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Mechanisms underlying the production of carapace vibrations and associated waterborne sounds in the American lobster, *Homarus americanus*

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Summary

American lobsters produce carapace vibrations, which also lead to waterborne acoustic signals, by simultaneously contracting the antagonistic remotor and promotor muscles located at the base of the second antenna. These vibrations have a mean frequency of 183.1 Hz (range 87–261 Hz), range in duration from 68 to 1720 ms (mean 277.1 ms) and lead to waterborne sounds of similar frequencies. Lobsters most often produce these signals using only one pair of muscles at a time and alternate between the muscles of the left and right antennae when making a series of vibrations. Occasionally, they vibrate their carapace by simultaneously contracting both sets of muscles. While the remotor muscle is required for

producing carapace vibrations, the promotor appears to play a secondary role. Electrical stimulation of the remotor, but not the promotor, results in the production of vibrations, while lesions of the remotor, but not promotor, eliminate the ability of lobsters to vibrate their carapace. Lobsters of all sizes and both sexes produce these signals when startled, grasped or threatened. However, at this time, the behavioral significance of vibration and/or sound production by American lobsters is not known.

Key words: sound, acoustics, American lobster, *Homarus americanus*, crustacean, antenna, vibration.

Introduction

A variety of crustacean species are known to be soniferous, including: white shrimp, *Penaeus setiferus* (Berk, 1998); snapping shrimp of the genera *Alpheus* and *Synalpheus* (Hazlett and Winn, 1962a; Brandt, 1963; Horch, 1975); crabs of the genera *Acanthocarpus*, *Matuta*, *Menippe*, *Ocypode* and *Uca* (Ewing, 1989); and spiny lobsters of the family Palinuridae (Moulton, 1957; Hazlett and Winn, 1962a,b; Meyer-Rochow and Penrose, 1976; Meyer-Rochow et al., 1982; Patek, 2002; Patek and Oakley, 2003). In all of these species, sound is produced through exoskeletal movements, such as stridulation of two body parts, percussion of two body parts or percussion of a body part and the substrate.

Sound production in the American lobster (*Homarus americanus* Milne Edwards 1837) may be unique amongst crustaceans because it seems to be produced by contraction of internal musculature. Fish (1966) first hypothesized this mechanism when he observed differences in the spectral qualities of American lobster sounds versus sounds from stridulatory sound producers. While sound production by stridulation (such as in spiny lobsters and many insects) typically consists of wide band sounds with no harmonic component, Fish observed low-frequency (100–130 Hz in six animals), tonal, short-duration sound pulses in American lobsters. These sound pulses are, in fact, most similar to sounds produced by some insects, such as cicadas, and some teleost fish species, including toadfish, searobins, sculpins, black

angelfish and plainfin midshipmen (Barber and Mowbray, 1956; Moulton, 1958; Tavalga, 1964; Winn, 1964; Fish and Mowbray, 1970; Rome et al., 1996; Vance et al., 2002; Ladich and Bass, 2003; Connaughton, 2004). These fish typically produce sound by contracting muscles that vibrate the swim bladder or pectoral girdle.

Fish (1966) further suggested that the remotor muscle, located at the base of the second antenna, is the muscle responsible for the low-frequency, waterborne ‘buzzing’ sounds he recorded from the American lobster. The remotor muscle is a large muscle, divided into two distinct bundles, often termed the large and small bundles (Mendelson, 1969; Bevingut et al., 1993), which originate at the coxopodite of the second antenna and insert into the carapace of the cephalothorax (Mendelson, 1969; Rosenbluth, 1969; Bevingut et al., 1993). Besides being a putative sonic muscle, the remotor muscle serves to articulate the basipodite and coxopodite at the base of the antenna, causing antennal movement.

The two fiber bundles found within the remotor muscle have distinct compositions and are likely to serve distinct functions. The small bundle is composed of myofibrils with long sarcomeres (>6 μm), while the large bundle has myofibrils with short sarcomeres (2–4 μm) (Bevingut et al., 1993). The length of the sarcomere is directly related to the speed of fiber contractions, with long sarcomere muscles contracting slower than those with short sarcomeres. Therefore, the large bundle of

the remotor muscle can contract faster than the small bundle and has been termed the fast division (Mendelson, 1969). The fast division of the remotor muscle also has a prominent array of T-tubules and voluminous sarcoplasmic reticulum (up to 60% by volume *versus* 15% in the small division; Bevingut et al., 1993), which are common anatomical features of sonic muscles and an adaptation for producing fast contractions (Mendelson, 1969; Bevingut et al., 1993). Additionally, mitochondria are limited in the fast division, probably because these fibers do little mechanical work and are only intermittently active (Rosenbluth, 1969). Mendelson (1969) suggested that the fast division of the remotor muscle is capable of contracting at frequencies up to 100 Hz, which is comparable to the 100–130 Hz sounds recorded by Fish (1966). Fish (1966) further speculated that these high-frequency contractions were made possible by a pair of motor neurons that alternately activated the muscle. The anatomical composition of the remotor muscle suggests that each division might serve a unique function, such that the small bundle (slow division) is responsible for antennal movement and posturing, while the fast division is used to produce sound.

