



FEATURE ARTICLE

Rumbling in the benthos: acoustic ecology of the California mantis shrimp *Hemisquilla californiensis*

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ABSTRACT: Although much research has focused on acoustic mapping and exploration of the benthic environment, little is known about the acoustic ecology of benthic organisms, particularly benthic crustaceans. Through the use of a coupled audio–video system, a hydrophone array, and an autonomous recording unit, we tested several hypotheses about the field acoustics of a benthic marine crustacean, *Hemisquilla californiensis*. Living in muddy burrows in southern California, these large mantis shrimp produce low frequency ‘rumbles’ through muscle vibrations. First, we tested whether acoustic signals are similar in the field and in the laboratory, and discovered that field-produced rumbles are more acoustically and temporally variable than laboratory rumbles, and are typically produced in rhythmic series called ‘rumble groups.’ Second, we verified if the sounds were indeed coming from mantis shrimp burrows and explored whether rumble groups were produced by multiple individuals. Our results suggest that during certain time periods, multiple mantis shrimp in the vicinity of the hydrophone produce sounds. Third, we examined the relationship between behavioral and acoustic activity, and found that *H. californiensis* is most active during crepuscular periods. While these crustaceans make a substantial contribution to the benthic soundscape, omnipresent and acoustically overlapping boat noise may threaten their acoustic ecology.

KEY WORDS: Acoustic ecology · Autonomous recording unit · Benthic · Crustacean

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The California mantis shrimp communicates acoustically by producing low-frequency ‘rumbles’.

Watercolor: E. R. Staaterman

INTRODUCTION

The acoustic soundscape of the benthic zone is a cacophony of snaps, squeaks, hums, grunts, and rasps produced by animals such as snapping shrimp (Au & Banks 1998), clawed lobsters (Henninger & Watson 2005), spiny lobsters (Patek & Oakley 2003), hermit crabs (Dumortier 1963), and fishes (Tavolga 1977). Given the low-light environment in which most benthic organisms live, the acoustic modality can play important roles—attracting mates, repelling rivals, deterring predators, or maintaining territories. Moreover, daily patterns in the acoustic activity of fishes

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(McCauley & Cato 2000, Locascio & Mann 2008), snapping shrimp (Lammers et al. 2008), and sea urchins (Radford et al. 2008) suggest that the benthic zone is an acoustic environment with distinct diel trends. However, compared to the extensive literature on acoustic behaviors in other marine taxa such as cetaceans, few investigations have explored acoustic communication among benthic invertebrates, particularly benthic crustaceans.

Mantis shrimp (Crustacea, Stomatopoda) are benthic marine crustaceans that are well known for their fierce predatory strikes (Patek et al. 2004) and excellent visual systems (Cronin & Marshall 2004). When the raptorial appendage of this animal makes contact with a prey item or the substrate, a sound is produced (Alcock 1900, Kemp 1913, Hazlett & Winn 1962, Caldwell 1979, Patek & Caldwell 2005), and stridulation may occur between the uropod and the telson (Brooks 1886, Giesbrecht 1910, Balss 1921, Dumortier 1963). The only record we could find of mantis shrimp sounds in the field is an anecdotal report of 'groaning' noises emanating from burrows of a large temperate stomatopod, the California mantis shrimp *Hemisquilla californiensis* (Haderlie et al. 1980).

Hemisquilla californiensis was the focus of the first comprehensive laboratory study of mantis shrimp sounds, which were referred to as 'rumbles' (Patek & Caldwell 2006). Individuals were held in tanks, and sounds were recorded from 50 % of the males ($n = 12$), and none of the females ($n = 6$). Whether or not females are capable of generating rumbles remains unknown. Rumbles appeared to be produced by vibrations of posterior mandibular remoter muscles located underneath the carapace (Fig. 1). Most rumbles lasted <2 s and the mean dominant frequency was 45 Hz (± 10 SD, $n = 53$ rumbles).

While previous experiments have focused on either laboratory based sound production or the general ecology of *Hemisquilla californiensis*, the present study is, to our knowledge, the first to investigate the acoustics of this species in its natural habitat. *H. californiensis* occurs off the coast of California and Mexico and lives in self-constructed muddy burrows, which provide a safe place for feeding, mating, and molting (Basch & Engle 1993). During the mating season (March to June), which is the time period of the present study, pairs of males and females reside together for several weeks. Males guard their burrows intensely, especially during crepuscular periods, when individuals are most active. *H. californiensis* typically closes its burrow with a mucous cap during periods of bright daylight and at night, presumably for protection from predators, which range from octopus to benthic-feeding elasmobranchs (Basch & Engle 1989, Basch & Engle 1993, Gray et al. 1997). We addressed 3 main questions: (1) Do rumbles in the field differ from those produced in the laboratory? (2) Are rumble groups produced by multiple individuals? (3) Do patterns of acoustic activity match previously documented patterns of behavioral activity?

