

The acoustics and acoustic behavior of the California spiny lobster (*Panulirus interruptus*)

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Numerous animals produce sounds during interactions with potential predators, yet little is known about the acoustics of these sounds, especially in marine environments. California spiny lobsters (*Panulirus interruptus*) produce pulsatile rasps when interacting with potential predators. They generate sound using frictional structures located at the base of each antenna. This study probes three issues—the effect of body size on signal features, behavioral modification of sound features, and the influence of the ambient environment on the signal. Body size and file length were positively correlated, and larger animals produced lower pulse rate rasps. Ambient noise levels (149.3 dB re 1 μ Pa) acoustically obscured many rasps (150.4 ± 2.0 dB re 1 μ Pa) at distances from 0.9–1.4 m. Significantly higher numbers of pulses, pulse rate, and rasp duration were produced in rasps generated with two antennae compared to rasps produced with only one antenna. Strong periodic resonances were measured in tank-recorded rasps, whereas field-recorded rasps had little frequency structure. Spiny lobster rasps exhibit flexibility in acoustic signal features, but their propagation is constrained, perhaps beneficially, by the noisy marine environment. Examining the connections between behavior, environment, and acoustics is critical for understanding this fundamental type of animal communication. © 2009 Acoustical Society of America. [DOI: 10.1121/1.3097760]

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I. INTRODUCTION

Surprisingly few studies have examined the acoustics of antipredator sounds in the marine environment even though these sounds have been observed across a wide range of taxa in an array of marine habitats. For example, when interacting with intruders or potential predators, nephropid lobsters vibrate antennal muscles (Mendelson, 1969; Henninger and Watson, 2005), ocy podid and pagurid crabs stridulate (Guinot-Dumortier and Dumortier, 1960; Field *et al.*, 1987), astacid crayfish squeak with their abdomen (Sandeman and Wilkens, 1982), mantis shrimp rumble using muscles attached to their carapace (Patek and Caldwell, 2006), and fish produce a myriad of sounds using mechanisms from muscle contractions to stridulatory jaws (Fish and Mowbray, 1970). Antipredator sounds have been shown experimentally to deter predators (Alexander, 1958; Masters, 1979; Lewis and Cane, 1990; Sargent, 1990) and function through a variety of mechanisms, including the effects of startle, warning or predator memory enhancement (Gittleman and Harvey, 1980; Gamberale and Tullberg, 1996; Speed, 2000; Sherratt and Beatty, 2003; Ruxton *et al.*, 2004; Caro, 2005).

There are two key factors when examining antipredator sounds: signal propagation through the environment and the effect of, or information contained in, the signal features. In terms of signal propagation, the emission of sound has the potential to attract other predators to the scene; this may make the situation for the prey item even more dangerous or, alternatively, it may increase conflict between the predators and thereby increase the odds that the prey item escapes

(reviewed in Chivers *et al.*, 1996). In either case, the propagation of antipredator signals through the environment—given the ambient background noise and the effects of the physical structure of the habitat—is an important factor in how the signal functions.

Antipredator signal features are relevant to their function and performance in deterring predators. Most antipredator signals, whether acoustic, chemical, or visual, capitalize on being noxious or generally startling to either deter the predator or trigger a predator's memory that the prey item is not palatable (Edmunds, 1974; Ruxton *et al.*, 2004). Furthermore, it is generally advantageous for the prey to appear as threatening as possible by exaggerating size (e.g., eye spots). Although these general principles of antipredator signal design are widely accepted, the features of acoustic antipredator signals are rarely characterized.

Most spiny lobster species (Palinuridae), including the California spiny lobster (*Panulirus interruptus*), generate antipredator sounds called “rasps” (Parker, 1878; 1883; Lindberg, 1955; Moulton, 1957; George and Main, 1967; Meyer-Rochow and Penrose, 1974; Smale, 1974; Meyer-Rochow and Penrose, 1976; Mulligan and Fischer, 1977; Patek, 2001; Patek, 2002; Patek and Oakley, 2003; Latha *et al.*, 2005; Patek *et al.*, 2006). Documented for over a thousand years (Athenaeus, 300), these sounds are produced when spiny lobsters are handled by potential predators. The rasps function to deter predators; spiny lobsters that have been silenced (i.e., the sound-generating apparatus has been disabled) are attacked more frequently and with greater success than spiny lobsters with intact sound-producing structures (Bouwma and Herrnkind, 2004; Bouwma, 2006; Bouwma and Herrnkind, 2007).

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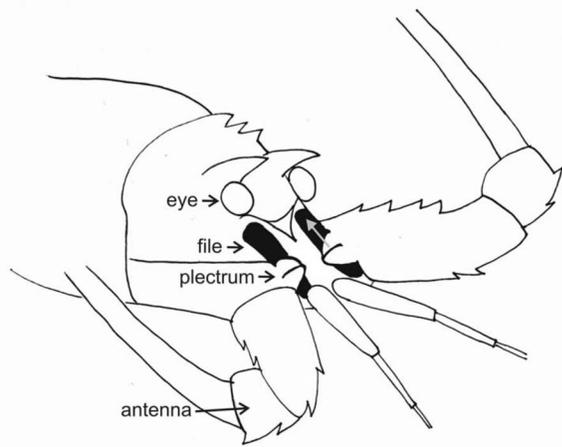


FIG. 1. The sound-producing anatomy of a California spiny lobster (*Panulirus interruptus*). A plectrum is found at the base of each antenna and rubs over a file beneath each eye. Sound is produced when the plectrum slides posteriorly (arrow) over the file. Adapted from (Summers, 2001).