While the anatomical composition of the remotor muscle suggests that it is a sonic muscle, data supporting this hypothesis are limited. There are only two published reports concerning sound production in the American lobster: Fish (1966) recorded waterborne sounds from six animals and felt body vibrations in 25 (of 100) lobsters, and Mendelson (1969) successfully recorded remotor muscle activity in lobsters while they produced body vibrations; however, he did not rigorously determine whether the muscles caused the vibrations. The overall goal of the present study was to build on this limited empirical data and develop a more complete understanding of the mechanisms underlying carapace vibrations and sound production in the American lobster. First, we recorded the body vibrations produced by lobsters and characterized them in terms of frequency and duration. Second, we tested whether the body vibrations produced by lobsters give rise to waterborne acoustic signals by making simultaneous vibration and sound recordings using an accelerometer attached to the carapace and a hydrophone. Finally, to determine if the muscles of the second antenna were, in fact, the underlying cause of body vibrations and waterborne sounds, we recorded electromyograms (EMGs) from antennal muscles, while simultaneously monitoring body vibrations, in both normal lobsters and lobsters with lesioned muscles. Our results demonstrate that lobsters use both the remotor and promotor muscles of the second antenna to produce vibrations of the carapace, which in turn give rise to waterborne sounds.

Materials and methods

Carapace vibration surveys

A total of 1622 legal-sized lobsters [83–160 mm carapace length (CL)] were surveyed between October 2003 and September 2004 (~135 each month) to determine which cohorts of lobsters (size class and sex) are most likely to produce body vibrations when grasped. These surveys were

conducted at The Little Bay Lobster Company in Newington, NH, USA using lobsters that were captured in various offshore areas in the Gulf of Maine. Additional surveys of sublegal (<83 mm CL) and small legal-sized lobsters ($N=101$; 42–95 mm CL) were conducted in the months of October 2003, November 2003, July 2004 and September 2004 using lobsters caught in UNH (University of New Hampshire) traps deployed in inshore waters off Newcastle Island, NH, USA. In both surveys, lobsters were grasped around their dorsal carapace and lifted three times. The presence or absence of a body vibration each time they were lifted was recorded, in addition to their size and sex. Any lobster that vibrated at least once during the three trials was identified as a vibration producer. There was no distinction made between lobsters that vibrated once or multiple times. Statistically significant differences in the percentage of lobsters vibrating in each sex, in each 10 mm CL size class and in each month were calculated using analysis of variance (ANOVA) and Tukey's *post-hoc* tests (Systat version 10; Systat Systems Inc., Point Richmond, CA, USA).

Vibration and sound recordings and spectral analysis

In the laboratory, acoustic signals and carapace vibrations were recorded from known vibration-producing lobsters and characterized according to both their frequency and duration. To determine whether body vibrations and waterborne signals were produced simultaneously, acoustic signals and carapace vibrations were recorded from lobsters in an aquarium by two means: (1) measuring vibrations of the carapace using an accelerometer glued to the carapace and (2) recording the associated waterborne acoustic component with a hydrophone placed near the lobster. Henceforth, signals recorded with the accelerometer are reported as vibrations whereas those recorded with the hydrophone are referred to as sounds.

A waterproof, general-purpose accelerometer (1.25 cm × 2.70 cm; Sales Technology Inc., League City, TX, USA) was used to record carapace vibrations. The threaded end of the accelerometer was screwed into a nut embedded in a curved epoxy tab, which was secured to the lobster's dorsal carapace with cyanoacrylate glue. The output of the accelerometer was displayed and recorded on a Macintosh laptop using a Powerlab 8SP analog-to-digital interface (ADInstruments, Colorado Springs, CO, USA) and Chart Software version 4.2 (ADInstruments). A sampling rate of 4000 samples s⁻¹ was used to ensure proper representation of the accelerometer signal. The accelerometer was tested with known frequencies of sound generated by a low-frequency oscillator (model 202c; Hewlett Packard, Palo Alto, CA, USA) in the range of 10–2000 Hz, to confirm that it could collect accurate data at this rate of sampling.

Lobsters' vibrations were recorded by the accelerometer in a small chamber (26.7 cm × 29.2 cm × 15.2 cm, width × length × depth) filled with chilled seawater (10–15°C). Successful recordings were obtained from a total of 17 lobsters out of ~50 that were tested for use in the electrophysiological studies. Twelve of the lobsters, from three different size classes [<65 mm CL (56F, 63M, 54M, 61M, 65M), 74–82 mm CL

(75F, 78F, 82M, 74M) and >90 mm CL (92M, 90M, 90M)] were intermolt, while five lobsters were soft, postmolt animals (69M, 81F, 84F, 90M, 95M). Soft lobsters (69M and 84F) not falling into the aforementioned size categories were excluded for size class comparisons. Lobsters were induced to produce sound either by lightly grasping or tapping on the dorsal carapace or tail or by passing a shadow above them.

In order to test whether lobsters were producing waterborne acoustic signals concurrent to body vibrations, a hydrophone (model AQ-9; Aquarian Audio Products, Anacortes, WA, USA) was placed in the test chamber, anterior to, and within 10 cm of, four lobsters. Both types of signals (hydrophone and accelerometer) were simultaneously displayed and recorded using the aforementioned MacLab hardware and software, and the spectral characteristics of both recordings were measured and compared. Hydrophone recordings of waterborne acoustic signals were recorded from four additional lobsters using the spectral software Canary version 1.2.4 (Cornell Ornithology Laboratory, Ithaca, NY, USA).

A one-way ANOVA (Systat version 10) was used to compare differences in body vibration frequencies and durations between size classes, and unpaired *t*-tests (Instat version 2.01; GraphPad Software Inc., San Diego, CA, USA) were used to compare differences between sexes and molt stages (postmolt *versus* intermolt). Typically, intensity was not determined from accelerometer recordings because the location of the accelerometer on the carapace in relation to the sound source and the amount of contact the epoxy tab made with the carapace varied among individual animals. For waterborne acoustic signals recorded using Canary software, spectrograms were produced and peak frequency (in Hz) and mean intensity (in dB) were determined.