MATERIALS AND METHODS

We utilized 3 approaches. (1) We used 2 recording systems to identify and characterize rumbles produced in the natural habitat of *Hemisquilla californiensis*. (2) A hydrophone array allowed us to calculate the locations of rumbles. (3) An autonomous recording unit provided acoustic data that were used to describe diel patterns of mantis shrimp acoustic activity. Field recordings were obtained at 2 locations along the coast of Santa Catalina Island, CA, USA, in the early mating

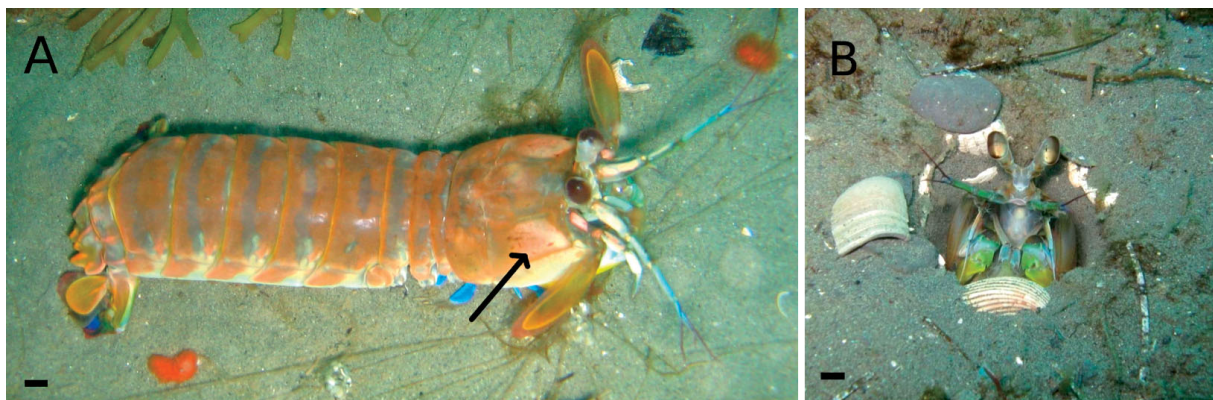


Fig. 1. *Hemisquilla californiensis* is a large mantis shrimp that builds burrows in the muddy benthic zone off the coast of southern California. (A) Individuals regularly leave their burrows to forage and interact with neighboring mantis shrimp. Males possess red patches on either side of the carapace, which lie just above the sound-producing muscles (arrow). (B) Individuals can often be seen guarding their burrows. During the mating season, males decorate the edges of their burrows with shells, presumably to attract females (J. Engle pers. comm.). Scale bar: ~1 cm

season (March 2009 and March 2010). We deployed each recording device using SCUBA and anchored it to the substrate near an *H. californiensis* burrow (~12 to 18 m depth, 13°C temperature, 33 salinity). During both field seasons, sunrise was at ~06:45 h and sunset was at ~19:15 h.

Identifying and characterizing rumbles generated *in situ*. To test whether rumbles in the field differed from those produced in previous laboratory experiments (Patek & Caldwell 2006), we first identified and described rumbles produced by *Hemisquilla californiensis*. Sounds were recorded at a total of 4 burrows over the course of 4 dives in the waters near Two Harbors, Santa Catalina Island. Two recording systems were used: a hydrophone that was connected to an underwater video camera (HTI-94-SSQ series, High Tech; sensitivity: -167.4 dB re:1 V μPa^{-1} , frequency response: 2 to 30 kHz; camera: DCR-VX2100, Sony Electronics; housing: VH-2100, Amphibico) and another hydrophone that recorded onto a digital audio recorder (Type 8104 hydrophone, Brüel and Kjaer; sensitivity: -207.9 dB re:1V μPa^{-1} , frequency range: 0.1 to 10 kHz; recorder: PMD670, Marantz; 16 bit, 48 kHz sample rate). We positioned the recording systems ~30 cm from the nearest burrow, and we left the area once the equipment was in place to minimize potential interference on the recordings from SCUBA bubbles.