The stick-slip frictional mechanism of spiny lobster sound production is unusual in the biological world, and the paired structures potentially yield flexibility in signal features. Analogous to bowed-stringed instruments, spiny lobsters produce pulses of sound through stick-slip frictional interactions between the plectrum and file surfaces such that the plectrum sticks and slips due to friction as it is pulled posteriorly over the file; a pulse of sound is produced during each “slip” (Patek, 2001, 2002; Patek and Baio, 2007). The plectrums are located at the base of each antenna and traverse the oblong files located on each side of the antennular plate (Fig. 1). Each rasp sound is produced when the plectrum is pulled posteriorly and generates a series of sound pulses as it sticks and slips over the surface of the file (Fig. 2). Because there is a pair of plectrum/file units, sounds can be produced by rubbing only one plectrum over the file, both plectrums in series, or both plectrums concurrently. This flexibility in the deployment of the sound-producing structures potentially offers spiny lobsters additional variation in the range of signal features.

While the above studies have addressed the functional morphology, evolutionary history, and behavioral context of

sound production, the acoustics of these sounds have been examined exclusively in laboratory settings and, thus, the amplitude and frequency structure of these sounds in nature are not currently known. Furthermore, little is known about the influence of using paired structures on the signal features and the scaling of signal features with body size in adult lobsters (Meyer-Rochow and Penrose, 1976; Patek and Oakley, 2003). Examination of the sounds in the laboratory and field offers important insights into the use of these signals by spiny lobsters and, more generally, the role and function of antipredator sounds in the marine environment. In this study, as in all previous analyses of spiny lobster antipredator sounds, we measure the rasps generated during handling, simulating the lobster’s experience once a predator has successfully caught the prey and is attempting to process it; this leaves open the possibility that a different suite of acoustic signals are used during predator approach or for signaling to distant predators, although no such sounds have been documented to date in spiny lobsters.

Thus, the goals of this study were to examine the acoustics and acoustic behavior of the California spiny lobster (*Panulirus interruptus*) from the following three perspectives: (1) *Body size and signal features*: Which acoustic parameters are correlated with body size? Do spiny lobsters vary rasp duration by increasing number of pulses or decreasing pulse rate? (2) *Plectrum activation and rasp variation*: Are single, sequential and concurrent plectrum activation patterns correlated with specific rasp features, such as greater rasp duration, higher pulse rate or greater number of pulses, and particular behaviors, such as tail flipping or leg movements? (3) *Rasps and their acoustic environment*: How does the acoustic environment influence rasp signal features, specifically when comparing recordings made in a tank versus in the field?

II. METHODS

A. Animal collection and care

California spiny lobsters, *Panulirus interruptus* (Crustacea, Decapoda, Palinuridae), were collected at the University of Southern California, Wrigley Institute for Environmental Studies (WIES, Santa Catalina Island, CA,) in baited lobster

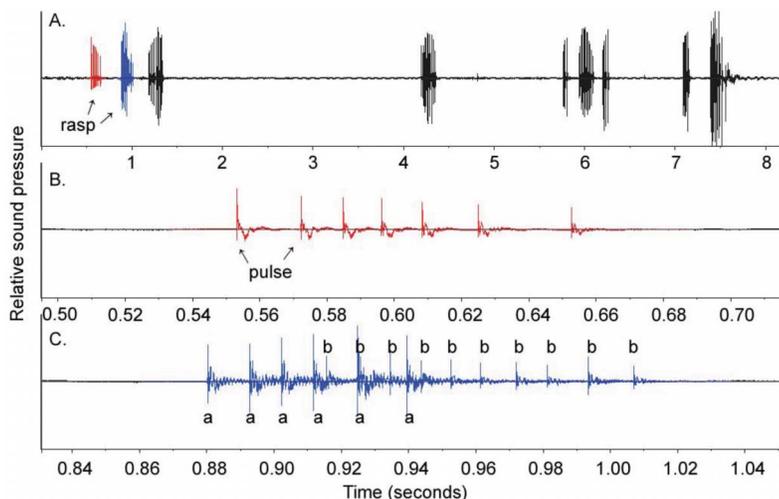


FIG. 2. (Color online) Spiny lobsters typically produce a series of rasps (A) each consisting of a series of pulses (B). In a rasp produced by a single plectrum (the first rasp in panel A), seven pulses are visible (B). The second rasp in A was generated with two plectrums activated concurrently (C), beginning with the first plectrum producing a series of pulses labeled “a” and the second plectrum generating the overlapping series of pulses labeled “b.” Series a and series b are distinguishable by differences in both amplitude and temporal spacing.

traps or by hand (CA Department of Fish and Game Permit No. SC-5751). One small lobster was borrowed from the WIES “touch tank.” Lobsters that were brought back to the laboratory were maintained in cylindrical holding tanks (1.5 m diameter, 0.8 m height) with a continuous supply of sea water (14–16 °C). They were fed bait fish daily.

Experiments were conducted during three different field seasons, and the lobsters were captured shortly before each set of experiments. In the first field season (2005), we conducted the temporal acoustic analysis experiments in which we recorded 24 individuals (2 males and 22 females; 44–102 mm carapace length; 14–15 °C water temperature). In the second field season (2006), we conducted audio-video experiments of acoustic behavior and comparisons of rasp acoustics in tank versus field conditions. In these experiments, we recorded 20 individuals (6 males and 14 females; 50–113 mm carapace length; 8–18 mm file length; 14–15 °C water temperature). In the third field season (2008), we recorded 13 more individuals (12 females, 1 male; 65–93 mm carapace length; 19.8 °C water temperature) in the field and measured pressure levels of the rasps and ambient field environment. The specific sample sizes used in each experiment are detailed below.