Vibration production mechanism: sonic muscle electrophysiology

To determine if the remotor and promotor muscles were active during the production of body vibrations, electrical activity was recorded from the left and right promotor and remotor muscles of 10 lobsters while they were induced to vibrate [see fig. 1 in Bevingut et al. (1993) for an excellent illustration of these muscles]. Two small holes were created in the carapace over each muscle using a 26-gauge hypodermic needle (Becton-Dickinson and Co., Franklin Lake, NJ, USA), and pairs of electrodes, made of 30-gauge insulated wire with 2 mm of insulation stripped from the tips, were inserted into the holes and secured to the carapace with cyanoacrylate glue and squares of duct tape. The electromyograms (EMGs) were amplified and filtered using A.C. pre-amplifiers (P5 series; Grass Medical Instruments, Quincy, MA, USA) and recorded with a Powerlab 8SP interface (ADInstruments) and Chart version 4.2 software (ADInstruments). *t*-tests (Instat version 2.01) were used to examine differences in the frequency and duration of vibrations produced with one set of muscles (i.e. left or right remotor and promotor) *versus* those produced with both sets of muscles simultaneously.

The remotor and/or promotor muscles of 12 lobsters were

lesioned to test whether the activity of the muscles was responsible for producing carapace vibrations and whether both sets of muscles (right and left antennae) and/or both types of muscles (remotor and promotor) were necessary for production of carapace vibrations and waterborne sounds. Lesions were performed on one set of muscles at a time (right or left antennae). In six cases, both muscles were lesioned; in three cases, just the remotor was lesioned; and in three further cases just the promotor was lesioned. Lesions were performed by cutting a small window in the carapace just posterior to the insertion of the target muscle(s) onto the carapace and separating the muscle tissue from the insertion on the carapace; the rest of the muscle tissue, including the origin at the antenna, was left intact. The window in the carapace was then covered with duct tape, and lobsters were allowed to recover in a holding tank for a minimum of 1 h. After this recovery period, the electrical activity of both the intact and lesioned muscles, as well as carapace vibrations, was recorded as previously described. *t*-tests (Instat version 2.01) were used to evaluate differences in the vibration frequency between lobsters with intact and lesioned muscles.

To further test the hypothesis that the muscles of the second antenna are responsible for production of carapace vibrations in the American lobster, the remotor and promotor muscles were electrically stimulated while vibrations were recorded using an accelerometer, as described above, in five lobsters. To stimulate the muscles, wire electrodes inserted into the muscles of interest were connected to S9 stimulators (Grass Medical Instruments), and muscles were stimulated with trains of pulses of varying frequencies, intensities and durations.

Results

Carapace vibration surveys

American lobsters occasionally produce a body vibration ('buzz') when grasped. To determine if there were any sex- or size-related differences in the production of body vibrations, 1723 lobsters were surveyed. Overall, 7.5% (129 of 1723) of the lobsters surveyed vibrated. There were small, but significant, differences in the proportion of lobsters that vibrated in each size classes ($P < 0.001$), with the highest percentage of vibrations detected in the 120–149 mm CL size classes (Fig. 1A). There were also statistically significant differences in the proportion of lobsters that vibrated each month ($P < 0.001$), with November having the most soniferous lobsters and August having the smallest percentage of lobsters that vibrated (Fig. 1B). There was no significant difference in the probability of vibration production between male and female lobsters ($P = 0.94$), suggesting that these signals are not used by males to attract females during courtship.

Vibration and sound recordings and spectral analyses

The mean frequency of body vibrations produced by 17 soniferous lobsters in response to being disturbed, as measured by the accelerometer, was 183.1 ± 2.3 Hz (reported as mean \pm S.E.M. unless otherwise noted; range 87–261 Hz). The mean

duration of these ‘buzzes’ was 277.1 ± 15.6 ms and was highly variable (range 68–1720 ms; Fig. 2). Statistically significant size-dependent differences were seen in both the frequency and duration of body vibrations. Lobsters 74–82 mm CL in size vibrated at frequencies significantly lower than lobsters <65 mm CL, and lobsters >90 mm CL produced vibrations significantly shorter in duration than those in the <65 mm CL

size class ($N=5$ per size class; Table 1; Fig. 3). Soft postmolt lobsters ($N=5$) produced vibrations that were significantly lower in mean frequency ($P<0.001$) but not significantly different in duration ($P=0.09$) than hard intermolt lobsters ($N=12$) of the same size (Table 1). There was no significant difference in the frequency of body vibrations between intermolt males ($N=11$) and females ($N=4$; $P=0.41$), while male vibrations were longer in duration than female buzzes ($P=0.05$). There was high variability in the production of carapace vibrations amongst the lobsters tested. While some lobsters repeatedly vibrated in response to limited stimulation, other lobsters produced very few signals, and only after repeated stimulation. We found no correlation between the likelihood that a lobster would vibrate, or the amount of stimulation needed to elicit vibrations, and size or sex; however, soft postmolt lobsters did tend to vibrate in response to less stimulation. This trend was not quantified because of the small sample size of soft lobsters combined with the large degree of variability inherent in these responses.

Body vibrations gave rise to simultaneous waterborne sounds of similar frequencies (Fig. 4). Seven waterborne sound events, with a mean frequency at peak intensity of 182.9 ± 21.7 Hz and a mean intensity of -18.5 ± 0.5 dB (dB references: standard seawater reference, 0.65 aW m^{-2}), were recorded in Canary Software from four lobsters with a hydrophone located approximately 10 cm in front of the lobster. Each of the seven sound events was closely associated with an exoskeleton vibration of comparable duration and frequency.

Sound and vibration production mechanism: sonic muscle electrophysiology

Electromyograms of the remotor and promotor muscles of the second antenna revealed that both muscles are active during the production of body vibrations (Fig. 5A). Typically, lobsters only used the pair of muscles from one side at a time when producing carapace vibrations. Remotor and promotor muscle contractions were tightly coupled but not synchronous (Fig. 5B). A clear relationship was seen between each peak of a vibration event and muscle activity, with each carapace movement apparently resulting from a single remotor and promotor muscle contraction.