Waveforms and spectrograms of these recordings were used to identify individual rumbles for analysis. For the video files, the audio component was first extracted into a 2-channel clip (iMovie 4.0.1, Apple; 16 bit, 48 kHz sample rate). Then each file from the 4 dives was downsampled to 2000 Hz (Matlab v. 2007b, The Mathworks) and low-pass filtered at 500 Hz (Raven Pro 1.4, Cornell Lab of Ornithology, Ithaca, NY). The following spectrogram parameters were used to view and analyze these recordings: for the files from the first recording system—Hann window, 8192 Pt. fast Fourier transform (FFT), 90% overlap (yielding a frequency resolution of 0.244 Hz); for files from the other recording system—Hann window, 16384 Pt. FFT, 90% overlap (yielding a frequency resolution of 0.122 Hz). For each rumble, we measured duration, lowest frequency, highest frequency, dominant frequency (the frequency, in Hz, with the highest sound level), and peak power (the sound level, in relative dB, at the dominant frequency). For the data from the recording units described above, we report the average for the dominant frequency and duration. However, these hydrophones were not calibrated, so for peak power, we report relative levels and limit our comparisons to data from the same recordings.

The field recordings revealed rumbles that were produced in groups of 2, 3, or 4. Therefore, we introduced the term ‘rumble group’ to describe a short series of

rumbles (e.g. Fig. 2) that have similar dominant frequency and peak power and occur within 0.25 s of each other. Rumble groups were usually produced in long repetitive series, lasting from several minutes to hours, which we call ‘rumble bouts’ (Fig. 3). In order to define the structure of a typical rumble group, we used data from multiple rumble bouts, which were recorded on different days and at different locations (and were assumed to be independent; Figs. 2 & 3). We analyzed bouts which had at least 9 rumble groups with at least 2 rumbles per group (minimum $df = 8$), allowing us to make 17 comparisons. Matched pairs *t*-tests were used to examine the differences in peak power and duration between the first and second rumble of each group (JMP v. 7.0, SAS Institute).

Within certain recording periods, we observed acoustically distinct rumble bouts which either alternated or overlapped temporally. To test whether these varying rumble bouts could have been produced by different individuals, we examined their dominant frequency (which could differ due to a physical quality such as body size) and relative peak power (which could differ due to body size and distance from the hydrophone). We assigned labels to distinct rumble bouts (i.e. Bout A, Bout B, etc. as in Fig. 3) and tested for significant differences in dominant frequency and peak power using Kruskal-Wallis test (JMP, SAS). Because the first rumble of each group was typically the most consistent, we only compared these.

Locating the source of mantis shrimp rumbles. In order to confirm that rumbles originated from mantis shrimp burrows and not another unidentified source, we deployed a 3-element hydrophone array to localize the source of the sounds (array engineered by the Cornell Lab of Ornithology; 3 HTI-94-SSQ hydrophones, High-Tech; sensitivities: -169.4 , -169.4 , -169.2 dB re:1V μPa^{-1} , frequency response: 2 to 30 kHz). We

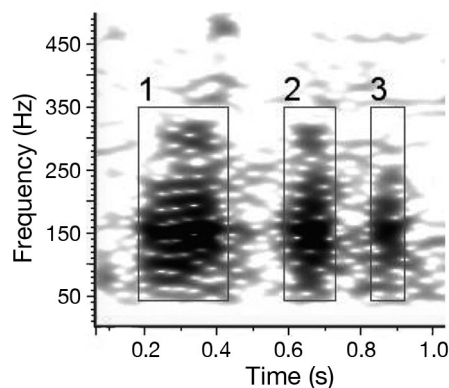


Fig. 2. *Hemisquilla californiensis*. Typical rumble group, consisting of 3 rumbles (labeled 1, 2, and 3). Spectrogram parameters: Hann window, 256 samples; 3 dB filter bandwidth, 11.2 Hz; discrete Fourier transform (DFT), 8192 samples; overlap, 90%; 50 to 500 Hz bandpass filter

