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Recommended Citation

Ward, D., F. Morison, E. Morrissey, K. Jenks and W.H. Watson III. 2011. Evidence that potential fish predators elicit the production of carapace vibrations by the American lobster. *J. Exp. Biol.* 214: 2641-2648. <https://doi.org/10.1242/jeb.057976>

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RESEARCH ARTICLE

Evidence that potential fish predators elicit the production of carapace vibrations by the American lobster

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Accepted 27 April 2011

SUMMARY

American lobsters (*Homarus americanus*) will on rare occasions produce sounds by vibrating their dorsal carapace. Although this behavior can be elicited in the laboratory by handling lobsters, the stimulus that triggers the production of sounds in the lobster's natural habitat is not known. We investigated the influence of two fish that are known to prey on lobsters, cod (*Gadus morhua*) and striped bass (*Morone saxatilis*), on the production of sounds by American lobsters. In addition, we examined the response of the same fish to the sounds the lobsters produced. Although solitary lobsters spontaneously produced sounds at a low rate of 1.2 ± 0.23 sound events per 30 min, the presence of a single cod or striped bass led to an increase in the rate of sound production (cod: 51.1 ± 13.1 events per 30 min; striped bass: 17.0 ± 7.0 events per 30 min). Most ($74.6 \pm 6.6\%$) of the 292 sound events recorded occurred when a fish came within 0.5 m of a lobster, but a fish did not have to come into contact with a lobster to elicit sounds. Immediately following the production of a sound by a lobster, fish turned and swam away significantly faster than when they encountered a lobster that did not make a sound. Moreover, after striped bass (but not cod) experienced a number of these sound events, they subsequently tended to avoid swimming close to the lobsters. These data, taken together, suggest that sound production by American lobsters may serve to deter potential fish predators.

Supplementary material available online at <http://jeb.biologists.org/cgi/content/full/214/15/2641/DC1>

Key words: lobster, acoustics, carapace, cod, striped bass, predators.

INTRODUCTION

It is well known that decapod crustaceans are capable of sound production using a variety of mechanisms (Moulton, 1957; Popper et al., 2001). Much of our current understanding of sound production by crustaceans is the result of experiments conducted with selected species of spiny lobsters (e.g. *Panulirus argus*, *Panulirus guttatus*). They produce sounds by rubbing the plectrum at the base of each antenna over a 'file' under each eye (Moulton, 1957; Patek, 2001; Patek, 2002; Patek and Baio, 2007). The resulting sound has been described as a low rasping or slow rattle noise (Moulton, 1957; Hazlett and Winn, 1962; Mulligan and Fischer, 1977).

All spiny lobsters of the stridentes lineage produce sounds, often in response to being handled or engaging in an encounter with a potential predator (Hazlett and Winn, 1962; Meyer-Rochow and Penrose, 1976; Patek, 2001; Patek, 2002; Patek and Oakley, 2003). However, while it is generally accepted that these sounds are produced to deter predators, until recently there was little direct evidence supporting this hypothesis (Childress and Jury, 2006). Two recent studies, however, provide strong evidence that sounds might serve as a valuable defense mechanism. First, Bouwma reported that two species of spiny lobsters (*P. argus* and *P. guttatus*) reliably produce sounds during encounters with triggerfish (*Balistes caprisicus*), and triggerfish that experienced confrontations were reluctant to initiate future encounters (Bouwma, 2006). Second, Bouwma and Herrnkind demonstrated that spiny lobsters (*P. argus*) which produced sounds when they were attacked by octopuses (*Octopus briareus*) were more likely to escape unharmed (Bouwma and Herrnkind, 2009). Therefore, at least for these species, it is very

likely that sound production capabilities evolved, at least in part, to help deter predators.

