Marine and Freshwater Behaviour and Physiology
June 2006, 39(2): 99–111

The stomatopod rumble: Low frequency sound production in *Hemisquilla californiensis*

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(Received 12 July 2005; in final form 8 December 2005)

Abstract

Stomatopods (mantis shrimp), numbering over 450 species, are renowned for their exceptional visual and chemosensory abilities and yet virtually nothing is known about their use of acoustic signals. We present acoustic recordings and analyses of the sounds of a stomatopod, *Hemisquilla californiensis*. This species generates tonal, low frequency sounds, which we term 'rumble', that are spectrally similar to those produced by African and Asian elephants. The fundamental frequency of the stomatopod rumble ranges from 20 to 60 Hz, with a strong second harmonic. *Hemisquilla californiensis* appears to generate these sounds through contractions of the posterior mandibular remotor muscle which is coupled to a stiff, lateral extension of the carapace. The sides of the carapace are covered by large, polarized, red spots which vibrate during sound production. Thus, the animals may generate a multi-modal signal by coupling vibrational and visual signals. *Hemisquilla californiensis* generates the rumble while interacting with potential predators and burrow intruders, suggesting a defensive or territorial function for the sound.

Keywords: *Sound production, crustacean, stomatopod, bioacoustics, acoustic signalling, behavior,* Hemisquilla californiensis

Introduction

Crustaceans produce sounds with a myriad of mechanisms, ranging from stridulation in crabs (Guinot-Dumortier & Dumortier 1960), muscle buzzing in nephropid lobsters (Mendelson 1969), drumming in grapsid crabs (Mulstay 1980) and stick and slip friction in palinurid lobsters (Patek 2001), to name but a few. Several authors have reviewed the diversity of sound production in crustaceans (Busnel 1963; Ewing 1989; Greenfield 2002; Schmitz 2002), and yet the acoustic behavior of mantis shrimp (Order: Stomatopoda) has remained virtually unexamined.

Remarkably, there appear to have been no analyses or recordings of stomatopod acoustic signals, other than a few descriptive observations. For an entire order of animals, consisting

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ISSN 1023–6244 print/ISSN 1029–0362 online/06/020099–111 © 2006 Taylor & Francis
DOI: 10.1080/10236240600563289

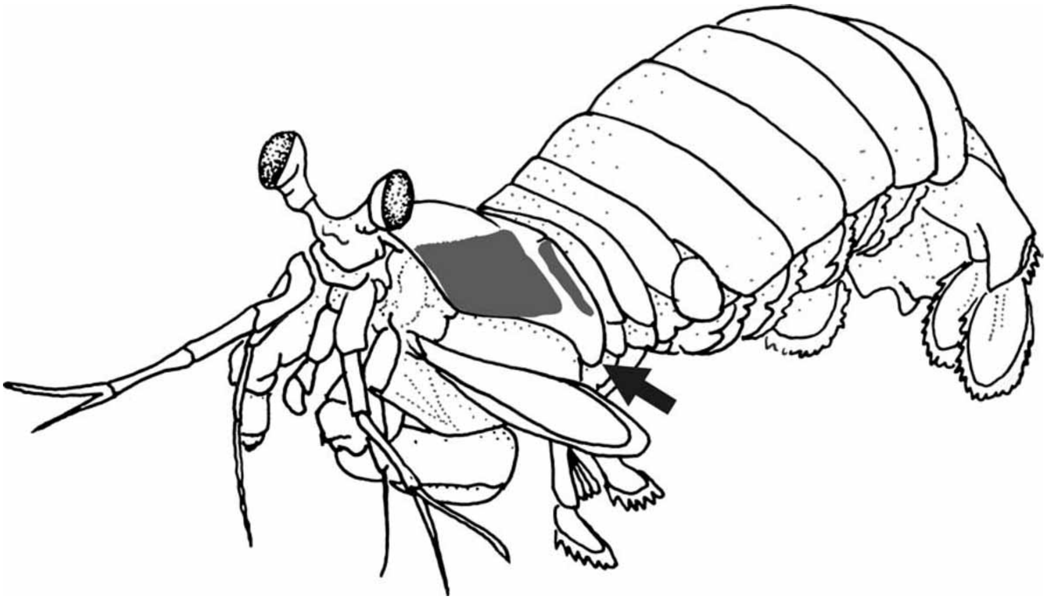

Figure 1. *Hemisquilla californiensis* in a typical pose. Polarized, red patches of color are located on each side of the carapace. The arrow indicates the location of the hypothesized acoustic musculature beneath the curved posterior edge of the carapace.