Lobsters tended to produce buzzes by alternating between the muscles of one side of the body and those of the opposite side of the body. However, in some cases, they used both sets of muscles simultaneously (unilateral $n=156$; bilateral $n=10$; Fig. 6). There was no significant difference in the mean frequency ($P=0.74$) or duration ($P=0.16$) of carapace vibration events between vibrations

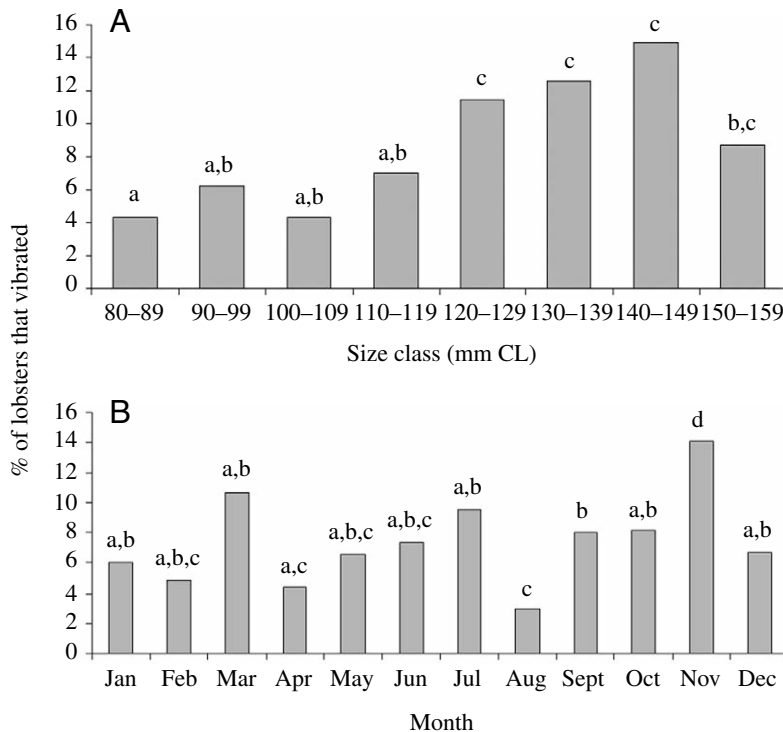


Fig. 1. The percentage of lobsters that vibrated in (A) each size class and (B) each month during body vibration surveys. Different letters denote statistically significant differences in the percentage of lobsters that vibrated in each group ($P=0.05$).

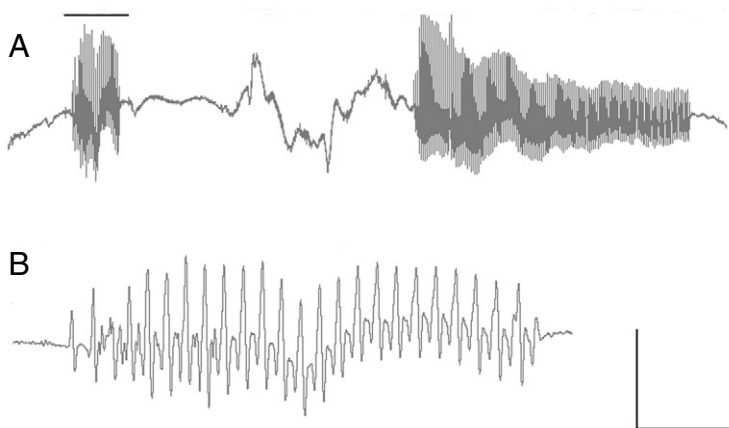


Fig. 2. Body vibrations recorded from a 78 mm CL intermolt female. Individual lobsters often produced signals of variable durations. (A) As an example, the first vibration shown was 170 ms long while the second vibration was 1590 ms in duration. (B) Expanded view of the first body vibration, denoted with a bar in A. Scale: A, 20 mV, 250 ms; B, 20 mV, 25 ms.

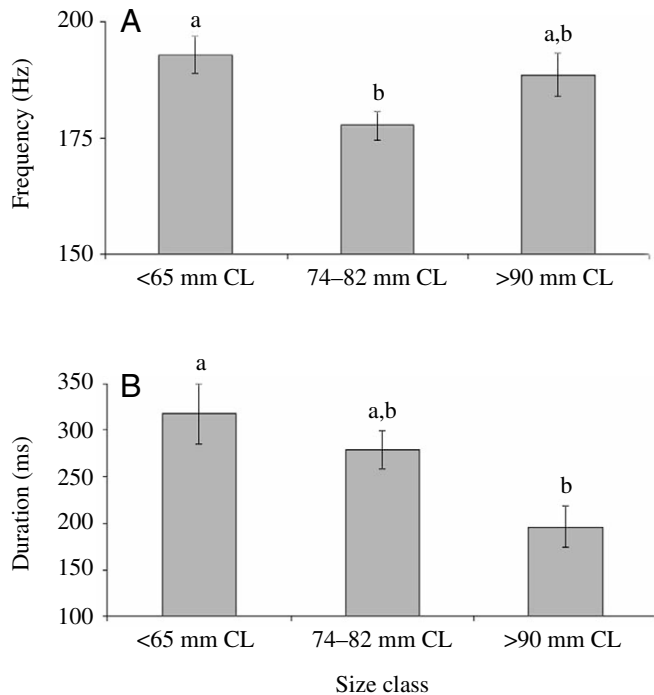


Fig. 3. (A) Mean frequency and (B) duration of body vibrations produced by three size classes, each of five lobsters (<65 mm CL, 75–84 mm CL, >90 mm CL). Different letters denote statistically significant differences ($P=0.05$).

produced unilaterally *versus* those produced bilaterally (unilateral, frequency 181.0 ± 2.9 Hz, duration 287.8 ± 20.3 ms; bilateral, frequency 178.5 ± 6.7 Hz, duration 461.5 ± 112.2 ms).