The American lobster (*Homarus americanus*) occasionally produces carapace vibrations that can travel through the water as a sound wave (Fish, 1966; Henninger and Watson, 2005). It is one of the few crustacean species known to produce sound internally (Fish, 1966; Patek and Caldwell, 2006). Carapace vibrations result from the contraction of antagonistic remoter and promoter muscles located at the base of the second antennae (Henninger and Watson, 2005). Sound production occurs in lobsters regardless of age, size or sex (Henninger and Watson, 2005), suggesting that it does not have a role in mating, like the sounds produced by many other animals. Moreover, at least in the laboratory, only 7.5% of lobsters tested vibrated. This could represent the proportion that actually produce sounds in the wild, or it might be a function of the assay used, which simply involved picking animals up out of the water.

The behavioral significance of sound production in the American lobster is unknown. As for spiny lobsters, vibrations are most readily elicited by grasping animals, and American lobsters rarely produce sounds spontaneously or in the presence of other lobsters (Henninger and Watson, 2005) (W.H.W., personal observations). A variety of New England fish are known to prey upon lobsters, including tautog (*Tautoga onitis*), shorthorn sculpin (*Myoxocephalus scorpius*), cunner (*Tautoglabrus adspersus*), white hake (*Urophycis tenuis*), Atlantic cod (*Gadus morhua*) and striped bass (*Morone saxatilis*) (Bigelow and Schroeder, 1953; Richards and Cobb, 1986; Barshaw and Lavalli, 1988; Hanson and Lanteigne, 2000; Nelson et al., 2003). Moreover, some of these fish can detect sounds that are at the same

frequency as those produced by lobsters (~190 Hz) (Olsen, 1969; Myberg, 1981; Hawkins, 1986). Atlantic cod, in particular, can detect sounds between 50 and 540 Hz, which encompasses the entire range of sound production by *H. americanus* (Fish, 1966; Olsen, 1969; Henninger and Watson, 2005). While specific hearing thresholds and frequency ranges have not been identified for all fish, the anatomy of the ear of many hearing generalists, such as striped bass, suggests that the auditory system is similar to that of cod, and therefore would have a similar sensitivity (Popper and Fay, 1993; Popper et al., 2001).

Given the tendency for American lobsters to produce sounds when disturbed, the sensitivity of various fish to the frequency of sounds produced by the American lobster, and the strong evidence that sound production serves an anti-predator role in spiny lobsters, it is possible that American lobsters also produce sounds, in part, to deter fish predators. The objective of this study was to begin to test this hypothesis by addressing the following two questions. First, do American lobsters produce sounds when they are approached or contacted by a potential fish predator? Second, when lobsters produce sounds, do fish find it aversive and move away from the lobsters?

We discovered that American lobsters reliably produce sounds when approached by striped bass and cod, even if the fish never attack or touch the lobsters. In contrast, lobsters rarely produce sounds spontaneously or when approached by other lobsters. When lobsters do produce sounds, fish appear to be startled and find it aversive, quickly turning and moving away from the lobster. Moreover, after experiencing several sound events, striped bass avoid lobsters that produce sounds and stop moving close enough to them to elicit sound production. Thus, the approach of a fish that might be a predator is the most likely natural stimulus that elicits sound production in American lobsters and, because fish tend to move away from lobsters when they produce sounds, it is possible that this behavior reduces the probability that they will be attacked.

MATERIALS AND METHODS

Animal collection

A total of 47 adult intermolt American lobsters (*Homarus americanus*, H. Milne-Edwards 1837), ranging in size from 81 to 107 mm in carapace length (CL), were used in this study. In general, an equal number of males and females were used for each experiment. Thirty-one of the 47 animals were selected from hundreds of lobsters examined at the Island Seafood Company in Elliot, ME, because they demonstrated a high probability of producing carapace vibrations when handled. Only a small percentage of American lobsters vibrate when grasped (Henninger and Watson, 2005) and, because the goal of this study was to determine whether lobsters would make sounds in response to fish, we sought to select lobsters that had a high probability of sound production. Therefore, when interpreting the data from this study, one should take into account that, as a group, the lobsters used were much more likely to make sounds than most of the lobsters in the natural population. Each lobster was grasped around the dorsal carapace, lifted from the holding tank, and held in the air for 3 s. If a body vibration was noted, the lobster was set aside. After 1000 lobsters were surveyed, the lobsters that vibrated at least once were tested again. Any lobster that produced a vibration on multiple occasions was retained and then transferred to the University of New Hampshire (UNH) campus and held in a large seawater tank in a quiet room until trials began. Another 16 lobsters, that did not tend to produce vibrations when handled, were selected from those collected locally in UNH research traps, and they served as 'non-

vibrating' controls. These control lobsters were used to determine fish responses to the presence of a lobster that did not vibrate. Some control lobsters were used in more than one trial. All lobsters were fed intermittently while being held for up to 1 week prior to starting any trials.