of over 450 species (17 families) (Ahyong 2001), this is a notable lack of information. In a review of stomatopod sound production, Dumortier (1963) reported several studies in which stridulation by the uropod against the telson was observed in species of *Squilla* and *Lysiosquilla* (Brooks 1886; Giesbrecht 1910; Balss 1921). Several other researchers have noted the sounds produced during a raptorial strike (Alcock 1900; Kemp 1913; Hazlett & Winn 1962; Patek & Caldwell 2005). In addition, Caldwell (1979) documented raptorial appendage substrate pounding in *Neogonodactylus* (previously *Gonodactylus*) species during interactions with potential conspecific intruders. The stomatopod *H. californiensis* (Figure 1), the subject of this study, has been thought to produce sound, based on the 'groaning' noises emanating from their burrows which have been heard by divers (Haderlie et al. 1980), although no recordings were made.

Here we present the first acoustic analyses of *H. californiensis*, coupled with observations of their acoustic behavior and a hypothesis for the underlying mechanism of sound production. Our goals for this study were as follows: (1) record and document sounds generated by *H. californiensis*; (2) categorize and analyze the recorded sounds; and (3) identify and describe the underlying mechanism of sound production. It is generally accepted that crustaceans do not hear the far-field pressure component of sound, and instead they detect the near-field particle vibrations that dominate within approximately one wavelength of the sound source (Hawkins & Myrberg Jr 1983; Kalmijn 1988; Budelmann 1992; Popper et al. 2001; Lovell et al. 2005). This leads to some terminological difficulties when referring to acoustic recordings of crustaceans, specifically whether these signals should be described as vibrations or sounds. In light of the ambiguous function of the stomatopod sounds described here, and the fact that their piscine predators may detect pressure waves (Tavolga et al. 1981), we use the term 'sound' to encapsulate the near-field, far-field and seismic components of this acoustic signal.

Biology of Hemisquilla californiensis

Little is known about the ecology and behavior of *H. californiensis* outside of field observations made off the coast of the southern California mainland (Basch & Engle 1989, 1993). This mantis shrimp species is large, with body lengths ranging up to 30 cm, and hunts for food using its large raptorial appendages (Figure 1) (Basch & Engle 1989, 1993). At depths from 4–90 m in sandy substrates, *H. californiensis* excavates cylindrical burrows with a single entrance (Basch & Engle 1989, 1993). The burrow entrance of an adult is flush with the substrate and extends downward at 60° for 1–2 body lengths, and then runs horizontally for about 1 m. The burrow diameters range from 7 to 95 mm, depending on animal size and locale, with most burrow diameters falling in the 30–45 mm size class (Basch & Engle 1989, 1993). Although animals are observed during both day and night, most of their activity appears to occur during crepuscular periods (Basch & Engle 1989, 1993). They close their burrows before sunset and are active again at dawn, but then at least partially close their burrows during the middle of the day (Basch & Engle 1989). The animals leave their burrows to forage on a wide variety of prey items, many of which they bring back to their burrows for consumption (Basch & Engle 1989, 1993). They are thought to be preyed upon by nearshore predators such as sea bass and grouper (E. Sigler, personal communication, as cited in Basch & Engle 1993; Murillo et al. 1988).

Methods

Study animals

Eighteen adult *H. californiensis* (Gonodactyloidea: Hemisquillidae), including twelve males and six females, were maintained in artificial, recirculating saltwater at 15–19°C. Adult males are easily recognizable by the regions of bright red coloration on their carapace. Sizes ranged from 34–45 mm carapace length (18–20 cm body length). Individuals were housed individually in polyvinyl chloride (PVC) tubes with 7 cm inner diameter and approximately 30 cm in length. The mantis shrimp were fed frozen shrimp and vitamin-fortified freeze-dried shrimp (Selcon, American Marine Inc., CT, USA). The animals were obtained from collaborators who captured animals during trawls. We also purchased animals from a local 99 Ranch supermarket which is periodically supplied with *H. californiensis* during the spring when the animals are caught as by-catch during trawls by local fishermen. Recordings were made in glass tanks containing approximately 38–190 L of saltwater at depths of approximately 28–41 cm.