B. Temporal acoustic analyses

We tested for the presence of correlations between body size and temporal components of the rasp, including rasp duration (s), number of pulses (total number of pulses per rasp), and average pulse rate (pulses s⁻¹: number of pulses per rasp divided by rasp duration) (Fig. 2). A hydrophone (1 Hz–170 kHz, TC4013, Reson, Slangerup, Denmark) was connected to a band-pass filter (high-pass: 10 Hz, low-pass: 15 kHz; 1 Hz–1 MHz VP2000 voltage preamplifier, Reson, Slangerup, Denmark) and a digital audio recorder (48 kHz sample rate, maximum 20 kHz frequency response [–0.5 dB], PMD670, Marantz, NJ). Individuals were hand-held at variable depths in a fiberglass tank (1.5 m diameter, 0.8 m height) with the hydrophone suspended approximately 60 cm from the anterior end of the lobster.

Rasp waveforms were measured using acoustic software (RAVEN 1.2.1, Cornell Laboratory of Ornithology, NY). We defined rasps as consisting of at least two pulses that occurred within 45 ms of each other. Sometimes, a single pulse of sound was produced in isolation; these pulses were not included in the analyses. Pulse duration was not measured, because previous studies have shown that tank reverberations obscure the ending time of each pulse (Patek and Baio, 2007). When the rasps were difficult to resolve against excessive background noise, they were omitted from the analyses.

In many recordings, the sounds generated by the two plectrums were distinguishable from each other, either temporally or through amplitude differences. We split the dataset into rasp waveforms unambiguously produced by one plectrum only and compared them to rasp waveforms clearly showing activity from two plectrums (Fig. 2); when this distinction was not clear, the rasps were not included in this particular analysis. Using these distinct patterns, we docu-

mented three modes of plectrum activation: (1) “single plectrum” in which only one plectrum was used to generate one rasp, (2) “sequential plectrums” in which the same plectrum was used repeatedly or two plectrums were used in sequence to generate multiple rasps, and (3) “concurrent plectrums” in which two plectrums concurrently generated one or more rasps (see Fig. 2 and further explanation in Sec. III). We limited this dataset to individuals that produced at least three rasps each of single plectrum and dual plectrum activation.

We analyzed the relationships among these acoustic variables and between these variables and body size. Least-squares linear regressions were used to examine the correlation between carapace length and mean values for acoustic features across individuals. A general linear model [analysis of covariance (ANCOVA)] was applied to examine the effects of plectrum activation on the temporal acoustic features, as well as the effects of individual, and individual by plectrum usage on the resulting correlations. Similarly, an ANCOVA was used when examining the correlation between pulse number and rasp duration within and across individuals. Statistics were performed with JMP v. 5.0.1 software.

C. Comparison of acoustic frequencies in tank versus field conditions

The acoustic frequencies of *P. interruptus* rasps were compared between field and tank recordings. Each individual lobster was recorded in the field and then recorded in the tank so that the spectral characteristics could be compared both within and among individual lobsters.

Field recordings were taken in 7.3 m water (14 °C) with the lobsters hand-held at 42 cm depth. The distance of the hydrophone from the anterior end of the focal lobster was held at a constant 31 cm in the field and ranged from 31–66 cm in the tank. The tank recordings were performed in a cylindrical, fiberglass tank (1.5 m diameter, 0.8 m height) at 15 °C. Calibrated recordings were taken with a hydrophone (0.1 Hz–10 kHz ± 1.5 dB, sensitivity: –206.1 dB ± 0.25 dB re 1 V/μPa, Type 8104 hydrophone, Brüel and Kjaer, Nærum, Denmark) and amplifier (set at high-pass filter 2 Hz and low-pass filter 10 kHz; 0.2 Hz–200 kHz, Type 2635 charge amplifier, Brüel and Kjaer, Nærum, Denmark) which were connected to a digital data acquisition system (50 kHz sample rate, NIDAQ 6062E PCMCIA data acquisition card, National Instruments, TX; custom data acquisition software, MATLAB, The Mathworks, Natick, MA). Using a custom MATLAB program, the data were converted to “.wav” files by scaling the voltage amplitude by a factor of 0.1 and running a 20 Hz high-pass Butterworth filter.

The dominant frequencies (the two frequencies with greatest acoustic power) were identified for each rasp and compared to ambient background noise in each recording (RAVEN v. 1.2.1 and 1.3, Cornell Laboratory of Ornithology, Ithaca, NY). Temporal measurements were calculated from the acoustic waveforms; frequency analyses were measured from power spectra using a discrete Fourier transform (settings: Hanning window, 2000 sample window size, 3 dB filter bandwidth at 36 Hz resolution).

We examined correlations between acoustic features and body size using least-squares linear regressions. We performed a t-test to examine whether recording conditions significantly affected the dominant frequencies. Statistics were performed using JMP software (v. 7.0, SAS Institute, Inc., NC).

