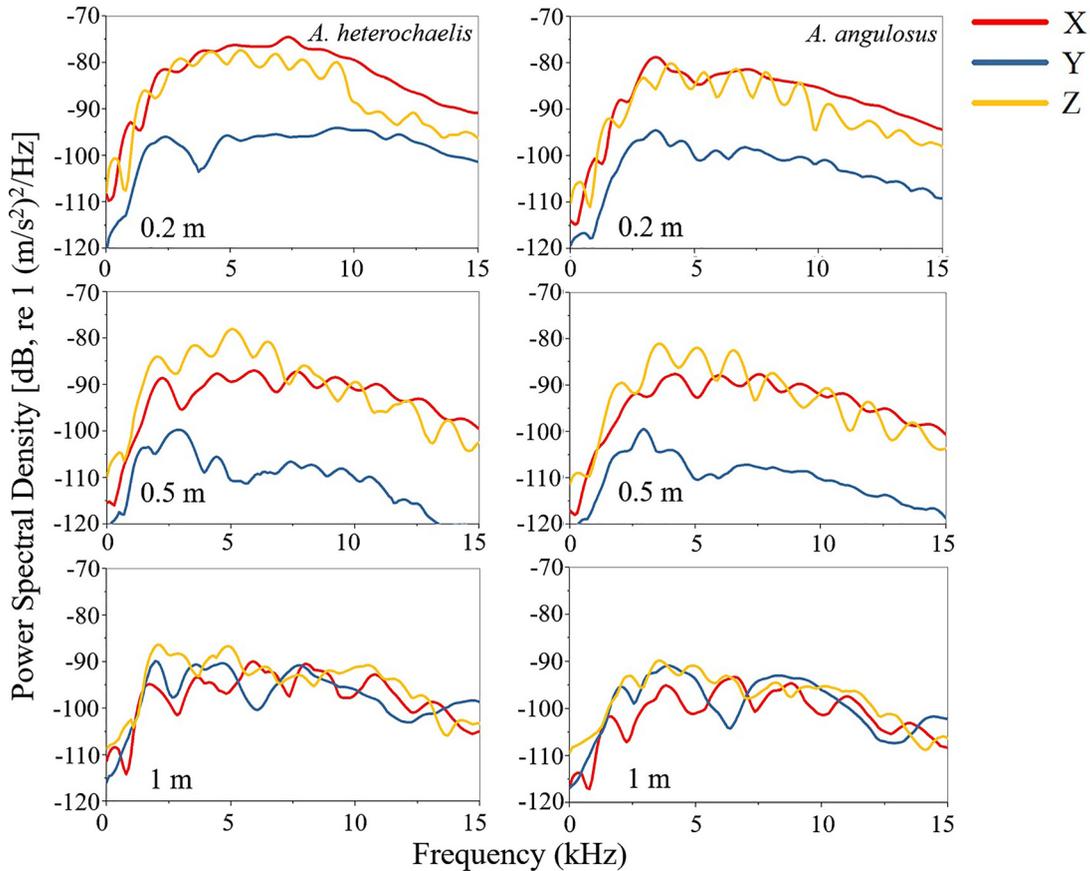


FIG. 9. (Color online) The mean power spectral density of the particle acceleration along the x , y , and z axes recorded at 0.2, 0.5, and 1 m for *A. heterochaelis* and *A. angulosus*.

The greater acceleration along the horizontal axes (x and z axes) may provide information that could serve as a directional signal. This directionality is reduced at the 1 m distance, where the amplitudes across the three axes were similar (Figs. 7 and 9). At 0.2 and 0.5 m, *A. heterochaelis* produced snaps with higher total accelerations (Fig. 8) than those of *A. angulosus*. At 1 m, the total acceleration for the two species was similar. We analyzed the peak frequency of the acceleration component in the x direction (Fig. 10) as

the relatively higher amplitude in this direction suggests that the particle motion along this axis may act as an acoustic signal in communication. The mean peak frequency along the x axis measured at 0.2, 0.5, and 1 m for *A. heterochaelis* was 6.1 ± 1.4 kHz ($n = 60$), 6.0 ± 2.6 kHz ($n = 57$), and 6.8 ± 1.7 kHz ($n = 85$), respectively. There was a significant difference in the x axis acceleration when comparing the frequency at the three distances ($H = 9.273$, $df = 2$, Kruskal-Wallis ANOVA, $p < 0.01$). For *A. angulosus*, the mean