Acoustic recording and analyses

Sounds of animals when freely moving around the tank or occupying their burrows were recorded. A hydrophone (20–15,000 Hz; HTI-94-SSQ, High Tech, Inc., Gulfport, MS, USA) was placed within 10 cm of the focal animal and sounds were elicited by approaching the animal with the hydrophone or a stick. The hydrophone was connected to an analog audio tape recorder (TCD5M, Sony Corp., Tokyo, Japan). These recordings were subjected to a low-pass filter (15 kHz cut-off frequency, 24 dB/octave attenuation, Model 3362, Krohn-Hite, Brocton, MA, USA) and then digitized in Matlab (v. 6, The Mathworks, Natick, MA, USA) using a 16-bit analog–digital computer board (SoundBlaster Audigy 2, Creative Labs, Milpitas, CA, USA) set at 44 100 samples per second. Sounds were analyzed using Raven software (v. 1.2, Cornell Lab of Ornithology, Ithaca, NY, USA). Temporal sound measurements were taken from the waveforms, whereas frequency analyses were conducted using a discrete Fourier transform as implemented in Raven (settings: Hanning window, 19 000 sample window size, 3 dB filter bandwidth at 3.34 Hz resolution). We measured the duration of each discrete burst of sound, the dominant frequency (harmonic frequency with greatest amplitude), the fundamental frequency (the first harmonic), and the frequency modulation (maximum change in dominant frequency during a single sound burst).

One-way analyses of variance (JMP 5.0.1, SAS Institute, Inc., NC, USA) were used to test for significant differences among individuals across the measured acoustic parameters (sound duration, dominant frequency, frequency modulation). A standard least squares linear regression analysis (JMP 5.0.1, SAS Institute, Inc., NC, USA) tested whether body length was correlated with the above acoustic parameters.

Acoustic morphology and behavior

We recorded audio and video images simultaneously (DCR-VX2100 Sony digital video camera connected to the hydrophone described previously) in order to identify any stereotyped behaviors which accompany sound production. We identified the source of the vibrations by scanning freely-moving individuals with a hydrophone. The animals were also held in hand, in both air and water, and the musculature contracting simultaneously with the carapace vibrations was observed. The polarization and coloration of the vibrating carapace was assessed using a linearly polarizing filter (52 mm, polar filter, Nikon). The filter was rotated until the polarized patch was maximally red and then rotated further until the coloration disappeared.

Results

Acoustic analyses

We attempted to record sounds from all eighteen individuals, and successfully recorded sounds from six reproductively mature males. Given that we sampled twice as many males as females, it is ambiguous whether females in fact do not produce sound or instead that we did not elicit sounds in females simply due to a low sample size.

The dominant frequencies and frequency modulations of the stomatopod sounds are notably similar to the sweeping tonal 'rumble' sounds (15–30 Hz) produced by African and Asian elephants (Payne & McVay 1971; O'Connell-Rodwell et al. 2001). Thus, we propose the name 'rumble' for the low frequency, tonal sounds produced by *H. californiensis* (Table I).

Ninety-one percent of the 58 recorded stomatopod sounds were rumbles. The dominant frequency and the fundamental frequency were the same and ranged from 20 to 60 Hz, with a mean frequency of 45 Hz (SD = 10, Table I) (Figures 2 and 3). The overall mean duration was 1.9 s (SD = 1.4) and the median duration ranged from 0.7 to 1.8 s across six individuals. The mean frequency modulation was 10 Hz (SD = 5) with a range of 1.3–21.5 Hz. In all but two cases, the starting dominant frequency was higher than the dominant frequency at the end of the sound.

The majority of the recorded rumbles (70%) were less than 2 s and exhibited a gradual decrease in dominant frequency (Figure 2). Rumbles that exceeded 2 s in duration were less common (30%) and typically exhibited both increases and decreases in dominant

Table I. Signal features of the rumble. *N* is the number of sounds analyzed per individual; each row represents one individual. All individuals were reproductively mature males. Sample sizes varied within individuals because it was not possible to analyze all signal parameters in all recordings. Except in two recorded rumbles, the frequency modulations began at a higher frequency and ended at a lower frequency.