This work was approved by the University of New Hampshire, Institutional Animal Care and Use Committee (IACUC no. 080801), and the NH Fish and Game Department (approval no. mfd0918).

Vibration and sound recordings

Carapace vibrations and sounds were recorded by two means, as described previously (Henninger and Watson, 2005): (1) vibrations were measured directly using an accelerometer glued to the dorsal carapace; and (2) the acoustic component of the waterborne signal was recorded using a hydrophone (Model AQ-9; Aquarian Audio Products, Anacortes, WA, USA) located in the center of the 1.82 m diameter test tank (Fig. 1). The waterproof accelerometer (CMCP-1100; 1.24×2.7 cm; Sales Technology Inc., League City, TX, USA; sensitivity: 100 mV g⁻¹; frequency range: 0.32 Hz–10 kHz) used to record carapace vibrations was screwed into a nut embedded in a curved epoxy tab, which was secured to the lobster's carapace with cyanoacrylate glue. The accelerometer was wired directly to a power source (12 V DC) and the A–D interface described below. This connection also served to restrict lobsters to a certain area of the tank, which facilitated data analyses. The main advantage of the accelerometer method was that it produced a clear signal that was not distorted by other noises in the tank. The outputs of both the accelerometer and hydrophone were recorded using a Powerlab analog-to-digital interface (ADInstruments, Colorado Springs, CO, USA) and Chart Software version 5.4 (ADInstruments) running on a Macintosh computer (see Fig. 1). Sampling rates were typically >2 kHz and a high frequency filter was occasionally used to reduce background noise.

Lobster sound intensity

Sound pressure levels (SPL) were calculated using the following formula (Au and Hastings, 2008): $SPL = |M_n| - G + 20 \log V$, where M_n is the voltage sensitivity of the hydrophone (in dB re 1 V/μPa), G is the gain of the amplifier and V is the voltage recorded. The hydrophone used was an Aquarian Audio Products H2a-XLR hydrophone with a sensitivity of -180 dB re 1 V/μPa and a gain of 17 dB. The useful range of the hydrophone was >10 Hz to <100 kHz. Voltage values were obtained from the entire duration of the hydrophone sound signature using the root mean square function of the Chart analysis software.

Overview of experiments

In this study we carried out three separate experiments designed to determine: (1) whether lobsters would make sounds in the presence of fish and, if so, to quantify the response of the fish to these sounds; (2) whether lobsters would vibrate in response to other lobsters; and (3) whether lobsters would make sounds in response to fake fish. In these three experiments, sound-producing lobsters or fish were never used more than once. However, some of the control lobsters that did not make sounds were used more than once. The specific protocols for these three experiments are summarized below.

Lobster–fish interactions

This experiment had two goals: first, to determine whether fish would elicit sound production from lobsters; second, to determine how fish responded when sounds were produced. Trials were performed inside a 1.82 m diameter tank that was located in a quiet