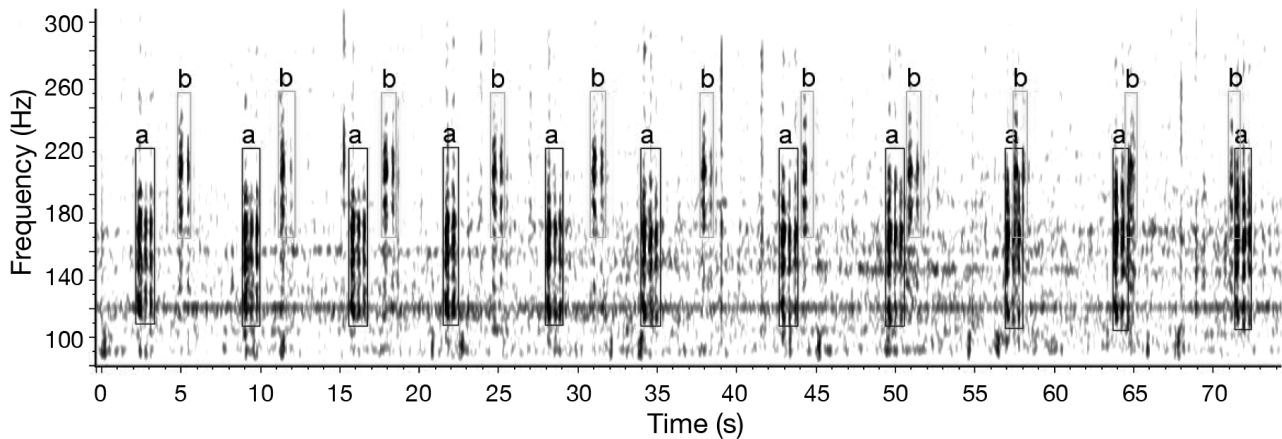


Fig. 3. *Hemisquilla californiensis*. Rumble groups alternated and sometimes overlapped, suggesting that multiple individuals were producing the sounds. The spectrogram shows 2 rumble bouts (labeled a and b); these data correspond to example no. 11 in Table 1 and data presented in Fig. 4. Boxes surround rumble groups, not individual rumbles. Spectrogram parameters: Hann window, 256 samples; 3 dB filter bandwidth, 5.62 Hz; DFT, 1024 samples; overlap, 90%; 50 to 500 Hz bandpass filter

identified a focal male and its burrow at a depth of 14 m by SCUBA diving. We placed the hydrophones in an equilateral triangle (5 m side⁻¹) centered around the burrow, and recorded sounds between 25 to 28 March 2010. Hydrophone cables were extended to the surface and into a boat where sounds were recorded on a computer with Raven Pro software, with a sample rate of either 5 or 20 kHz and a sensitivity range of either ± 0.5 or $\pm 5V$ (16 bit, NIDAQ USB-6251, National Instruments).

Although we recorded sounds for several hours, we only analyzed a small subset of rumbles that were free of boat noise and/or other obscuring sounds. For the analysis, all data were bandpass filtered (10 to 500 Hz). We used the XBAT software program (www.xbat.org; Figueroa 2005) to compute multi-channel spectrograms (Hanning window, 2214 or 512 Pt. FFT depending on sample rate of file), visually and aurally confirm the occurrences of rumbles, and annotate individual rumbles. A second customized Matlab-based program was used to compute the location of rumbles based on their times of occurrence at each of the 3 hydrophones (Clark et al. 1996, Clark & Ellison 2000). To assure correct localization, we limited our analysis to rumbles with waveforms that could be clearly observed on all 3 channels.

Identifying patterns in mantis shrimp acoustic activity and vessel noise. To test whether patterns in mantis shrimp acoustic activity matched previously documented behavioral activity (Basch & Engle 1989), we deployed an autonomous recording unit for almost 8 d, from 21 March at 16:20 h until 29 March 2009 at 10:30 h (Cornell Lab of Ornithology; HTI-90-U hydrophone, High-Tech; sensitivity: -197.3 dB re:1V μPa^{-1} , frequency response: 2 to 20 kHz, continuous sampling at 16 bit, 32 kHz sample rate). The unit was deployed

~9 km from the Two Harbors site and anchored 3.8 m from the nearest male *Hemisquilla californiensis* burrow at 18 m depth.

In order to examine patterns across each day, acoustic data were downsampled to 1000 Hz and combined to create 24 h files. These were converted into daily spectrograms, and each day of data was visually and aurally analyzed by the same trained investigator to identify rumble patterns and boat noise. We established operational definitions to describe whether these rumble rates should be considered 'rhythmic' (occurring in groups, <0.25 s apart, as defined above) or 'sporadic' (occurring as single rumbles). Power spectral density distribution levels (dB re:1 $\mu\text{Pa}^2 \text{Hz}^{-1}$) and sound levels (dB re:1 μPa) were computed based on hydrophone sensitivities and gain settings of the recording systems.

RESULTS

Rumble characteristics. Rumbles measured at different burrows and on different days had similar acoustic features, but exhibited high variability in dominant frequency. For all rumbles, we measured an average dominant frequency of 167.0 Hz (± 0.66 SE, range 53 to 257 Hz) and an average duration of 0.20 s (± 0.0013 SE, range 0.06 to 0.6 s). The initial rumble in a group had significantly higher relative sound levels than the second rumble in 16 out of 17 comparisons made (average difference = 5.1 dB, average SE = 0.71, matched pairs *t*-tests, $p < 0.01$ for all tests). The first rumble was also significantly longer in duration than the second rumble in 14 out of 17 comparisons (average difference = 0.092 s, average SE = 0.015, matched pairs *t*-tests, $p < 0.01$ for all tests).