N	Dominant frequency (Hz) mean (SD)	Frequency modulation (Hz) mean (SD)	Duration (s) mean (SD)
12	50 (10)	5 (5)	0.9 (0.3)
7–9	50 (15)	10 (5)	1.1 (0.5)
18–21	45 (5)	10 (5)	1.8 (0.8)
4–8	35 (5)	10 (10)	1.6 (0.6)
2	55 (5)	10 (5)	1.1 (0.1)
5–8	45 (10)	15 (5)	1.7 (0.3)

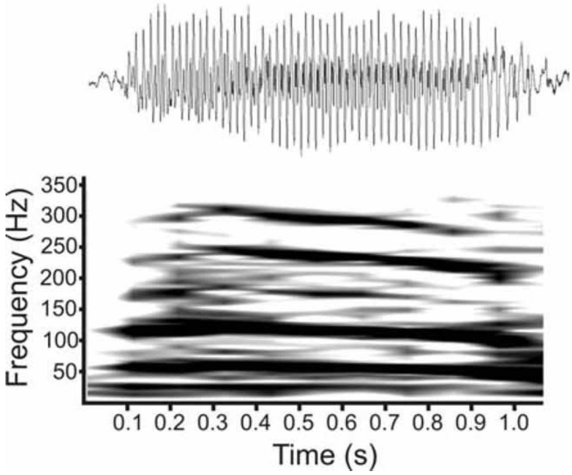

Figure 2. A typical rumble lasting approximately 1 s. A waveform is shown in the top panel with the corresponding spectrogram in the lower panel. Seventy percent of the recorded rumbles were under 2 s in duration. Note the strong dominant frequency at 60 Hz, and the weak third harmonic (second overtone) of the fundamental. This rumble shows a net frequency modulation of 8 Hz when the onset dominant frequency is compared to the dominant frequency at the end of the rumble. A 35 Hz high pass filter was applied to this signal. A recording of this sound is available as supplementary material online.

frequency (Figure 3). Both of these types of rumbles were recorded when the animals were either in the burrows or freely moving around the tank.

In addition to the rumbles, we also recorded 10 pulsed broadband rattles from four different individuals (1–3 rattles per individual) (Figure 4). Pulsed broadband rattles are defined as sound bursts consisting of a series of discernable pulsatile units with a broadband frequency spectrum which lacks clearly defined tonal harmonics (Figure 4). The sound pulses were produced at rates between 25 and 60 pulses s^{-1} (mean 42 pulses s^{-1}) with the total number of pulses per rattle ranging from 5 to 73 pulses (mean 37 pulses). Durations ranged from 0.2–2.0 s with an overall mean of 1.1 s.

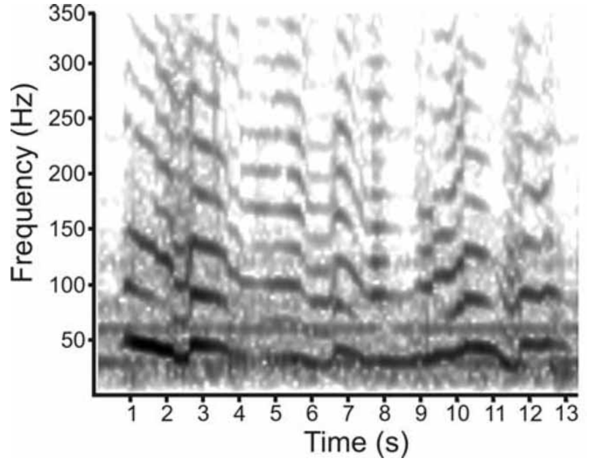

Figure 3. An exceptionally long duration rumble produced over a period of 13 s. Long rumbles, exceeding 2 s, were infrequently produced and constituted only 30% of the total number of recorded rumbles. This rumble shows a net frequency modulation of 19 Hz when the onset dominant frequency is compared to the dominant frequency at the end of the rumble. Noise generated by external pumps was present in the constant 30 and 60 Hz frequency bands; the 60 Hz band obscures some of the rumble harmonics. A recording of this sound is available as supplementary material online.