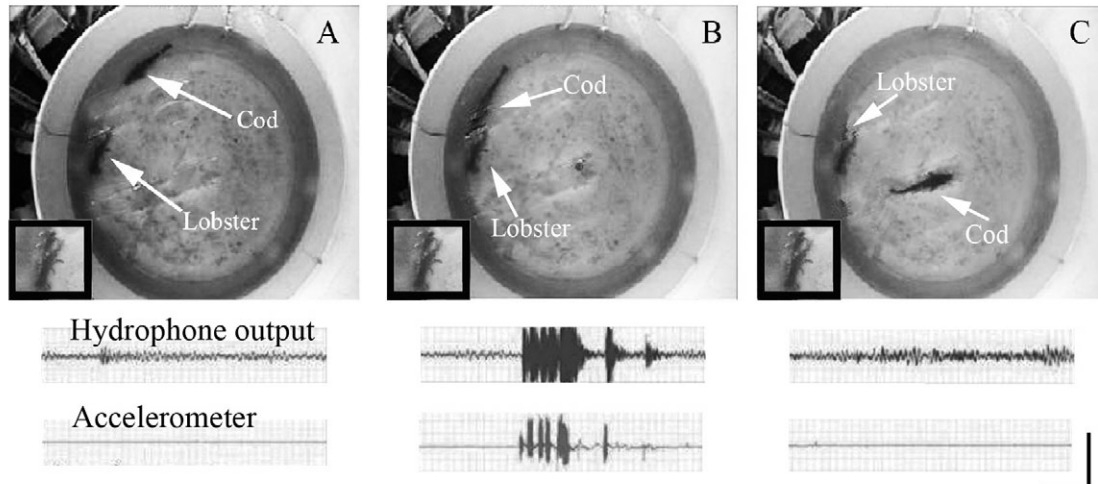


Fig. 1. Experimental setup used to record interactions between lobsters and fish. The top panels are individual frames taken from digital video that was shot during an experiment (total time elapsed, 24 s). Magnified images of the lobster have been inserted to show that the lobster did not alter its posture or change its behavior before, during, or after the interaction with the fish. The bottom panels show recordings from a hydrophone that was located in the middle of the tank and the output of the accelerometer attached to the dorsal carapace of the lobster. (A) Top: the approach of a cod (44.9 cm) towards a lobster (94 mm in carapace length); bottom: outputs of the hydrophone and accelerometer during the 8 s time span when the cod was approaching the lobster. (B) Top and bottom (captured during the next 8 s time span): the vibration produced by the lobster when the cod came within 20 cm of it. (C) Top and bottom: the cod immediately turned and swam away, after the lobster produced a sound. A video showing the lobster making sounds in response to the approach of a fish can be viewed at: www.lobsters.unh.edu.

room in the basement of Rudman Hall on the UNH campus. All pumps and chiller units that were part of the recirculating seawater system were turned off and removed during all trials to avoid any acoustic interference. The tank was illuminated *via* dimmed fluorescent lights suspended above the tank, providing sufficient lighting for digital video recording of all trials. All trials were captured with digital video to eliminate the need for an investigator's presence near the tank, thus limiting the impact of personnel on the behavior of the animals being studied. Digital video (15–30 frames s^{-1}) was captured using the Quick Capture module within Chart Software version 5.4 (ADInstruments). This module was used to synchronize digital video with accelerometer and hydrophone recordings so that precise behavioral analyses could be carried out subsequent to each trial (Fig. 1).

Twelve Atlantic cod (*Gadus morhua* L.; mean size 51.5 ± 1.5 cm; s.e.m. used here and throughout the text), and three striped bass (*Morone saxatilis*, Walbaum 1792; 62.8 ± 0.7 cm) were used in these experiments. The cod were taken from a holding pen in Newcastle, NH at the UNH Marine Research Pier, between July 2008 and March 2009. All of the cod were grown from juveniles by the Atlantic Marine Aquaculture Center (Durham, NH, USA). All striped bass were captured in the Great Bay estuary, NH, using hook and line, during either July 2008 or July 2009. Although both cod and striped bass are known to prey on lobsters in the field, the ones used in this study were probably too small to successfully attack and consume lobsters of the size range used in this study. All fish were returned to the waters from which they came as soon as possible after each experiment was over.