Table 1. *Hemisquilla californiensis*. Tests performed from recordings collected at 12 distinct days and times. Within each test, 2 temporally overlapping and acoustically distinct bouts were identified. For each bout, the number of rumble groups tested (RG), mean number of rumbles per group (R G⁻¹), dominant frequency (F_{Dom}; Hz ± SE), and relative peak power (P_{Peak}; relative dB ± SE) are shown, as well as the differences in dominant frequency (F_{Diff}; Hz) and peak power (P_{Diff}; relative dB). Kruskal-Wallis tests were used to compare the dominant frequency and peak power between Bouts A and B, using only the first rumble of each group; **bold**: statistically significant comparisons

Test	Bout A				Bout B				Comparisons					
	No. of RGs	R G ⁻¹	F _{Dom} (Hz)	P _{Peak} (dB)	No. of RGs	R G ⁻¹	F _{Dom} (Hz)	P _{Peak} (dB)	F _{Diff}	H	p	P _{Diff}	H	p
1	22	4	197.2 ± 1.0	70.8 ± 0.19	11	3	230.1 ± 9.62	62.1 ± 0.60	33.0	8.0	0.005	8.7	21.4	0.0001
2	8	3	205.5 ± 0.95	70.8 ± 0.25	6	1	148.5 ± 1.76	76.6 ± 0.41	57.1	9.7	0.002	5.8	9.6	0.0002
3	15	4	169.5 ± 4.4	83.2 ± 0.26	15	2	143.7 ± 0.49	92.1 ± 0.59	25.8	21.8	0.0001	8.9	21.8	0.0001
4	12	4	140.9 ± 0.49	71.1 ± 1.10	7	2	207.9 ± 2.31	69.0 ± 1.13	66.9	12.6	0.0004	2.1	1.8	0.176
5	13	4	132.9 ± 0.58	91.9 ± 0.19	8	2	185.8 ± 3.08	82.5 ± 0.81	52.9	14.2	0.0002	9.4	14.2	0.0002
6	24	2	163.1 ± 0.86	70.7 ± 0.29	24	3	141.8 ± 5.18	68.8 ± 0.22	21.3	7.5	0.006	2.0	19.4	0.0001
7	17	3	145.1 ± 0.92	71.3 ± 0.46	16	1	135.5 ± 7.05	64.5 ± 2.1	9.6	3.4	0.065	6.8	23.3	0.0001
8	13	3	144.7 ± 2.97	73.5 ± 0.44	8	1	184.5 ± 0.99	66.2 ± 0.42	39.9	14.5	0.0001	7.3	14.2	0.0002
9	19	3	119.4 ± 1.54	74.3 ± 0.18	13	3	163.6 ± 3.36	70.9 ± 0.39	44.2	23.5	0.0001	3.3	18.4	0.0001
10	17	2	171.5 ± 2.28	72.3 ± 0.34	22	3	149.2 ± 1.19	71.8 ± 0.34	22.3	24.9	0.0001	0.51	0.54	0.46
11	13	3	167.7 ± 3.38	66.5 ± 0.47	15	1	213.4 ± 4.08	59.9 ± 0.59	45.8	19.3	0.0001	6.5	19.7	0.0001
12	38	1	164.7 ± 0.34	74.3 ± 0.019	26	2	178.9 ± 0.69	64.5 ± 0.37	14.1	47.0	0.0001	9.8	45.6	0.0001

Differences between overlapping rumble groups.

We found 12 examples (from different days and recordings) in which co-occurring rumble bouts differed in either dominant frequency or relative peak power of the rumbles (Table 1). We found 9 examples in which both the dominant frequency and the peak power differed significantly (Fig. 4) between the 2 bouts. In several cases, rumbles overlapped temporally (see example in Fig. 3).

Locations of mantis shrimp rumbles.

We estimated the location of 52 rumbles (Fig. 5). The locations were clustered; some rumbles originated from inside the hydrophone triangle, closest to No. 3, while others originated outside the triangle (Fig. 5). In a few cases,

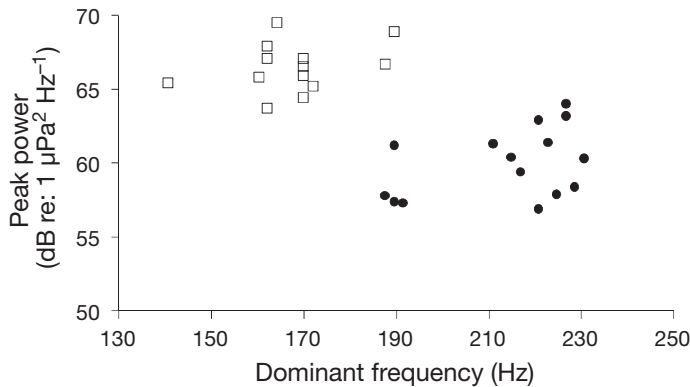


Fig. 4. *Hemisquilla californiensis*. Although relative peak power (dB re: 1 μPa² Hz⁻¹) and dominant frequency (Hz) were not correlated, 2 bouts of rumble groups showed distinct clusters for these 2 parameters (Series A = open square, Series B = filled circle). Each point represents data from the first rumble of each of the rumble groups analyzed (for A, n = 13; for B, n = 15). These data correspond to example no. 11 in Table 1 and the spectrogram shown in Fig. 3

rumbles that were <2 s apart originated from locations that were several meters apart.