D. Rasps in the field environment

The pressure levels of the rasps and background noise were measured in the field. Lobsters were held by hand in 7.3 m water at 45 cm depth with the hydrophone positioned at 97 cm depth. Thus, the effective diagonal distances between the lobster and hydrophone were 0.9, 1.1, 1.3, and 1.5 m. The equipment and settings were the same as in Sec. II C. Absolute average power (dB) was calculated by converting RAVEN software's dimensionless units to pascals using the calibration provided by the hydrophone and amplifier manufacturer and the conversion factors provided by RAVEN software (version 1.4, Hanning window, 2000 sample window size, 3 dB filter bandwidth at 36 Hz resolution). These calibration methods are explained in the RAVEN software support documents and are also available upon request from the authors. The average power (dB) was calculated relative to 1 μ Pa (the standard for aquatic measurements) and also calculated relative to the baseline noise level measured in each recording.

E. Audio-video analyses of acoustic behavior

In order to test whether rasp features and plectrum activation were correlated with specific behaviors, we used synchronous audio and video to record spiny lobsters producing rasps. Each individual was held approximately 36 cm deep, 1.5 m from the camera, and recorded until it produced 5–10 rasps (20–15 000 Hz; HTI-94-SSQ hydrophone, High Tech, Inc., Gulfport, MS; Sony DCR-VX2100 Handycam video camera, Tokyo, Japan; Amphibico VLAL0010 underwater housing, Montreal, Canada). Rasps were elicited by holding and gently squeezing or tickling the lobster.

We identified behavioral units typically associated with escape or arousal in lobsters (Atema and Cobb, 1980). The two most consistent and identifiable behaviors were leg movements and tail flips. Tail flips are an escape response in which the tail is rapidly tucked under the body causing the animal to rapidly jet backwards. Leg movements were noted if they were vigorous and continuous (as distinguished from the slow or small movements associated with resting behavior).

Sound production and behavioral units were counted and binned over 10 s intervals. The onset of each 10 s bin occurred when the spiny lobster first started to produce rasps. Sound production and behavior were measured for 10 s in all individuals with the exception of one individual for which only 6 s were recorded. We tested whether including this individual affected the results by running the analyses with and without it. We logged the time at which each behavioral unit and sound occurred and noted the identity of the plectrum(s) (right plectrum, left plectrum, or both) producing the sound. We then calculated the rate of rasp production (the

TABLE I. Temporal features of rasps. Sample size was 19 individuals with 5–21 rasps recorded per individual. The minimum number of pulses in a rasp sequence was set at two pulses; single pulses were not included in the analysis. A one-way analysis of variance tested for differences across individuals. ** indicates $p < 0.0001$.

	Minimum–maximum	Mean \pm std. dev.	F-ratio
Pulse rate (pulses s^{-1})	24–192	71 \pm 20	**7.9982
Rasp duration (ms)	15–303	108 \pm 35	**6.4656
Number of pulses	2–19	7 \pm 3	**8.5686

number of rasps divided by the 10 s bin during which they occurred) and the proportion of rasps produced by a single plectrum or both plectrums (including both sequential and concurrent movement) out of the total number of rasps produced during the 10 second time period.

We tested whether the behavioral units (tail flip and antennal movement) were correlated with the rate of rasp production and the number of rasps produced using both plectrums concurrently. These data were not normally distributed (Shapiro-Wilks Goodness-of-Fit test; $p < 0.0001$), therefore the nonparametric Kruskal–Wallis test was used in place of a t-test (JMP 5.0.1, SAS Institute, Inc., NC).

Results are presented as mean \pm one standard deviation.

III. RESULTS

A. Acoustic features and body size correlations

The temporal rasp features varied substantially both within and across individuals (Table I). File length (Fig. 1) was positively correlated with carapace length (Fig. 3) ($N = 18$; $R^2 = 0.6178$, $F = 25.8664$, $p = 0.0001$). Carapace length was negatively correlated with mean pulse rate, but not correlated with mean rasp duration or mean number of pulses per rasp (Fig. 3; Table II). Rasp duration was positively correlated with number of pulses (Fig. 4) ($df = 18$; whole model: $R^2 = 0.6998$, $F = 24.7785$, $p < 0.0001$; number of pulses: $F = 181.4677$, $p < 0.0001$; individuals: $F = 12.5963$, $p < 0.0001$). Because pulse rate was calculated using values from rasp duration and pulse number, it was not statistically valid to examine the relationships among the three variables. The rasps produced with two plectrums concurrently had a significantly greater number of pulses than rasps produced by one plectrum alone or two plectrums sequentially; rasp duration and pulse rate were also greater in rasps produced with two plectrums (Table II).

Dominant frequencies were not correlated with body size in the tank nor in the field (Fig. 3) (least-squares linear regression, $p > 0.4$ in all tests). Body size was not correlated with average power when pooled across all recording distances (Fig. 3) ($R^2 = 0.302$, $df = 12$, $F = 4.76$, $p = 0.05$).