In this experiment the behavior of an individual fish was examined when it was in the tank alone, in the presence of a lobster that did not make sounds (control) and in the presence of a sound-producing lobster. While the control lobsters were used in more than one trial, each fish and sound-producing lobster was used only once. Thus, we exposed three different lobsters capable of producing carapace vibrations to three different wild-caught striped bass (*M. saxatilis*), and 12 lobsters capable of producing carapace vibrations to a total

of 12 Atlantic cod (*G. morhua*). The mean size of all sound-producing lobsters was 91.8 ± 1.4 mm CL. The protocol for these experiments was as follows. First, an individual cod or striped bass was placed in the tank and their spontaneous movements were recorded for 30 min to document normal swimming behavior and determine whether they had any preferences for certain areas of the tank. After 30 min, a banded control lobster was introduced into the tank, with an accelerometer attached to its dorsal carapace. The accelerometer was used to confirm that control lobsters did not produce sounds throughout the experiment. Lobsters were always placed in approximately the same area of the tank because they were attached to the accelerometer. Because the fish tended to move away from the person conducting the experiment when they approached the tank, these trials almost always commenced with the fish on the opposite side of the tank from the lobster. The behaviors of the control lobster and fish were then recorded for a period of 30 min to quantify the swimming behavior of the fish in the presence of the control lobster. After 30 min the control lobster was replaced by a banded 'sound-producing' lobster, and the trial was continued for another 30 min. Thus, test fish were first exposed to control lobsters that did not make sounds, and then to lobsters that did make sounds. The order of the experiment was not randomized because once certain fish experienced several sound events they tended to avoid lobsters. Therefore, if we exposed fish to sound-producing lobsters first, it would bias their subsequent behavior in the presence of control lobsters. All recordings of vibrations and sounds were saved, along with the digital video, for subsequent analyses.

The data obtained during the aforementioned trials were analyzed to determine: (1) whether fish would elicit sound production from lobsters and, if so, how close they needed to approach a lobster in order to elicit a sound event; and (2) whether fish responded differently to lobsters that produced sounds in comparison to lobsters that did not.

Lobsters tended to vibrate when a fish approached them. To quantify this, the distance between a fish and a lobster was measured each time a lobster produced a sound. These data were used to

calculate how close, on average, a fish needed to be to a lobster in order to elicit a vibration (we called this distance the 'area of influence'). In order to determine how lobster sounds affected fish behavior, we determined how far a fish swam from a lobster after a sound was produced and compared this to their swimming behavior when they interacted with a lobster that did not produce a sound. The distance a fish moved away from the lobster was measured every 2 s, for a total of 10 s, using Logger Pro software 3.7 (Vernier Software & Technology, Beaverton, OR, USA). Because control lobsters did not produce sounds, we initiated measurements of the distance between a fish and a lobster at the time when the fish moved to a position that would normally elicit sound production by a sound-producing lobster (inside the area of influence).

In preliminary studies it was apparent that lobster sounds also had a long-term influence on the swimming behavior of striped bass, but not cod. In order to quantify this effect we tracked the movements of striped bass before, during and after encounters with lobsters and compared the overall swimming pattern against their activity when no lobsters were present in the tank. Videos of each experiment, with the three different striped bass, were replayed and the x,y location of the striped bass was determined, using Logger Pro 3.7 software, every 10 s, for 30 min before a sound-producing lobster was placed in the tank, and then for 30 min while a sound-producing lobster was in the tank.

Sounds produced in response to other lobsters

This experiment was designed to determine whether lobsters produce carapace vibrations either spontaneously, when they are alone, or in the presence of other lobsters. We recorded the number of sounds produced in 30 min by 13 sound-producing lobsters while they were alone in the tank (no other lobsters or fish present), as well as during the 30 min after a control lobster was placed in the tank. The mean sizes of the two groups of lobsters were similar (sound-producing lobsters: 91.5 ± 2.9 mm CL; control lobsters: 90.5 ± 0.9 mm CL).

Lobster sound production in the presence of a fake fish

The goal of the third experiment was to determine whether lobsters relied on vision to assess the presence of potential predatory fish. On three occasions we recorded carapace vibrations and sound production from lobsters when we approached them with a plastic fish. The three lobsters used came from the pool of 47 that were selected from the Island Seafood Company, described above. The fake fish used was a 52.1 cm long plastic replica of a hammerhead shark that was hung

by clear fishing line from a pole and lowered into the tank. The pole was then manipulated to gradually move the fish towards the lobster. Approaches were repeated over a period of approximately 10 min, while monitoring lobster sound production. The number of approaches used in each of the three trials ranged from 22 to 62.