When the posterior insertions of both the remotor and promotor muscles were lesioned, carapace vibrations ceased (Fig. 7), even though muscle contractions still occurred in the lesioned muscles. When the muscles on only one side of the body were lesioned, lobsters could still produce vibrations by using the intact muscles of the other side (Fig. 7). Lobsters continued to alternate between the muscles of each side of the body as they did before the lesion, rather than avoiding the use of the lesioned muscles. Lesions of the promotor muscle alone ($N=3$) did not inhibit carapace vibrations nor did they significantly change the frequency of carapace vibrations in

Table 1. The mean frequency and duration of body vibrations produced by lobsters of different sizes and molt stages

	Frequency (Hz)		Duration (ms)	
	Mean	Range	Mean	Range
<65 mm CL	192.8	125–261	317.8	68–1370
74–82 mm CL	177.6	87–243	279.2	115–1720
>90 mm CL	188.5	137–227	195.8	110–690
Postmolt	163.5	84–218	253.6	115–1220
Intermolt	188.5	87–261	295.8	68–1720

comparison with signals produced by the same animals with intact promotor muscles (non-lesioned vibrations, $N=10$, mean frequency 161.7 ± 14.6 Hz; lesioned vibrations, $N=19$, mean frequency 158.3 ± 9.2 Hz; $P=0.84$). However, when the remotor muscle alone was lesioned ($N=3$), carapace vibrations ceased.

In four lobsters, we directly stimulated the remotor and promotor muscles to induce carapace vibrations (Fig. 8). The stimulation parameters that yielded vibrations that most closely resembled natural vibrations were: frequency 150 Hz, duration ~20 ms, intensity 3–4 V. Vibrations were produced when both muscles were stimulated or when just the remotor was stimulated, but not when the promotor muscle was stimulated alone. In every case, the stimulation duration matched the body vibration duration, indicating that the stimuli caused the vibrations rather than causing the lobsters to be disturbed so that they vibrated on their own (Fig. 8).

Spontaneous vibration production

One lobster (74 mm CL, male) was recorded producing spontaneous carapace vibrations while acclimating to the test chamber. These vibrations were lower in frequency and shorter in duration than induced body vibrations [mean frequency 57.73 ± 18.9 Hz (\pm S.D.), mean duration 130.93 ± 38.1 ms (\pm S.D.); Fig. 9]. The lobster produced these signals on two occasions for periods of over 15 min. These were the only occurrences of spontaneous sound or vibration production recorded during the course of these experiments, despite all lobsters having the same opportunity to do so while acclimating to the testing chamber.

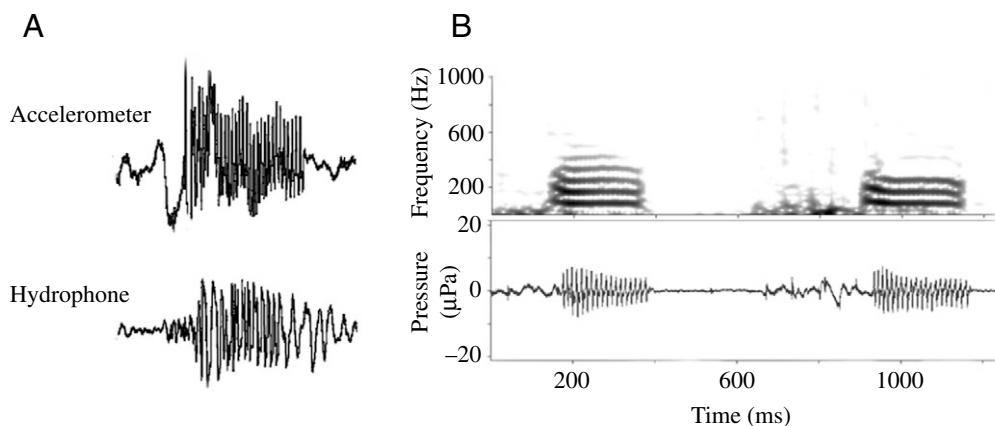
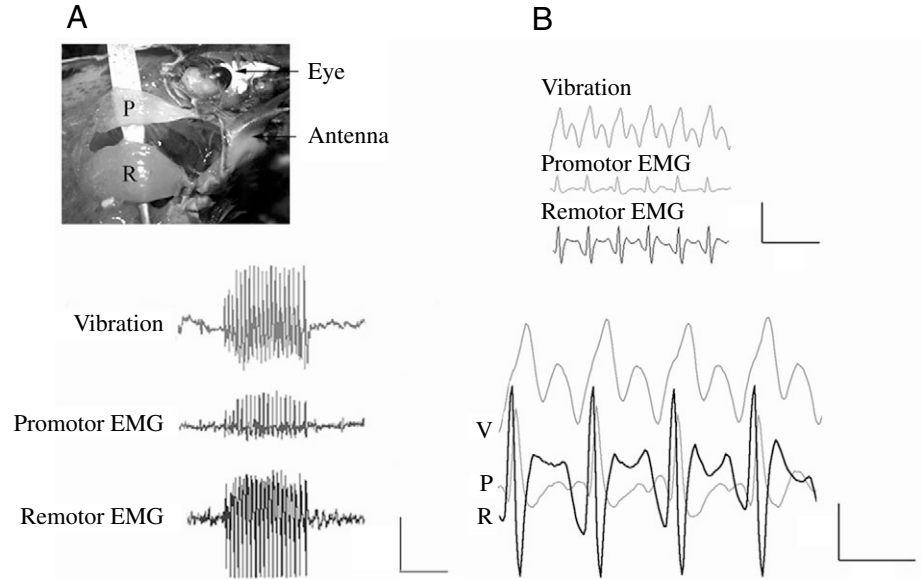


Fig. 4. Body vibrations give rise to waterborne acoustic signals. (A) Simultaneous recording of a 300 ms body vibration, recorded in Chart software, and a waterborne sound recorded using Canary software. (B) Expanded view of a waterborne sound recorded in Canary software. Notice in the spectrogram that the most intense sounds (darkest colors) are of a low frequency (<300 Hz).