B. Acoustic frequencies in the tank and the field

The frequency characteristics and background noise levels of the rasp recordings were different in the field and the

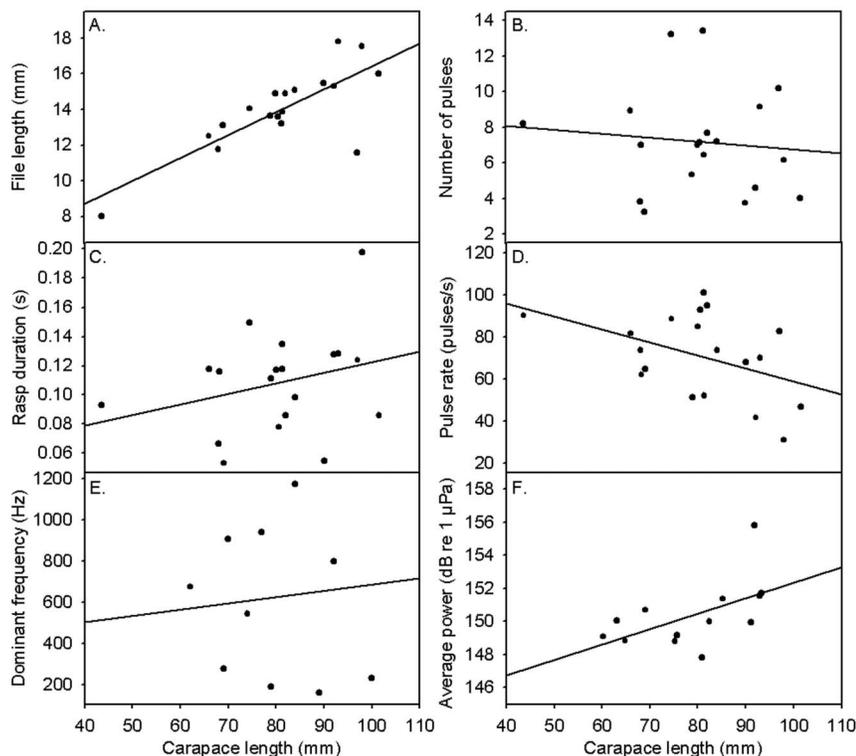


FIG. 3. The relationships between file length (A), temporal signal features [(B)–(D)], spectrographic features [(E)–(F)], and body size. Each data point represents the mean value for an individual lobster.

tank (Table III). The rasps from the field recordings typically had one distinct narrow peak below 500 Hz and another broader peak around 1.5–2 kHz (Fig. 5). Tank recordings lacked this predictable structure and exhibited a pattern of evenly spaced narrow peaks (Fig. 5). The dominant frequencies in the tank and field were significantly different (t -ratio=7.569, $p < 0.0001$), but the second most powerful frequency was not significantly different (t -ratio=1.212, $p = 0.24$).

C. Rasps in the field acoustic environment

The average power of the rasps was 150.4 ± 2.0 dB re $1 \mu\text{Pa}$ ($N=13$ lobsters; 281 rasps). The average background noise level was 149.3 ± 3.3 dB re $1 \mu\text{Pa}$ ($N=36$ recordings) and the rasps exceeded the background noise level by an average 1.6 dB (range: -7.5 to 9.5 dB) (Table IV; Figs. 6 and 7). 31% of the rasps had power less than the average ambient noise with the majority of the negative decibel ref-

TABLE II. The correlation between temporal rasp features, body size, and plectrum activation. Least-squares linear regressions were used to analyze the relationship between pulse rate, rasp duration, number of pulses, and carapace length. A general linear model (ANCOVA) was used to analyze the correlation between the use of one or both plectrums to generate sound and the temporal features of the rasp. This second analysis was restricted to individuals producing at least three rasps each of single plectrum and double plectrum activation, resulting in a dataset of five individuals. * indicates $p < 0.05$; ** indicates $p < 0.001$.

	Carapace length $N=19$ individuals	Plectrum activation $df=1,4$	
Pulse rate	* $R^2=0.2170$ $F=4.7110$	Whole model plectrum activation Individual plectrum activation \times individual	** $R^2=0.6501$, $F=10.9405$ * $F=4.1794$ ** $F=18.6654$ $F=0.2576$
Rasp duration	$R^2=0.0517$ $F=1.0308$	Whole model plectrum activation Individual plectrum activation \times individual	** $R^2=0.5289$, $F=6.6105$ ** $F=13.5364$ ** $F=9.4418$ $F=1.1452$
Number of pulses	$R^2=0.03826$ $F=0.6763$	Whole model plectrum activation Individual plectrum activation \times individual	** $R^2=0.5826$, $F=8.2215$ ** $F=45.2203$ * $F=4.4095$ $F=0.19512$

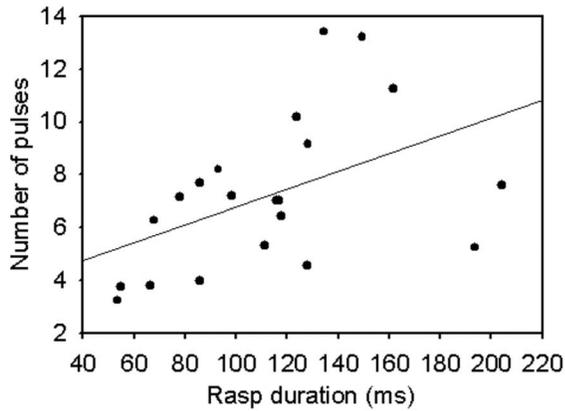


FIG. 4. The number of pulses scales positively and significantly with rasp duration. Each data point represents the mean value for an individual.

erenced to background noise rasps occurring at greater recording distances (Fig. 7). However, when the proportion of rasps below zero dB re background noise was calculated within each individual and then pooled across individuals for each distance, this pattern was less evident and was non-significant (least-squares linear regression: $R^2=0.5532$, $df = 1, 12$, $F=1.905$, $p=0.09$).