RESULTS

Production of carapace vibrations and associated acoustic signals by lobsters

This experiment clearly demonstrated that approaches by fish increased the probability that lobsters would produce carapace vibrations and the sounds associated with these vibrations. While lobsters spontaneously produced sounds while alone in the tank, it was a rare occurrence (Fig. 2A; 1.2 ± 0.2 sound events per 30 min trial, $N=13$ lobsters). The presence of another lobster significantly increased the number of carapace vibrations produced (Fig. 2A; 3.0 ± 0.4 sound events per 30 min trial, $N=13$ lobsters), but these events were also rare (Fig. 2A; unpaired Mann–Whitney test, $P=0.001$, $U=31.0$, $n_1=13$, $n_2=16$).

In contrast, in the presence of a striped bass, lobsters produced ~ 14 times more sounds during a 30 min trial (Fig. 2B; $N=3$) than when they were alone, and interactions with cod led to the production of significantly more sounds than when lobsters were alone (Fig. 2B; $N=12$, unpaired Mann–Whitney test, $P=0.0001$, $U=0.00$, $n_1=13$, $n_2=8$). Lobsters probably produced more sounds in the presence of cod than with striped bass because the striped bass tended to avoid the lobsters more than the cod, as described later in this paper.

The mean intensity of the sounds produced by lobster carapace vibrations was 118 ± 1.49 dB re $1 \mu\text{Pa}$ ($N=5$ lobsters). This is comparable to previously measured lobster sound intensity values (Fish, 1966; Henninger and Watson, 2005) (16 and 18.5 dB re $1 \mu\text{bar}$, which is equivalent to 116 and 118.5 dB re $1 \mu\text{Pa}$, respectively). The difference between the values results from the use of different units for the reference pressure in these previous studies (μbar vs μPa).

To determine how close a cod needed to come to a lobster in order to elicit sound production, we measured the distance between the lobster and the cod each time a lobster vibrated (12 lobsters exposed to 12 cod). Out of all the sound events recorded, $74.6 \pm 6.6\%$ took place when cod were within 0.5 m of a lobster (Fig. 3). Of these responses, $51.9 \pm 7.8\%$ occurred when fish were closer than 0.3 m. It should be noted that fish did not have to come into contact with lobsters in order to elicit sound production and typically sound production was not accompanied by any other displays or aggressive interactions (Fig. 1).

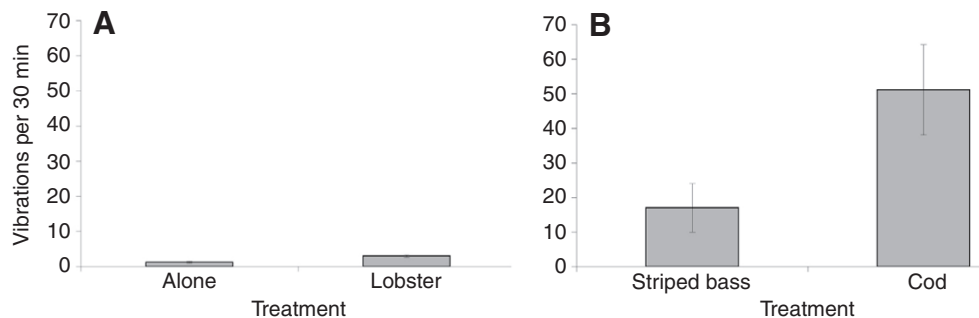


Fig. 2. The number of sound pulses (mean per 30 min trial, \pm s.e.m.) produced by lobsters when alone, in the presence of another lobster (A), or in the presence of either a cod or striped bass (B). (A) Lobsters produced very few sounds when alone and there was a small, but significant ($P=0.001$), increase in the number of sounds they produced when they were in the presence of another lobster ($N=13$). (B) The presence of a striped bass or a cod caused an increase in sound production, but this was only significantly different from controls ('alone' data from the trials in A) for the cod trials ($P=0.0002$). Fewer sounds were elicited by striped bass because they had a tendency to avoid the lobsters after being subjected to a few sound pulses.