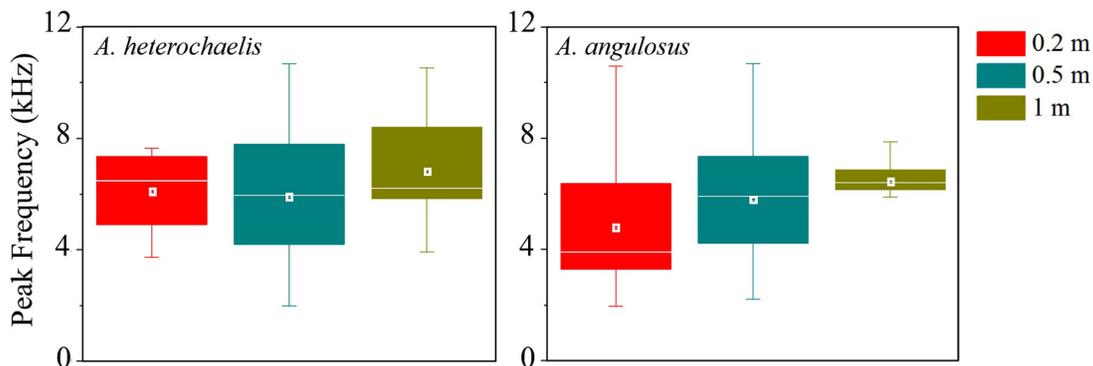


FIG. 10. (Color online) The peak frequency of the acceleration recorded along the x axis at 0.2, 0.5, and 1 m for *A. heterochaelis* and *A. angulosus*. The box bottom and top denote the 25% and 75% percentiles of the distribution, respectively, and the median and mean peak frequencies are represented by the white line and dot within each boxplot, respectively. The bottom and top line extensions of the box represent the lower and upper edge values, respectively.

peak frequency was 4.9 ± 1.8 kHz ($n = 199$), 5.8 ± 1.9 kHz ($n = 177$), and 6.4 ± 1.9 kHz ($n = 254$) at 0.2, 0.5, and 1 m, respectively, which also showed a significant difference across distances ($H = 84.836$, $df = 2$, Kruskal-Wallis ANOVA, $p < 0.01$).

C. Field recordings of snapping shrimp snaps

We extracted a total of 282 snaps from the field data collected in the May River Estuary, the location of the shrimp capture and presumably the same two species, for comparison to the laboratory-recorded snaps. The precise locations of the shrimp relative to the recorder in the field were unknown. The field snaps had a mean SPL_{pk-pk} of 158.9 ± 4.0 dB ($n = 282$) and showed a broadband spectrum within the recorded frequency range (Fig. 11). The mean spectrum was consistent with that recorded in the laboratory, suggesting that the recordings made in the laboratory environment can represent the acoustic parameters encountered in the field. Although there was a significant difference in the peak frequencies of the snaps recorded in the laboratory and field ($U = 38176.0$, $p < 0.01$; Mann-Whitney test), the frequency of the peak amplitude was consistently below 10 kHz in both data sets with most snaps showing a peak amplitude below 5 kHz. The mean peak frequency in the field data was 4.1 ± 1.9 kHz ($n = 282$) compared to the laboratory result of 3.2 ± 1.0 kHz ($n = 349$). The centroid frequency was not compared because of the limited sampling frequency in the field recordings (Nyquist frequency of 40 kHz).

IV. DISCUSSION

Snapping shrimps have long been known for their ability to produce short, broadband pulses at high amplitudes (Ritzmann, 1974; Schein, 1975, 1977; Au and Banks, 1998; Schmitz and Herberholz, 1998; Schultz, 1998). To date, the studies addressing the acoustics of these snaps have primarily focused on interpreting the pressure component (Everest *et al.*, 1948; Au and Banks, 1998) and have not

quantitatively addressed the particle motion. However, if snapping shrimp use their pulses for acoustic communication, they are likely detecting the particle motion component of the sound (Budelmann, 1992; Popper and Hawkins, 2018). The pressure signal, however, remains a key variable when passively monitoring marine habitats and addressing the “noise” that snapping shrimp produce. Both the pressure and particle motion were examined in this study. The distances (0.2, 0.5, and 1 m) were representative of the small-scale spatial distribution of shrimp that we observed in the oyster flats, where we collected individuals for this study, and reflect the distances over which acoustic communication may occur (Hughes *et al.*, 2014). The SPL_{pk-pk} measured at 1 m for the two study species were similar and the high amplitude and broadband characteristics of these sounds underscore their dominance in coastal soundscapes. The pressure component attenuated by approximately 17 dB over the 0.8 m range examined (from 0.2 to 1 m). Before the particle acceleration is masked by background noise in both amplitude and directivity, shrimp may use particle motion to discern the presence and position of conspecifics at a range greater than that enabled by the water jet alone (9 mm; Herberholz and Schmitz, 1998, 1999). Further, the water jet may often be impeded at short (several cm) distances due to obstacles (oyster shell hash and rocks) in their natural habitat. Interpreting the pressure component, we found that the peak and centroid frequencies did not change substantially over the distances measured (≤ 1 m), and the peak frequencies observed in the tank were similar to the snaps extracted from the field soundscape recordings. Taken together, these results allow us to consider, for the first time, the use of acoustic communication in snapping shrimps and enhance our understanding of the acoustic characteristics of one of the most pervasive sounds in the ocean.