D. Audio-video analyses of acoustic behavior

Two datasets were analyzed, one including all data and one excluding a short video sequence. The results were consistent whether or not the short video clip was included in the dataset; thus, the statistical results presented here include all available data. The number of rasps produced by both plectrums concurrently [Fig. 2(c)] was positively correlated with tail-flip behavior (Table V). Regardless of whether rasps were produced with a single plectrum or both, the rate of sound production increased significantly when an individual's legs were moving (Table V).

TABLE III. Comparison of frequencies in the field versus tank recordings and background noise versus rasps. Data are in the following format: mean frequency \pm s.d.; tank: $N=13$ individuals (3–22 rasps per individual); field: $N=11$ individuals (5–34 rasps per individual).

	Tank		Field	
	Background noise	Rasp	Background noise	Rasp
Dominant frequency (Hz)	126 ± 322	1794 ± 338	366 ± 706	633 ± 374
Second dominant frequency (Hz)	n.a.	1796 ± 303	n.a.	1590 ± 483

IV. DISCUSSION

The acoustics of the California spiny lobster's rasp were tied to the ambient environment, the individual behavior of the lobsters, and, to a lesser extent, the size of the lobsters. As we discuss below, the interconnections between the rasp characteristics and the environment may be central to the rasp's function as an antipredator signal.

A. Body size and signal features

Although the size of the sound-producing apparatus was tightly correlated with the body size of these animals, the acoustic features were less so (Fig. 3). Pulse rate was correlated with body size, such that larger animals produced rasps with a slower pulse rate [Fig. 3(d)]. However, dominant frequency and power were not strongly associated with body size [Figs. 3(e) and 3(f)]. Given that the rasps are broadband signals with little tonal definition, it is perhaps unsurprising that a significant correlation between body size and dominant frequency was not observed. Future studies should examine a broader range of body sizes and examine the effect of motivation on signal features. For example, the stick-slip mechanism of sound production may permit greater power output when individuals pull the plectrum more tightly against the file thereby generating a higher normal force and louder

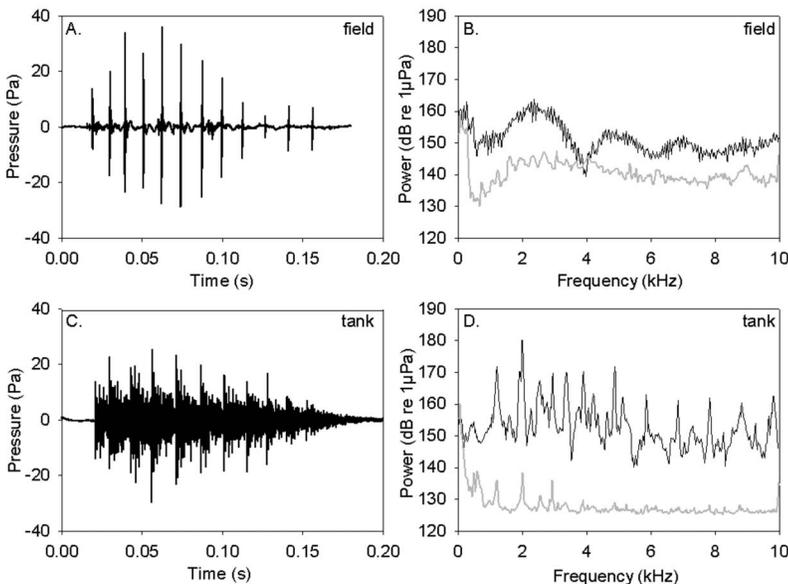


FIG. 5. Recordings of the same lobster producing a rasp in two different environments. In the field, the pulse structure of the rasp is evident (A) and the sound shows little resonant structure [(B) power spectrum settings as described in Sec. II]. In a tank, the reverberations obscure the pulse structure (C) and a series of harmonics are apparent (D). The grayed spectra in (B) and (D) indicate the signature of the ambient background noise. This particular lobster was positioned 53 cm from the hydrophone in the tank and 30 cm from the hydrophone in the field, which may also have caused spectral differences (Akamatsu *et al.*, 2002).

TABLE IV. Average power of rasps at varying distances in the field. Power is reported as dB re 1 μ Pa and dB re background noise \pm standard deviation. Samples sizes are number of individuals (N) followed by number of rasps recorded per individual.

	0.9 m N=8 (3–18)	1.1 m N=11 (3–22)	1.3 m N=9 (1–22)	1.5 m N=5 (1–9)
dB re 1 μ Pa	150.2 \pm 1.4	150.2 \pm 2.1	149.2 \pm 1.6	149.2 \pm 1.7
dB re background noise	1.8 \pm 1.6	1.3 \pm 2.2	0.45 \pm 2.1	1.0 \pm 2.4

sound (Patek and Baio, 2007). The fact that the lobsters were hand-held in this study may have elicited different signaling behavior than in freely-moving individuals (although their rapid escape responses preclude measuring calibrated power levels at known distances in freely-moving individuals). Also, repeated stimulation of the same individuals may have yielded habituation, again influencing signal feature patterns over the time-course of these experiments. This might explain the unexpected variation in power levels across the four field recording distances (Table IV).