Fig. 5. Sounds and body vibrations are produced by contractions of the remotor and promotor muscles. (A) Example of a simultaneous accelerometer recording of body vibrations and remotor and promotor muscle electromyograms (EMGs). The top photograph shows the anatomy of the two muscles (P, promotor; R, remotor). (B) Expanded view of a section of a different simultaneous recording of vibrations and muscle activity. There is a clear one-to-one relationship between each wave in the accelerometer recording (V), or carapace movement, and muscle activity. Scale: 10 mV for the top trace (vibration), 8 μ V for the EMG traces; time scale=200 ms; B, top, 8 mV, 20 ms; bottom, 4 μ V, 10 ms.



Discussion

Our findings support the hypothesis that, when American lobsters are disturbed, they occasionally produce carapace vibrations that give rise to waterborne sounds. We found that both male and female lobsters, of all sizes tested (56–143 mm CL), produced carapace vibrations of ~0.5–1 s in duration by simultaneously contracting the antagonistic remotor and promotor muscles located at the base of each second antenna.

While scattered reports exist, this study is the first to experimentally demonstrate muscle-generated carapace vibration production in a crustacean. Sound production in American lobsters is most similar to mechanisms of sound production employed by some teleost fish species, some insects and rattlesnakes (Rome et al., 1996; Ladich and Bass, 2003; Connaughton, 2004) rather than the stridulation and percussion mechanisms commonly reported in crustaceans (Hazlett and

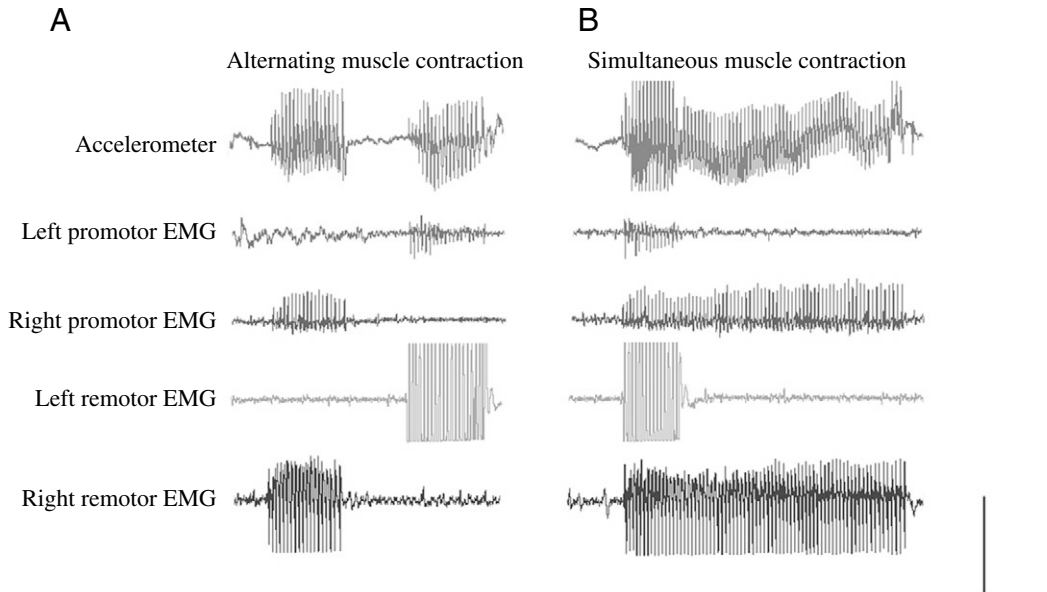


Fig. 6. Electromyogram (EMG) recordings of all four sonic muscles during the production of a series of vibration pulses. (A) Lobsters most often produced body vibrations by using the paired remotor and promotor muscles of only one antenna (i.e. left or right) and often alternated between sides. Every lobster tested used both sides in alternation, although in some individuals one side was favored and used most often. (B) Lobsters also used simultaneous contractions of the sonic muscles of both antennae to produce signals. In some cases, both sets of muscles were used during the entire vibration, or, as seen in B, one set was used for only part of the event. Vibrations produced by both sets of muscles were not significantly longer in duration or different in frequency than vibrations produced by one set. Scale: A and B, 20 mV for the top trace (accelerometer), 16 μ V for the EMG traces; time scale=200 ms.