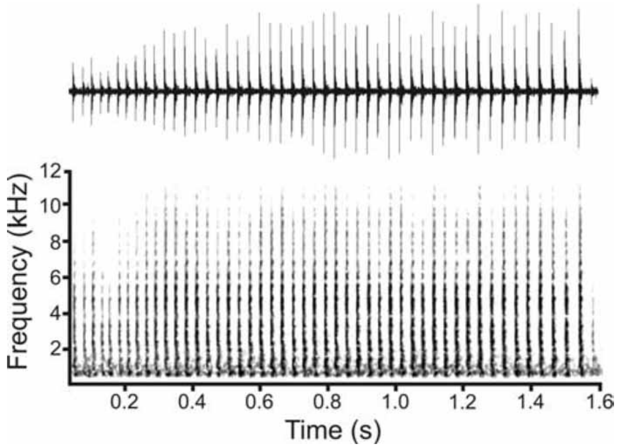

Figure 4. An example of a pulsed broadband rattle which was generated when a stomatopod vibrated its exoskeleton against the inside of a plastic burrow. A waveform is shown in the top panel with the corresponding spectrogram in the lower panel. This rattle was produced at an average rate of 32 pulses s^{-1}. While vibration against the substrate is probable in this species, the spectral features of this signal are highly unnatural given that they were produced in a PVC burrow, rather than in the sandy substrate of a natural burrow. A 500 Hz high pass filter was applied to this signal. A recording of this sound is available as supplementary material online.

Rattles only occurred when animals were in their burrows or when their appendages were resting against the side of the glass tank (see video analyses next). The broadband frequency of the pulsed sounds and their occurrence only when the animals were in contact with a hard surface strongly suggests that the sounds were produced by parts of the exoskeleton vibrating against the unnaturally hard surfaces of their aquarium habitat.

Significant differences ($P < 0.01$) were present among individuals for all measured rumble parameters (sound duration, dominant frequency, frequency modulation) (Table I). None of these parameters correlated with the body length ($P > 0.1$), although it must be noted that we recorded only a few similarly sized individuals (6) with a small sound sample size for some individuals (Table I).

Acoustic behavior

The animals exhibited a stereotyped suite of behaviors during sound production. When initiating sound production, the maxillipeds and, most notably, the raptorial appendages, were pulled postero-dorsally and antennule flicking ceased. The carapace was typically flexed toward the central body axis, resulting in a more depressed position of the edges of the carapace. At the conclusion of a burst of sound production, the carapace was released to a more elevated, less bowed position. While audio/video recordings primarily yielded rumbles (Figures 2 and 3), we also recorded rattling sounds when the raptorial appendages were resting against the sides of the glass tank. Like the PVC burrow rattles described above, the recorded vibrations against the glass aquarium walls were highly unnatural.

When individuals were scanned with a hydrophone, sound was audibly loudest along the dorsal carapace as compared to along the length of the abdomen. When inspected manually, the vibrations were most intense along the midline of the carapace and the edge of the carapace visibly vibrated. When the animal was flipped over, such that the ventral surface of the carapace was visible from an oblique view, it was possible to see a pair of muscles contracting and generating the carapace vibration. These combined observations led us to hypothesize that the sound was generated through contraction of these muscles which are attached to the lateral margins of the carapace. We describe and discuss this morphology in the next section.

Acoustic morphology

The pair of muscles observed contracting during the carapace vibrations originated on the posterior, lateral surfaces of the carapace and inserted on small posterior processes of the mandibular system. These muscles appeared to be the posterior mandibular remotor muscles, which are described as originating 'from the undersurface of the carapace, medial to the dorsal longitudinal muscles . . . and insert[ing] on the posterior mandibular apodeme' (Kunze 1981, p. 264). *Hemisquilla californiensis* also had a prominent tube-like structure extending around the muscle's origination site on the ventral surface of the carapace (Figure 5); however, Kunze's illustration of *Alima laevis* did not show this feature. In nine measured *H. californiensis* individuals, the tube's diameter ranged from 2.7–4.4 mm, and extended to approximately 5 mm from the lateral edge of the carapace. The posterior edge of the carapace extended 2–3 cm from the midline. Both males and females had proportionally similar sized musculature and tube diameters.

The carapace itself had several interesting features, most notably its size, shape and coloration. A stiff, ventrally-curved extension from the posterior, lateral edge of the carapace was present (Figure 5), whereas most gonodactyloid stomatopods have an evenly soft and flexible carapace with a straight lateral margin. Furthermore, in males, striking red coloration was present in two large lateral spots on each side of the carapace (Figure 1), as well as on the dorsal surface of the merus and along the dorsal proximal segments