Diel patterns in mantis shrimp acoustic activity.

At the site of the autonomous recording unit, we observed daily patterns in mantis shrimp acoustic activity (Table 2). Every morning and on 7 of 8 evenings (~17:00 to 19:30 h), we detected loud rhythmic rumble groups. At night (19:30 to 05:30 h), we observed sounds that closely resembled mantis shrimp rumbles but were less rhythmic; these rumbles occurred in isolation and were of lower received level and lower frequency than the more intensive and clearly discernible daytime rumbles. At mid-day (~11:30 to 01:30 h), we did not detect rumbles in 6 of 7 d, but periods without rumbles were more variable, and the compounding effect of vessel noise made it difficult to discern patterns.

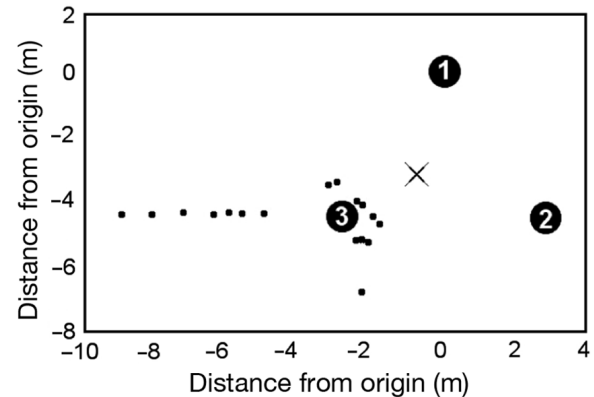


Fig. 5. *Hemisquilla californiensis*. Localization of rumbles using a 3-hydrophone array (black numbered circles) demonstrated that the sounds were emitted in close vicinity to the array, but not from the burrow opening (x); small dots: most likely location for each rumble, as calculated by a time-delay algorithm. Hydrophone no. 1 was used as the origin (0,0) for the grid in the time-delay algorithm

Table 2. *Hemisquilla californiensis*. Daily patterns in acoustic activity were consistent with published data on behavioral activity and burrow openings (data on open burrows from Basch & Engle 1989, their Fig. 3; n = 13 ind.). Sounds were recorded for almost 8 continuous days, but one mid-day period was missed

Period	Time of day	Acoustic activity	No. of days observed	Open burrows (%)
Morning crepuscular period	~06:30 – 08:30 h	Loud, rhythmic rumbles	8 of 8	50
Mid-morning	~09:30 – 11:30 h	Loud, rhythmic rumbles	6 of 8	nd
Mid-day	~11:30 – 01:30 h	No rumbling	6 of 7	15
Evening crepuscular period	~17:00 – 19:30 h	Loud, rhythmic rumbles	7 of 8	50–70
Night	~20:00 – 05:30 h	Quiet, sporadic, low-frequency rumbles	8 of 8	0

DISCUSSION

Compared to the relatively uniform sounds previously recorded in the laboratory (Patek & Caldwell 2006), the field-based recordings were more variable in their frequency and temporal characteristics. Patterns of acoustic activity matched previously published patterns of behavioral activity (Basch & Engle 1989). The timing of distinct rumble patterns, coupled with results from the hydrophone array, suggest that multiple individuals in an area produce sound simultaneously, possibly in a coordinated behavioral system. The power spectral density distribution of mantis shrimp rumbles was different from the background noise (Fig. 6), suggesting that these sounds make a substantial contribution to the benthic soundscape.

Characteristics of rumbles from the field

The most distinct difference between tank and field recordings was that rumbles in the field were produced in rhythmic groups. Across all recording types and days, certain parameters of rumble groups were conserved: the first rumble was the longest and loudest rumble of the group, and rumbles typically occurred

within a limited frequency band. However, the dominant frequency, relative peak power, and number of rumbles per group were significantly different across sampling days but also within sampling periods, suggesting that different individuals produced acoustically distinct rumbles. These results corroborate the findings of the laboratory experiment, which demonstrated variability between rumbles from different individuals (Patek & Caldwell 2006). Furthermore, our field data revealed recording periods in which different rumble groups overlapped temporally (Fig. 3). It seems unlikely that the 2 sound-producing muscles within 1 mantis shrimp could simultaneously produce 2 rumbles that differed in both dominant frequency and power. These results led us to conclude that several mantis shrimp within the vicinity of the hydrophone were generating rumbles simultaneously. Indeed, our hydrophone array located multiple sources of rumbles, which were several meters apart (Fig. 5). Although we cannot rule out the possibility that our focal animal was moving around while producing sound, examples of rumbles occurring <2 s apart at different locations provide strong evidence that 2 ind. were rumbling. Furthermore, there were many periods in which >2 mantis shrimp were audible, creating a cluttered spectrogram and perhaps representing a mantis shrimp 'chorus' (Fig. 7).