A. Variation in snap characteristics among individuals and species

We addressed the potential relationship between the size and snap amplitude from the perspective of the species,

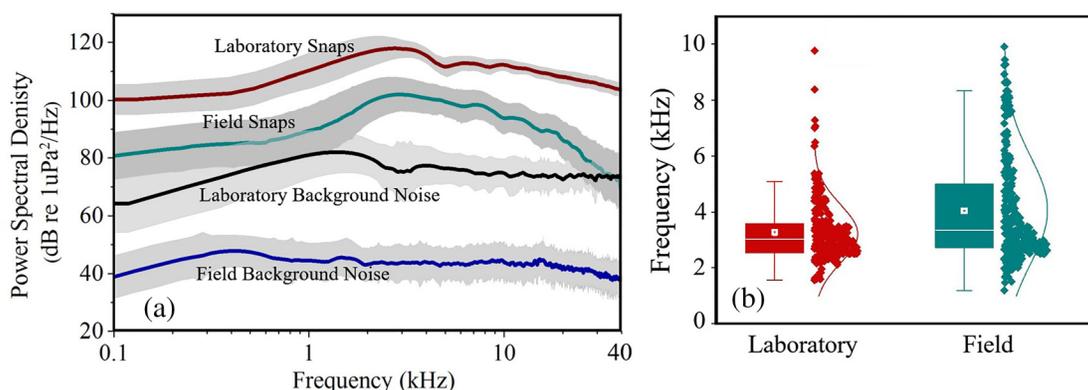


FIG. 11. (Color online) The comparison between the (a) mean and SD (gray shading) frequency spectra and (b) peak frequency from the snaps recorded in the laboratory and field. Note that the laboratory data include all of the snaps (recorded at 1 m) from both species *A. heterochaelis* and *A. angulosus*. The boxes reflect the range of the data from the 25% to 75% percentiles, and the white line and dot within each boxplot represent the median and mean values, respectively. The bottom and top line extensions of the box represent the lower and upper edge values, respectively.

individuals, and sex. Across all individuals, 5 *A. heterochaelis* and 20 *A. angulosus* produced variable snaps with respect to their energy and frequency properties. The factors that influence the acoustic characteristics of these snaps are both environmental (e.g., the viscosity and density of the seawater) and internal to the shrimp (e.g., the speed of the major chela closure). Given the controlled nature of these tank tests, where both temperature and water height remained consistent, it is unlikely that the environmental factors produced the range of amplitudes we observed within single individuals. Therefore, it appears that this variation between the snaps produced by a single individual may be driven by differences in closing the major chela. We opportunistically observed that some shrimp produced a series of snaps that would progressively diminish in amplitude, matching observations in Schmitz *et al.* (1995). This suggests that the animals may generate less force with each snap in the closing of the major chela during successive snapping. Generally, our induced snap rates of a dozen per hour was higher than the animals without any stimulus (Lillis *et al.*, 2017), suggesting fatigue as a possible cause. How this change in amplitude may translate to natural intraspecific interactions and *in situ* signaling has yet to be determined.

The SPL_{pk-pk} measured at 1 m tended to fluctuate around 180 dB re 1 μ Pa, but this amplitude varied by ± 10 dB. One shrimp (the fifth boxplot for *A. heterochaelis* in Fig. 5) generated snaps with a consistently lower amplitude (mean = 170.1 dB) compared to the other *A. heterochaelis* individuals. Another individual (first boxplot for *A. heterochaelis* in Fig. 5), produced snaps with a substantially higher mean SPL_{pk-pk} of 185.9 dB. This variability did not appear to depend on the major chela or body size in our analyses, counter to the observations of Au and Banks (1998) in which the SPL_{pk-pk} (at 1 m) was positively correlated with these measurements in *S. paraneomeris*. It is likely that this individual variation in the snap amplitude is the result of physiological processes that were not measured here, such as individual fitness or changes in the major chela during the molting process. Our small sample size of *A. heterochaelis* does limit our ability to assess the correlation between the shrimp size and snap SPL_{pk-pk} as the largest size differences in our study occurred between the two species. Our results, however, do suggest that the amplitude variation may be driven by the variation in the cock-and-trigger mechanism that generates the bubble or potentially other factors intrinsic to the shrimp (e.g., health, fatigue) that may have an important influence on the snap SPL_{pk-pk}.