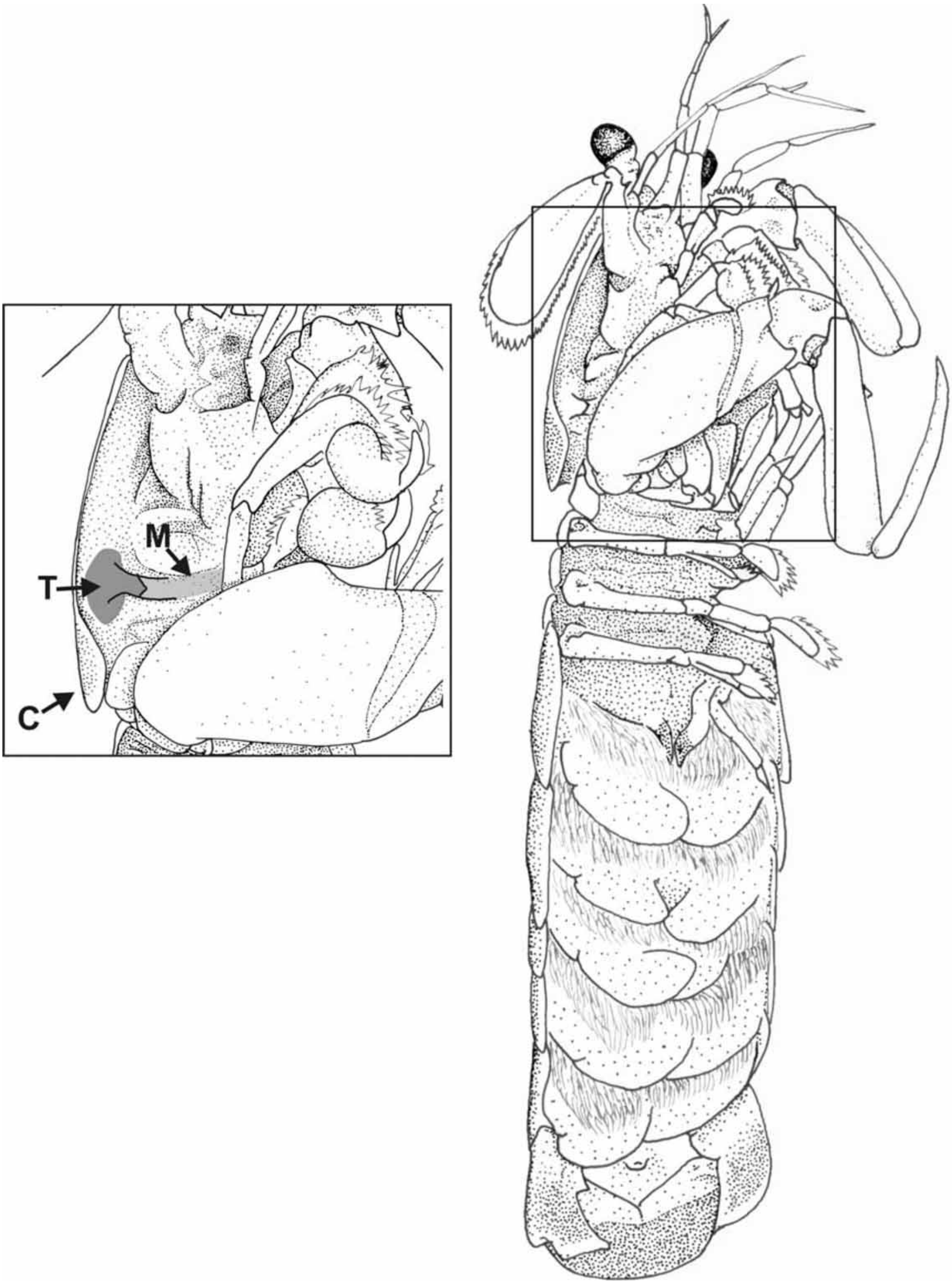

Figure 5. Ventral view of *H. californiensis* with the left inset illustrating the ventral–lateral region of the carapace. Hypothesized acoustic musculature consists of the posterior remotor muscle (M) and the tube-like attachment (T) to the carapace. The posterior, lateral margin of the carapace in *H. californiensis* is ventrally elongated and forms a stiff curve (C).

of the antennules. A polarizing filter revealed that these areas of red coloration were linearly polarized.

Discussion

Hemisquilla californiensis produces sounds which are remarkably reminiscent of the sweeping tonal 'rumble' sounds (15–30 Hz) produced by African and Asian elephants (Payne & McVay 1971; O'Connell-Rodwell et al. 2001). Thus, we proposed the name 'rumble' for the low frequency tonal sounds produced by *H. californiensis*.