Scaling of sound with body size has been examined previously in several spiny lobster species and across the family as a whole (Meyer-Rochow and Penrose, 1974; 1976; Patek, 2002; Patek and Oakley, 2003; Patek and Baio, 2007). Across the palinurid family, and within *Panulirus argus*, pulse rate and number of pulses were positively correlated

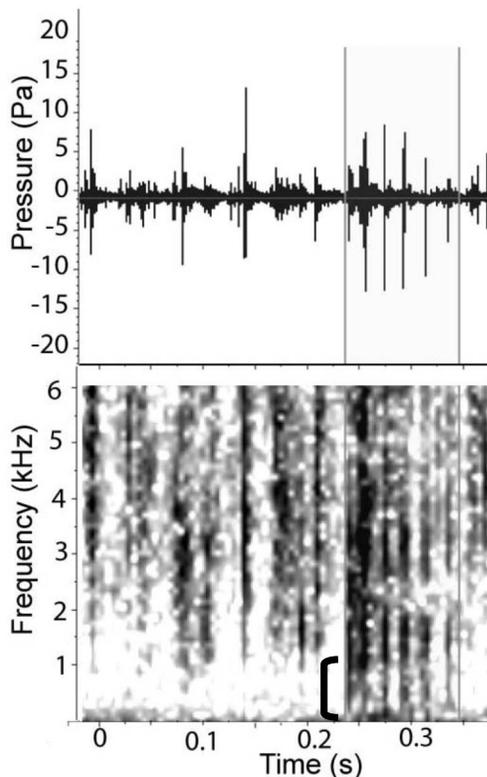


FIG. 6. A rasp produced by a lobster in the field at 1.1 m from the hydrophone. The rasp is highlighted and is shown as a waveform (upper) and spectrogram (lower; RAVEN PRO software v. 1.4, Hanning window, 512 sample window size, 3 dB filter bandwidth at 140 Hz resolution). The bracket indicates the energy extending below 1 kHz from the rasp, whereas the ambient background noise is less powerful in this frequency range.

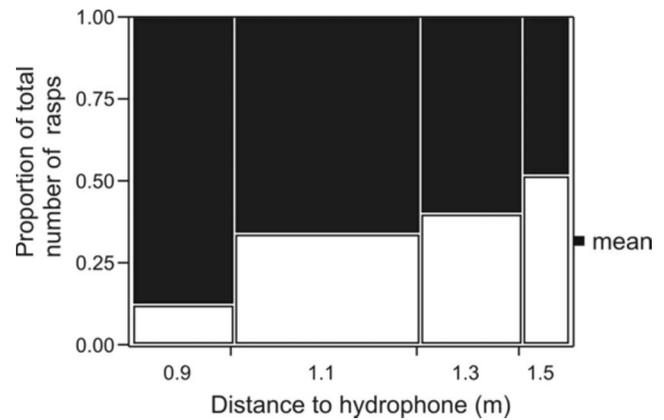


FIG. 7. The proportion of rasps with power levels above the background noise (black bars) and below background noise level (white bars) at four distances from the hydrophone. The width of the horizontal bars represents the relative number of rasps recorded (0.9 m: 65 rasps; 1.1 m: 118 rasps; 1.3 m: 65 rasps; 1.5 m: 29 rasps). The overall mean is indicated to the right.

with the length of the file while rasp duration was negatively correlated with file length (Patek and Oakley, 2003). At early developmental stages, correlations between dominant frequencies and size were not found (Meyer-Rochow and Penrose, 1974); however, across juvenile and adult *Panulirus longipes*, a positive correlation between body size and rasp duration was found, and, similar to the results of this study, there was a negative correlation between size and pulse rate (Meyer-Rochow and Penrose, 1976).

B. Plectrum activation and rasp variation

While the lack of body size and signal feature correlation in spiny lobsters might be explained by the study's limited body size range, another key factor is the behavioral use of the dual sound-producing apparatuses. For example, when examining temporal features of rasps, a larger number of pulses yielded a longer duration rasp (Fig. 4). While this was not explained by body size variation, it may instead be attributed to the lobster's use the pair of plectrums rather than a single plectrum to generate sounds.

Behavior, particularly the use of one or both plectrums had strong influences on the temporal features of the rasp. When two plectrums were used concurrently, the number of pulses, rasp duration, and pulse rate were greater (although these results may be confounded by individual differences; Table II). Furthermore, concurrent activation of both plectrums was correlated with the attempt to escape by tail-flipping and the overall activity of the animal. Thus, the be-

TABLE V. Correlation between plectrum activation and behavioral units (tail flip and leg movement). A nonparametric, two-sample Kruskal-Wallis test was used to test whether these behaviors were associated with rasp rate and plectrum use. Sample size was 20 individuals each sampled once. * $p < 0.05$.

	Overall rate of rasp production	Number of rasps when both plectrums were concurrently active
Tail flip	$Z=0.6622$; $p=0.51$	$Z=2.3437$; $p=0.019^*$
Leg movement	$Z=-2.2955$; $p=0.022^*$	$Z=-1.7812$; $p=0.075$

havioral motivation of the animal may more directly influence signal characteristics than the body size even though body size corresponds closely with the size of the sound-producing apparatus.

The relevance of behavior to signal features has been suggested previously in spiny lobsters (Patek and Oakley, 2003) and demonstrated in other systems with multiple signal-generating devices. For example, the searobin (*Priotonotus carolinus*) has a pair of sonic muscles which it can contract simultaneously to generate greater amplitude or sequentially to produce a higher fundamental frequency (Connaughton, 2004). The California mantis shrimp (*Hemisquilla californiensis*) may also use its paired sonic muscles to vary signal features (Patek and Caldwell, 2006).

The behavioral manipulation of the signal features may be important for tailoring an acoustic response to particular predators. For example, multiple studies have shown that vertebrates produce signal features specific to the predator (e.g., Templeton *et al.*, 2005). Thus, it will be important in future studies to present a range of predators to spiny lobsters and assess whether they respond differently depending on the relative size, risk, and hearing capabilities of that particular predator.