Some snap parameters may be species dependent. For example, the snaps of *S. paraneomeris* (Au and Banks, 1998) had a shorter precursor compared to our study species (Fig. 2), which is also reflected in a previous study on *A. heterochaelis* (Versluis *et al.*, 2000). The SPL_{pk-pk} (recorded at 1 m) of the snaps of *S. paraneomeris* varied from 183 to 190 dB re 1 μ Pa (Au and Banks, 1998). This parameter ranged from 164.4 to 192.1 dB for *A. heterochaelis* and 164.9 to 187.7 dB for *A. angulosus* in this study. Considering these studies took place under different

environmental conditions, the upper range of the peak-to-peak source level of these three species is very comparable and suggests that the morphological attributes of a species may not heavily influence the amplitude characteristics of their snaps, supporting our null findings of the influence of the size. The differences in the lower extent of the range of the measured peak-to-peak source levels may be introduced by both environmental and internal factors as stated above.

B. Amplitude variation over distance

The snapping shrimp pulses may be used for acoustic communication and can be used to estimate the snapping shrimp population sizes (Schmitz, 1998, 2002). Understanding these applications requires knowledge of the snap's acoustic characteristics and variation in these parameters over the distance. As expected, the sound pressure level of the snaps measured at 1 m was less than the amplitudes measured at the two closer distances. For *A. heterochaelis*, the sound pressure level at 1 m was less than that measured at 0.2 m by an amount of 17.3 ± 2.1 dB re 1 μ Pa [mean and standard deviation (SD)], and the amplitude measured at 1 m was less than that measured at 0.5 m by an amount of 9.0 ± 2.2 dB. These differences were 17.2 ± 1.6 and 8.9 ± 1.6 dB re 1 μ Pa, respectively, for *A. angulosus*.

Comparing the snaps from the field and laboratory recordings allowed us to examine whether the frequency characteristics of the snaps measured in the tank are reflective of the snaps produced in the natural environment. Under laboratory conditions, we calculated the snap parameters using the direct path arrival of the snap, whereas in the field, the recorded snaps had interacted with features of the environment (e.g., the muddy substrate, sea surface, and hard features such as the oyster reef) before reaching the hydrophone. Yet, the snaps recorded from both the laboratory and field were generally similar with a broadband spectrum and the majority of energy below 10 kHz (Fig. 11). There was reduced energy in the field snap spectrum with an increasing frequency compared to the laboratory data [Fig. 11(a)], and this may have resulted from the longer travelling distance from the source to hydrophone in the field or the greater attenuation of high frequencies in the soft sediments. Further, high frequencies with shorter wavelengths interact with more features by reflection. These results suggest that the frequency distribution of our laboratory measurements is reflective of what the shrimp and other animals likely experience in the field. This maintenance of the snap frequency characteristics may enable snaps to function as stable acoustic signals or cues. Further, our results suggest that the sounds of snapping shrimps in ambient soundscapes can be used to understand the frequency characteristics of the local shrimp species.

Snapping shrimps have evolved multiple means of communication such as mechanosensory, chemical, visual, and antennal touching (Conover and Miller, 1978; Hughes, 1996, 2000; Herberholz and Schmitz, 1998; Vickery *et al.*, 2012). Here, we consider if acoustic signals may also play a

role in communication. The use of an acoustic signal for communication across distance would be particularly valuable in the turbid estuaries and waterways in which these shrimps live, where visual cues can be limited and chemicals quickly diluted. Further, the sounds of snapping shrimp are often highest at low-light hours (Bohnenstiehl *et al.*, 2016; Salas *et al.*, 2018) when visual displays (Hughes, 2000) are less likely to be effective; therefore, audible snaps may offer a valuable means of communication for potentially establishing and defending territory (Hughes *et al.*, 2014; Hughes and Heuring, 2018).