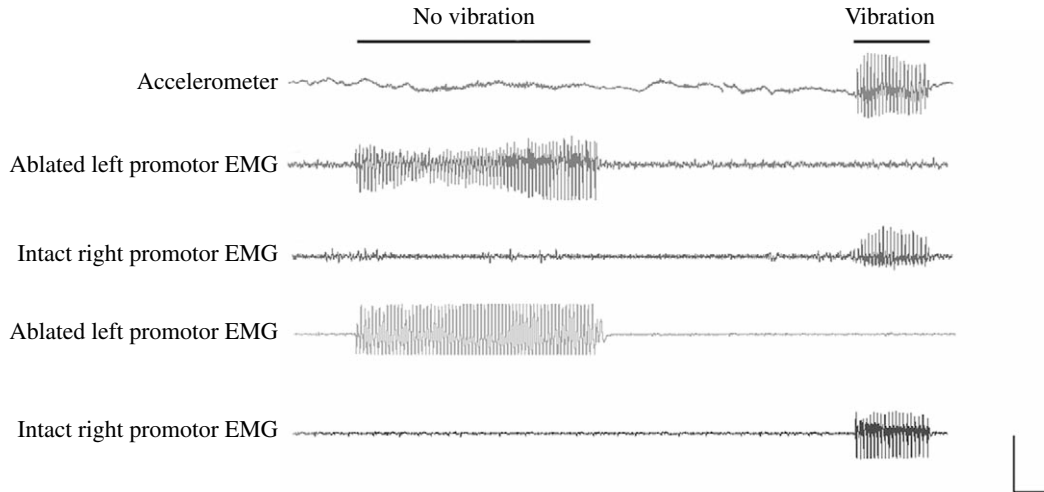


Fig. 7. Electromyogram (EMG) recordings of lesioned and intact muscles. In this example, the left antennal muscles (both remotor and promotor) were lesioned at their insertion into the musculature of the dorsal carapace, while the right antennal muscles were kept intact. While the muscles of the left antenna still contracted, they were unable to cause a vibration (recorded by the accelerometer in the top trace). However, when the intact muscles of the left antenna were active, they produced body vibrations. Lobsters continued to alternate between the muscles of each side and did not avoid using the lesioned muscles. Scale: 20 mV for the top trace (accelerometer), 16 μ V for the EMG traces; time scale=100 ms.

Winn, 1962a,b; Meyer-Rochow and Penrose, 1976; Meyer-Rochow et al., 1982; Ewing, 1989; Berk, 1998; Patek, 2002; Patek and Oakley, 2003).

A year-long survey of 1723 lobsters demonstrated that: (1) all size classes of lobsters can produce body vibrations; (2) the tendency is similar for males and females; (3) the prevalence of body vibrations between months, while statistically different in some months, varied within a small range of 2.96–14.10% and (4) carapace vibrations were often associated with meral spread posturing. These findings suggest that these carapace vibrations and/or the associated waterborne signals are used by all lobsters, possibly for defensive purposes rather than playing

a role in a behavior, such as mating, which is unique to a particular subset of lobsters.

Manually induced carapace vibrations and their associated waterborne signals had frequencies of \sim 183 Hz, with durations between 68 and 1720 ms. All lobsters produced signals of varying frequencies and durations, and it's likely that changes in duration, and possibly frequency, were influenced by the level of excitation and/or fatigue. Some differences in the frequency and duration of vibrations were seen between the three size classes sampled, but there were no clear trends across the size classes. The phenomenon of body size-dependent sound frequency production, as seen in mormyrids, drums and

Stimulation of both muscles

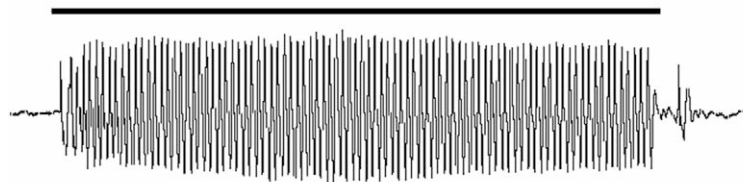
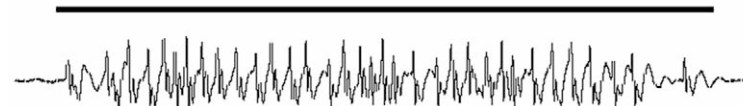
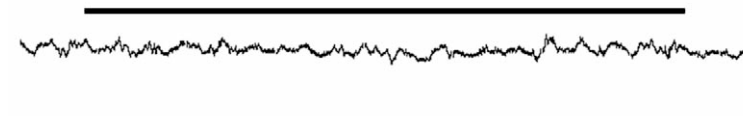


Fig. 8. Accelerometer recordings demonstrating that electrical stimulation of sonic muscles yielded carapace vibrations. Remotor muscle stimulation, and stimulation of both the remotor and promotor muscles simultaneously, resulted in body vibrations, while stimulation of promotor muscles did not cause body vibrations. Electrical stimulations involving both muscles created vibrations most similar in waveform and intensity to naturally produced sounds. Horizontal bars indicate the periods of stimulation. Scale: 5 mV, 150 ms.

Remotor-only stimulation



Promotor-only stimulation



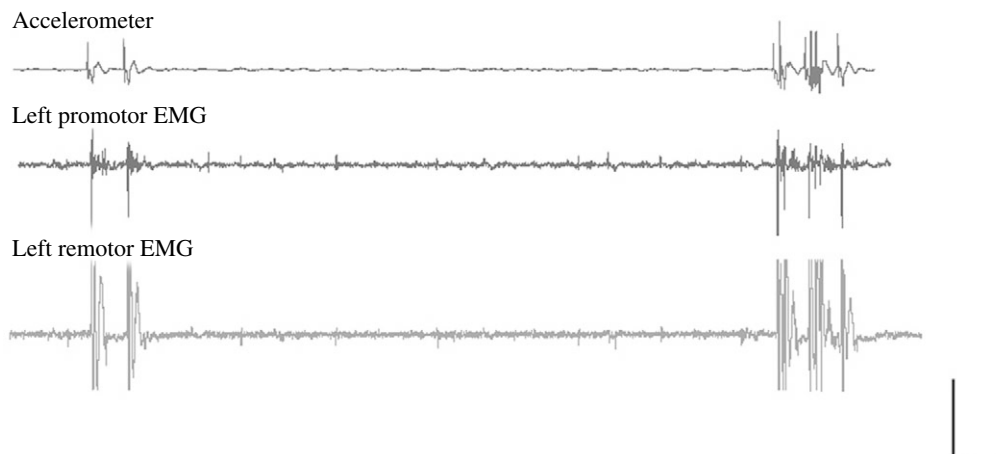


Fig. 9. Spontaneous carapace vibrations produced by a male lobster. The vibrations produced were lower in frequency and shorter in duration than those typically elicited by startling or threatening lobsters. Scale: 20 mV for the top trace (accelerometer), 8 μ V for the middle EMG trace, 16 μ V for the bottom EMG trace; time scale=125 ms.