The other differences between field and laboratory recorded rumbles (Patek & Caldwell 2006) were primarily due to differences in methodology and sampling environments. For example, in the tank experiment, individuals were approached by a hydrophone or a stick; these animals probably produced sounds in an anti-predator context (Bradbury & Vehrencamp 1998, Patek & Caldwell 2006, Staaterman et al. 2010). Furthermore, tank recordings typically distort the acoustic quality of animal sounds (Parvulescu 1967, Akamatsu et al. 2002, Patek et al. 2009).

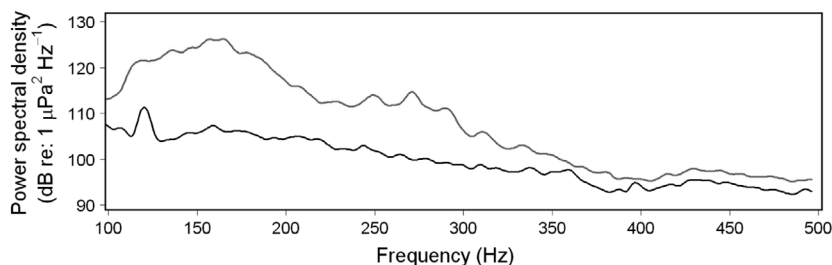


Fig. 6. *Hemisquilla californiensis*. Power spectral density measurements of mantis shrimp rumbles (grey line) were greater than background noise (black line) across the 100 to 500 Hz frequency band, but especially in the main communication band (~100 to 250 Hz). The peak in background noise at 120 Hz was from the autonomous recording unit's hard drive

Diel patterns in mantis shrimp acoustic activity

The daily patterns in acoustic activity were consistent with those described by Basch & Engle (1989). During crepuscular periods, individuals can be observed on foraging expeditions or guarding the entrance to their burrows (E. Staaterman pers. obs.). Acoustic activity was high during these times and rumbles were produced in groups. During periods of bright daylight and at night, *Hemisquilla californiensis* close their burrow with a mucous cap (Table 2; Basch & Engle 1989, 1993). Sporadic, lower-frequency, and relatively lower level sounds were recorded during these times. Differences in acoustic characteristics might result from the mucous plug covering the burrows or from the location of the animals within their burrows.

Acoustic ecology of *Hemisquilla californiensis*

The rhythmic nature of the daytime rumbles, and the variability in rumble characteristics for simultaneous rumble bouts, suggest that the rumbles serve a conspecific, communicative function (Bradbury & Vehrencamp 1998).

Many crustaceans are capable of detecting sound through a variety of mechanisms, including sensory hairs which function as particle motion detectors for both water-borne and substrate-borne signals (Breithaupt & Tautz 1990, Budelmann 1992, Taylor & Patek 2010). Like most crustaceans, *Hemisquilla californiensis* is covered with sensory hairs and is thus capable of detecting some forms of vibration. Although particle motion is dominant in the near-field region (usually <1 wavelength from the sound source), this region is 5× larger in water than it is in air, making this a behav-

iorally feasible range for communication in crustaceans (Ewing 1989). For example, the average mantis shrimp rumble with a dominant frequency of 167 Hz, traveling at 1500 m s⁻¹ in seawater, would have a near-field, free-field range of ~9 m. Given the measured population density of *H. californiensis* of 1 ind. per 12 m² (Basch & Engle 1993), mantis shrimp could detect rumbles from their neighbors. In addition, substrate-borne vibrations could further enhance signal detectability.

Why do individuals produce acoustically distinct rumbles? To address this question, we should consider the behavioral activity that occurs during the early mating season, when our recordings were collected. At all times of the year, this species is considered to be highly territorial and the spacing of burrows plays an important role in its ecology (Basch & Engle 1989, Basch & Engle 1993). During the mating season, males decorate their burrows with shells (Fig. 1) and recruit females to their burrows. Burrows are guarded especially intensely at this time, as intruder males have been seen evicting resident males in order to gain access to females (J. Engle pers. comm.). Therefore, we present 2 non mutually exclusive potential functions of the rumble: (1) maintenance of territory, and (2) attraction of mates.