Most rumbles were approximately 1 s in duration (Figure 2) whereas a smaller proportion of rumbles exceeded 2 s duration up to an exceptional 13 s duration (Figure 3). While the short duration rumbles exhibited a net decrease in dominant frequency during the sound (Figure 2), the dominant frequency of the long duration rumbles both increased and decreased throughout the sound (Figure 3).

In addition to the rumbles, broadband frequency rattling noises were recorded when *H. californiensis* individuals were in their hard plastic burrows (Figure 4) or resting against the walls of the glass aquaria. The pulse rates of these rattles were in the same range as the dominant frequencies of the rumbles. Thus, the rattles are most probably generated by the same carapace vibrations which generate the rumbles; the broadband frequencies of the rattles can be explained by the hard surfaces against which the carapace vibrated. The frequency spectra of these rattles are certainly unnatural in the sense that *H. californiensis* lives in a soft muddy substrate; however, the fact that these animals can generate sound by vibrating their carapace against a substrate does have potential implications for sound transmission, as will be discussed next.

A number of other species generate spectrally similar low frequency sounds, including whales and fish (Schevill et al. 1964; Payne & McVay 1971; Fine et al. 1977; Tavolga et al. 1981). By contrast, the only other well-studied crustacean that produces acoustic muscle vibrations is the American lobster (*Homarus americanus*); where high frequency muscle contractions in the second antennae generate tonal sounds with fundamental frequencies of 100–130 Hz (Fish 1966; Mendelson 1969; Henninger & Watson 2005).

Acoustic implications of the rumble

The low frequencies of *H. californiensis*' sounds have important ramifications for potential burrow resonances, production efficiency, propagation and reception in the surrounding marine environment. Sound travels nearly five times faster in water than in air, resulting in considerably longer wavelengths and faster propagation times (Zuckerwar 1997). Thus, the 20–60 Hz rumbles, traveling at approximately $1500\,\mathrm{m\,s^{-1}}$, have wavelengths of 75–25 m, respectively.

These very long wavelengths make it unlikely that the burrows of *H. californiensis* could act as resonators. In order for a burrow with a single opening to resonate a particular wavelength, the burrow's length must match at least a ¼ wavelength of a dominant harmonic (Ohanian 1989). Thus, unlike various species of frogs and crickets which use their burrows as resonators and therefore constructively match the appropriate fractional sound wavelengths to the burrow length (Bennet-Clark 1970; Bennet-Clark 1987; Lardner & bin Lakim 2002; Penna 2004), the wavelengths (12.5–75 m) of the first and second harmonics of the stomatopod rumble are mismatched with their 1.5–2 m burrow lengths (Basch & Engle 1989).

The spectral features of the rumble are well configured for signaling to predators and conspecifics within several meters, regardless of whether the receivers are sensitive to near-field, far-field or seismic signals. The long wavelengths of sound in water contribute to a much larger near-field region than would be present in air (Kalmijn 1988). Thus, an anti-predator sound would be effective over a radius of several meters against a wide range of taxa. Nonetheless, it takes a considerable amount of energy to generate sound frequencies with longer wavelengths than the size of the emitter (Bennet-Clark 1998), which explains why long-distance low-frequency acoustic pressure waves are only widely used by large mammals, such as elephants and whales. While low efficiency may limit the stomatopod's use of this sound as a long-range mating signal to conspecifics, it certainly could be used more locally as a territorial or attractive display over tens of meters.

The rattles which resulted from the vibration of *H. californiensis*' exoskeleton against the plastic tube (Figure 4) and glass tank walls suggest that these sounds may propagate via the substrate. Substrate vibration is an important component of many acoustic and vibrational signals in the aquatic environment (Popper et al. 2001; Cocroft & Rodriguez 2005). For example, the mottled sculpin (*Cottus bairdi*) generates, and responds to, substrate vibrations that are produced when the head is knocked against the substrate (Whang & Janssen 1994). Males of the fiddler crab genus *Uca* also generate both airborne and substrate vibrations via multiple mechanisms, including stridulation, substrate 'rapping', and leg vibration (reviewed in Salmon 1983). Furthermore, while far-field detectors remain elusive in crustaceans, crustaceans are known to be sensitive to substrate vibrations and low-frequency near-field signals (reviewed in Popper et al. 2001). Recordings and playbacks of substrate vibrations around the burrows of *H. californiensis* in the field would yield important insights into the relative importance of near-field, far-field and substrate vibrations of the rumble.