C. Rasps and their acoustic environment

Consistent with previous studies (Parvulescu, 1967; Meyer-Rochow and Penrose, 1976; Akamatsu *et al.*, 2002), there were significant effects of the tank and field on the frequency characteristics of the sound (Fig. 5; Table III). The tank recordings yielded average dominant frequencies of 1794 Hz, whereas in the field, the dominant frequencies averaged 633 Hz. The second most powerful frequency was similar in both settings—1796 Hz in the tank and 1590 Hz in the field—suggesting that the tank resonated the higher frequencies in the rasp or damped the lower dominant frequency. These substantial differences in frequencies and temporal structure between the tank and field strongly suggest that tank-based aquatic recordings should be interpreted with caution and are not useful for comparisons and characterizations of frequency-spectra.

The high intensity collapse of cavitation bubbles dominated the acoustic landscape around Santa Catalina Island, the site of this study. The majority of these sounds in other, similar environments have been attributed to snapping shrimp (Johnson *et al.*, 1947; Au and Banks, 1998; Versluis *et al.*, 2000), although it is likely that cavitation sounds are being produced by other organisms as well (Colson *et al.*, 1998; Patek *et al.*, 2004; Patek and Caldwell, 2005; Simon *et al.*, 2005). Consistent with our measurements of field background noise averaging 149.3 dB re 1 μ Pa, snapping shrimp (*Synalpheus paraneomeris*) generate signals at 183–189 dB re 1 μ Pa at 1 m from a hydrophone in a tank (Au and Banks, 1998).

The average power level of the rasps, 150 dB re 1 μ Pa, is quite loud compared to measurements of marine acoustic signals from similar sized organisms (excluding the sound of cavitation). A study of two spiny lobster species, *Panulirus homarus* and *Palinustus waguensis* (misspelled in the origi-

nal paper), documented power levels of 50–143 dB (Latha *et al.*, 2005); however, the reference level and distance from the recording device were not specified, so it is difficult to draw comparisons with the present data. The damselfish (*Abudefduf abdominalis*) generates courtship calls at 105–119 dB re 1 μ Pa at 0.5–1 m (Maruska *et al.*, 2007). Toadfish (*Halobatrachus didactylus*) acoustic power scales with body size, with pressure levels ranging from approximately 108–140 dB re 1 μ Pa (Vasconcelos and Ladich, 2008). *Opsanus tau* toadfish produce boatwhistle calls of an average 126 dB re 1 μ Pa at 1 m (Barimo and Fine, 1998).

Thus, the spiny lobster's rasp is loud, but so is the background noise (Figs. 6 and 7). A primary consequence of the loud background noise is that the rasps are obscured by the ambient background noise even though they attenuate minimally over the distances in which a predator encounter might occur. Given that the rasps are similar in power to the ambient background noise, the probability that they will be obscured is quite high—approximately 31% of the rasps recorded had a negative decibel level relative to the background noise (Fig. 7). This confers an advantage in the context of the antipredator function—the sounds are both loud and local, and perhaps less likely to attract additional nearby predators to the scene.

The frequency structure of the background noise relative to the rasp may also be important for propagation (Fig. 6). A quiet window is present below 1 kHz, a region in which the rasp's power output is relatively high. It is possible that spiny lobsters make use of such a “window” similar to gobies shown to communicate in the quiet low-frequency region in a noisy stream environment (Lugli *et al.*, 2003; Lugli and Fine, 2007). Like the gobies, it is also possible that antipredator communication is occurring in the near-field, thus measurements of particle velocity at close-ranges would yield a more accurate portrait of the rasp's acoustic landscape. While many of the spiny lobster's fish predators can detect pressure waves, most marine organisms are also sensitive to particle vibrations in the near-field. Characterizing the near-field of these local antipredator sounds is necessary both to understand the propagation of these signals and to determine the relevant signal features to attacking predators.

Various lobster species have been shown to detect vibrations in the near-field and at low frequencies (less than 200 Hz), yet the presence of pressure-sensitive hearing structures in crustaceans remains contentious (Cohen, 1955; Offutt, 1970; Tazaki and Ohnishi, 1974; Goodall *et al.*, 1990; Budelmann, 1992; Popper *et al.*, 2001; Lovell *et al.*, 2005; Lovell *et al.*, 2006). Previous research suggested that the rasps could function in the near-field to warn neighboring conspecifics (Lindberg, 1955; Meyer-Rochow *et al.*, 1982) via an “alarm signal.” However, given that palinurid larvae cycle for many months before settling (Phillips *et al.*, 2006), it is unlikely that they are genetically related and thus the fundamental assumption that alarm calls aid close relatives (Caro, 2005) would not be met.

In conclusion, there is a web of interconnections between the basic mechanism of sound production, the behavioral deployment, and the ambient environment in which these sounds are produced; each component is essential to

the production and propagation of the signal. Across the size ranges of the lobsters included in this study, there are no obvious signals to potential predators about body size. However, the overall behavior of the lobster strongly impacts the rasp features produced, suggesting that there may be a more important association between the stimulus and acoustic response than we addressed in these particular experiments. The loud natural environment plays a key role in masking the rasps even though the aquatic environment minimally attenuates sound over these small distances. This first analysis of antipredator acoustics and behavior in the California spiny lobster suggests that much remains to be learned in this rich frontier of marine bioacoustic research.

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