Given the spacing of the burrows and the presumed range at which rumbles are detectable, this may be a communication network in which a sender's signal is detected by multiple neighbors (McGregor 1993, 2005). In this case, acoustic signals may function to help individuals establish and maintain territories, as observed in other taxa (reviewed by McGregor 1993). For example, field crickets respond differently to loudspeakers playing highly degraded versus less degraded sounds of conspecifics, indicating that the quality of the sound helps crickets to determine the

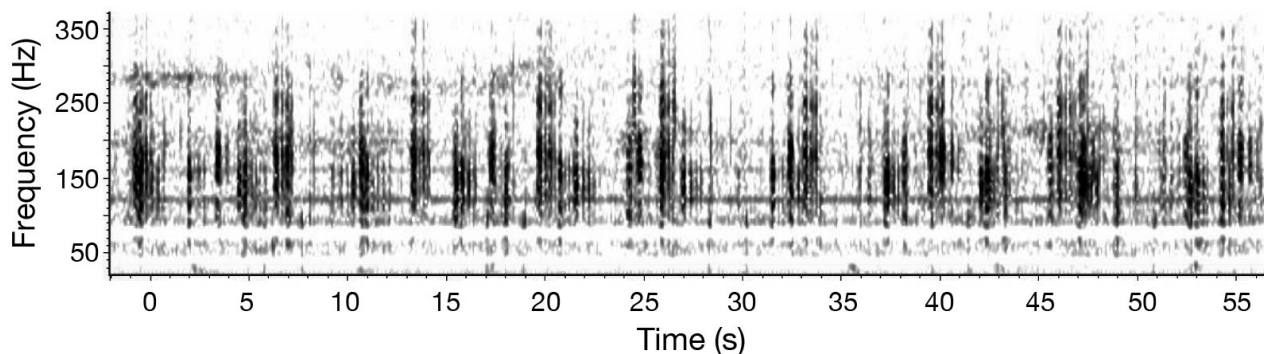


Fig. 7. *Hemisquilla californiensis*. Rumble groups from multiple individuals are visible in the spectrogram; note the differences in temporal patterning, intensity (as indicated by display darkness), and frequency. Some repetitive rumble groups are visible, but there is so much acoustic activity that it is difficult to discern exactly how many individuals are signaling. Sounds from the autonomous recording unit's hard drive have been filtered out, except for the 120 Hz 'hum' (horizontal line). Spectrogram parameters: Hann window, 256 samples; 3 dB filter bandwidth, 5.62 Hz; DFT, 1024 samples; overlap, 90%; bandstop filters at 35 Hz and 75 Hz

distance at which a neighboring individual is signaling. In electric fish, individuals respond less aggressively to signals produced by immediate neighbors than to signals produced by strangers. These 2 examples show that, in other taxa, the ability to distinguish the distance and identity of signaling conspecifics helps individuals determine the appropriate aggression levels with which to defend their territories (McGregor 1993). If mantis shrimp produce rumbles while exploring regions outside of their burrows, burrow residents would probably be able to detect movement of their neighbors (potential intruders) and use this information to respond appropriately. During one of the hydrophone array deployment dives, we observed a neighboring male shrimp near the burrow of our focal male (E. Staaterman & A. Gallagher pers. obs.). The data from the array revealed that there were 2 sound-producing individuals in the vicinity of the array. This neighboring male was probably the second individual that was detected on the array recordings, and these 2 individuals were perhaps using acoustic signals to maintain their territories.

The fact that only males produced this sound in the laboratory (Patek & Caldwell 2006), suggests another possible function of the rumbles: female attraction. A single male can recruit up to 2 females into its burrow (J. Engle pers. comm.). In the communication network of tree frogs, males use acoustic signals to attract females, and deliberately partition the acoustic space by adjusting either their temporal patterning or frequency (Grafe 2005). The considerable variability in temporal patterning and dominant frequencies observed in mantis shrimp rumbles makes this function highly possible. Furthermore, the differences in the dominant frequency, number of rumbles per group, and peak received level may convey important information to females about a male's reproductive status. For example, in a study on fiddler crabs, females showed preferences for certain characteristics of visual signals sent by males within a chorus, and males adapted their signals depending on the signaling behavior of neighboring males (Burford et al. 1998).

CONCLUSIONS

Our results demonstrate evidence of mantis shrimp 'chorusing,' in which multiple individuals produce sounds simultaneously. The prevalence of rumbles suggests that these sounds evolved to serve a critical function in their ecology. Increasing levels of low-frequency anthropogenic noise (Southall 2009) may mask these communication sounds as well as those from myriad undiscovered and under-represented benthic invertebrates.

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