Acoustic behavior of Hemisquilla californiensis

Lacking extensive field observations of the context in which sounds are produced, we can only speculate as to their function. In the laboratory, we recorded sounds from *H. californiensis* in an agonistic, defensive context when they were approached by a hydrophone or a stick. Occasionally the animals even attempted to strike the offending object shortly after rumbling. Rumbles were recorded only from reproductively mature males, and females did not respond acoustically to our attempts to elicit sounds.

These sounds could function as a warning to potential predators, such as fish and pinnepeds, that the stomatopod is willing and able to defend itself. This is similar to the body vibrations and warning squeaks produced by palinurid and nephropid lobsters (Fish 1966; Mulligan & Fischer 1977) and numerous other arthropods (Edmunds 1974; Guilford 1990). When concealed in its burrow, a stomatopod emitting low frequency sounds might be particularly effective at deterring predators or competitors because long wavelengths often are associated with relatively large sound producers (Ryan & Brenowitz 1985; Bennet-Clark 1998).

There is an intriguing possibility that vibration of the carapace could be visible to conspecifics as a rapidly alternating pattern of polarization. The angle of linear polarization of the red patches on the carapace of sexually mature males should change slightly as the carapace rapidly flexes and unflexes during sound production. This 'flickering' (rapidly changing plane of polarization) of the polarized signal should be visible to an attending *H. californiensis*. Gonodactyloids, including *H. californiensis*, have a complex set of polarized light detectors capable of discriminating in at least three different e-vectors

(Cronin et al. 2000; Cronin & Marshall 2004). Assuming that the angle of polarization changes at the fundamental frequency of 20–60 Hz, and the flicker fusion frequency of the polarizing detectors is faster, then *H. californiensis* should be able to see the vibrating carapace through the alternating e-vector. No measurement of flicker fusion values for *H. californiensis* are known, but values for the peripheral ommatidia of another stomatopod that occurs in a similar habitat, *Squilla empusa*, are as fast as 125 Hz (Trevino & Larimer 1969). If *H. californiensis* can indeed see the vibrations through a linearly polarized oscillation, this would be a unique multimodal signal.

Acoustic morphology

A number of interesting questions remain to be addressed about the muscle contractions and exoskeletal couplings that are presumed to generate the rumble. The visual observations of the muscle contractions provide a reasonable basis for the hypothesized mechanism; however, electromyographic recordings would offer a definitive identification of the vibrating muscles and also would elucidate how the muscle contractions are coupled to the observed frequencies and amplitudes. For example, the observed frequency and amplitude modulations could be due to alternate and synchronous contractions of the muscles, as are found in the searobin (*Prionotus carolinus*) which alternately contracts sonic muscles in order to generate higher fundamental frequencies or simultaneously contracts sonic muscles to generate higher amplitudes (Connaughton 2004). Furthermore, the carapace stiffness and shape may be coupled to the fluid medium and tuned to vibrate at particular frequencies, much like speaker elements and sound-producing insect wings (Bennet-Clark 1995, 1999). A comparison among closely related stomatopods also may yield insights into the acoustic function of the intriguing carapace shape and the tube-like attachment of the remotor muscle.

Conclusions

Hemisquilla californiensis generates low frequency, tonal sounds through carapace vibrations. The lateral extensions of the carapace are flexed and released during sound production to generate frequencies ranging from 20–60 Hz. This region of the carapace is colored by large, polarized red spots, suggesting a possible multi-modal signal that is coupled with the body vibrations. The use of the sound during agonistic interactions suggests an anti-predator or territorial function. In a clade thought to operate primarily in the visual realm (Cronin & Marshall 2004), these acoustic analyses offer a new glimpse into the sensory world of stomatopod crustaceans.

Acknowledgments

We are grateful to D. Cowles, L. Bartley and L. Haney for providing us with live specimens. C. Huffard illustrated the specimens shown here and we also thank E. Hebets, R. Hoy, A. Mates, D. Nguyen, C. Nunn, R. Tarter, and K. Weiss for assistance and discussions. We appreciate the constructive comments provided by three anonymous reviewers. This research was funded by the Miller Institute for Basic Research in Science (SNP) and a grant from the UC Berkeley Committee on Research (RLC).

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