If shrimps are able to acoustically detect the cavitation bubble produced by the snaps of conspecifics, they are likely doing so using particle motion (Budermann, 1992; Popper and Hawkins, 2018). At the shorter distances of 0.2 and 0.5 m, the acceleration in the horizontal directions (x and z axes) was greater than that in the vertical y axis, potentially conveying directional information. This could allow individuals to orient to the direction of neighboring shrimp (Popper and Schilt, 2008). At 1 m, the horizontal acceleration levels were similar to the vertical component, so although the back-and-forth vibratory vector was still present, the source direction may be more difficult to discern at this distance. Because shrimp are benthic, it is likely that the vertical axis is less important compared to the particle motion along the horizontal axes.

For the particle motion stimulus of a snap to be detected by a shrimp, the amplitude must exceed the shrimp's threshold for detection. We compared our results to the hearing sensitivities of *A. richardsoni* (Dinh and Radford 2021), the only known audiogram for a snapping shrimp species, to address if the snaps may be acoustically detectable by snapping shrimp. Dinh and Radford (2021) observed that the hearing range of their test species was below 1.5 kHz, well below the peak frequency of the snaps measured here and in a previous study (Au and Banks, 1998). The frequency of the highest auditory sensitivity was 100 Hz with thresholds between 70 and 80 dB re $1 \mu\text{m/s}^2$. The hearing thresholds increased to approximately 100 dB at 1 kHz. No clear electrophysiological responses were observed to sounds over 1.5 kHz. The snaps examined in this study did have significant energy below 1 kHz, and this portion of the signal overlaps with the tested audible frequency range of *A. richardsoni*. The mean accelerations along the x axis at 1 m for 100 Hz were 99.1 and 93.5 dB re $1 \mu\text{m/s}^2$ for *A. heterochaelis* and *A. angulosus*, respectively, which exceed the hearing threshold for *A. richardsoni* at 100 Hz. This indicates that the snaps may be detectable across ranges much farther than the detection distance of the water jet (9 mm; Herberholz and Schmitz, 1998, 1999). Individuals of *A. heterochaelis* and *A. angulosus* may be able to acoustically detect the snaps produced by conspecifics, assuming that these species have a similar hearing sensitivity as *A. richardsoni*, which is in the same family as the two study species. This comparison of auditory thresholds to our measurements of the snap amplitude suggests that there is sufficient energy in these snaps to potentially enable acoustic communication at distances up to 1 m. The field

measurements of the particle motion amplitude and directivity at the location of the shrimp's habitat would further inform the potential function of the snaps to serve as an informative acoustic signal.

V. CONCLUSIONS

We measured the snaps of the snapping shrimp species *A. heterochaelis* and *A. angulosus* in both sound pressure and particle motion. These data provide new and comparative data on these ubiquitous sounds, which are dominant features in the soundscapes of many coastal habitats. The peak-to-peak source levels of these temperate snapping shrimps were slightly lower in amplitude but comparable to those of a tropical counterpart. A similarity in the snap characteristics between the two study species and *Synalpheus parneomeris* (Au and Banks 1998) suggests a relative consistency in the acoustic characteristics across species. The snap amplitude attenuated rapidly, yet a pulse's properties in the frequency domain remained relatively consistent across short, communication-relevant distances. Further, frequency characteristics of the snaps recorded in the tank were similar to snaps recorded in the field, suggesting our laboratory-based analyses reflect the sounds encountered by animals in the field and soundscape recordings can inform the acoustic characteristics of the shrimp species. The particle acceleration was orientation and distance dependent, reflecting its potential to provide the source direction. Over short distances (≤ 1 m), the accelerations along the horizontal axes exceeded those measured along the vertical axis, which may allow a shrimp to discern the direction of a snap-producing conspecific. Overall, these data provide new insight into the potential communication parameters and context of the snapping behavior of snapping shrimps. These data triple the acoustic measurements of the snapping shrimp species, and the pressure measurements allowed us to consider the interspecific variation in the snap parameters across the different species. These data can also be compared to auditory thresholds to predict if shrimps are capable of detecting the acoustic signals of conspecifics within distances of 1 m.

ACKNOWLEDGMENTS

We appreciate the support of Richard E. Galat, Ed Doherty, and Scott Gallagher (Woods Hole Oceanographic Institution) and Michael Nicoletti (Raytheon BBN). We thank Bradshaw McKinney and Agnieszka Monczak from the University of South Carolina Beaufort for their help in the animal and data collection from the field. We are thankful to Wenzhan Ou for his help in conducting the micro-computed tomography scanning and acknowledge the China Scholarship Council for supporting Z.C.S. for his overseas study at the Woods Hole Oceanographic Institution. This research was funded by the National Science Foundation Biological Oceanography Award No. 15-36782, the Defense Advanced Research Projects Agency, and the Woods Hole Oceanographic Institution.

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