tiger fishes (Ladich and Bass, 2003), is related to the increasing size of the internal sound production and resonating structures as the animal grows. However, in the case of the American lobster, the differences seen in the data probably represent different levels of excitation and fatigue, not anatomical differences in the muscle-driven mechanisms, as all lobsters produced signals with a wide range of frequencies and durations. Differences in the frequency of body vibrations between soft, postmolt and hard, intermolt lobsters are probably not related to differences in the underlying sound-producing mechanism but are rather due to differences in the transfer and subsequent distortion of body vibrations when transmitted through a softer *versus* a harder carapace. It is also possible that differences are due to changes in the insertions of these muscles onto the carapace during the molt cycle. Soft lobsters were also more likely to vibrate as compared with their harder counterparts, possibly because they were more vulnerable to attack than lobsters with hard shells.

Both the remotor and promotor muscles are active during the production of carapace vibrations and there is a one-to-one relationship between contractions of these muscles and the carapace movements recorded with an accelerometer attached to the shell. This type of relationship is also seen in the sound-producing mechanisms of the toadfish (*Opsanus tau*) and the western diamondback rattlesnake, *Crotalus atrox* (Rome et al., 1996). Lobsters only need to use one pair of muscles to produce vibrations, and they often alternated the use of muscles from one side to the other when creating a series of signals. Northern searobins also use a mechanism of alternating muscle contractions to create sounds (Connaughton, 2004). However, while searobins alternately contract two sonic muscles during a single event, in order to increase the frequency of airbladder vibrations, it is not clear why lobsters use two antagonistic muscles to vibrate the carapace, given that the remotor muscle appears to be sufficient.

The remotor muscle has been previously implicated as an American lobster sonic muscle (Fish, 1966; Mendelson, 1969; Rosenbluth, 1969), yet this is the first study to demonstrate involvement of the promotor muscle. Interestingly, the

promotor muscle is the primary muscle responsible for the movement of spiny lobster antennae during stridulatory sound production (Patek, 2003). Both our lesioning and stimulation experiments indicate that the remotor muscle, the larger of the two muscles, is the primary muscle involved with sound and vibration production, while the promotor muscle may serve to modulate the signal. Results from lesioning manipulations and promotor muscle stimulation experiments indicate that the promotor muscle is not opposing the remotor as a way to hold the antennae still, nor is it essential to sound production. However, results from remotor-only and combined remotor and promotor stimulation experiments suggest that the promotor is important for maintaining the appropriate waveform and intensity of the vibrations. It is possible that the promotor muscle acts to tune the sound waves and facilitates transmission of sounds by modulating the tension of the carapace in a manner similar to the way dove superfast muscles control the tension of the syrinx as a means of trill pitch control (Elemans et al., 2004).

While various behavioral experiments designed to record the natural production of carapace vibrations and/or acoustic signals proved unsuccessful, the lobsters used in the experiments presented here predominantly produced signals when disturbed or threatened. Reports abound in the crustacean (Meyer-Rochow and Penrose, 1976; Mulligan and Fischer, 1977), fish (Winn, 1964; Connaughton, 2003) and insect (Dunning and Roeder, 1965; Sandow and Bailey, 1978; Masters, 1979, 1980; Evans and Schmidt, 1990) acoustic literature of vibration and sound production in response to disturbance or predator presence. These signals are often interpreted as defensive in nature; however, the true function of these signals is not well established, except perhaps in studies with insects (Dunning and Roeder, 1965; Masters, 1979; Evans and Schmidt, 1990). Moths of the family Arctiidae produce ultrasounds at night (Dunning and Roeder, 1965). Playback recordings of these sounds decrease the predatory effectiveness of echolocating bats, presumably because the sounds startle the bats or act as a warning of the moths' noxiousness (Dunning and Roeder, 1965; Evans and Schmidt, 1990). In addition, Masters (1979) found that both

wasp and beetle species use sounds produced by stridulation to deter predators, including spiders and mice. In this example, soniferous individuals were less aggressively attacked and more likely to survive than their aphonic counterparts, suggesting that these sounds are used as startle or aposematic signals. Similarly, for American lobsters, it is not hard to imagine that the carapace vibration of a grasped lobster could startle a fish or skate predator enough to cause them to momentarily release the lobster. Additionally, waterborne sound signals of lobsters, while not intense in nature, could serve as close contact warnings to predators, similar to the weak airborne sound signals produced by some insects in the presence of predators (Masters, 1980), and the more intense sounds of some fish and spiny lobsters when threatened (Mulligan and Fischer, 1977; Connaughton, 2003). Many of the fish known to attack lobsters can detect sounds in the range produced by disturbed lobsters (Popper, 2003). In our related work on sound detection, we found that lobsters can detect waterborne sounds produced by conspecifics at distances of one meter or less (H. P. Henninger and W. H. Watson, manuscript submitted), which supports the possibility that these signals could also serve a role in intraspecific communication. Studies are currently underway to determine when lobsters produce carapace vibrations and sounds in their natural habitat.

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