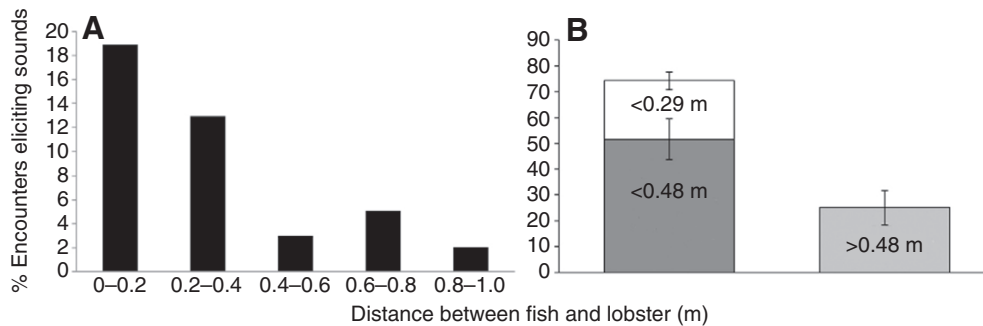


Fig. 3. The percentage of times sounds were produced when a fish moved within a certain distance of a lobster. (A) Data from 10 randomly chosen trials during which there were 60 sound events. Note that the majority of the sounds were produced when the fish approached to within 0.5 m of the lobster. Bins go from the lowest values to < the highest values (0.2 is included in the first bin but not the second). (B) Summary of the distances between fish and lobsters at the time when all 292 sound events were produced.

Lobster responses to fake fish

In order to determine whether lobsters perceive the presence of a fish using vision (in contrast to odors or sounds), we exposed lobsters to repeated approaches by a plastic fish. During three trials with three different lobsters, vibrations were produced during $39.4 \pm 2.1\%$ of the approaches. Moreover, as with real fish, all vibrations occurred when the plastic fish was moved to within 0.5 m of the lobster.

Fish responses to carapace vibrations

To determine how the waterborne component of the carapace vibration affected fish, comparisons were made between fish–lobster interactions that elicited a sound (from trials with lobsters known to vibrate) and fish interactions with control lobsters that did not make a sound. It should be noted that the banded lobsters did not typically display or express a threatening posture in response to an approaching fish, and often lobsters did not even turn around before producing a sound in response to a fish approaching from behind (Fig. 1). Rather, our data indicate that it was the sound produced by the lobster, and not any other noticeable behavior expressed by the lobster, that caused fish to almost instantaneously move away from lobsters after they vibrated.

The effect of lobster sound production on cod was evaluated by comparing the distance between fish and lobsters 2, 4, 6, 8 and 10 s after a sound was produced (from 5 sound-producing lobsters, a subset of the 12 total lobster–cod trials) vs when no sound was produced during a fish–lobster interaction (5 control lobsters) (Fig. 4). For the analysis using control lobsters that did not produce a sound, measurements were initiated from the time when fish came within the 0.3 m area of influence of the lobsters, which is when ‘soniferous’ lobsters typically produced a sound. The distance cod swam away from lobsters was significantly greater following a sound event compared with trials when sounds were not produced, at latencies of 4, 6 and 8 s (unpaired Student’s *t*-tests; 4 s: $t=2.35$, d.f.=8, $P=0.047$; 6 s: $t=2.43$, d.f.=8, $P=0.041$; 8 s: $t=2.18$, d.f.=8, $P=0.05$), but not at 2 and 10 s. The results at 10 s were likely due to the limitations imposed by the size of the test tank (diameter 1.82 m), because fish would swim away and then, after reaching the other side of the tank, would begin to circle back towards the lobster again. Overall, cod moved further away, faster, from lobsters that made sounds than from lobsters that did not. These results indicate that cod probably found the carapace vibrations and associated sounds produced by lobsters to be aversive.

The sounds produced by lobsters had a short-term impact on both species of fish, causing them to rapidly move away, and also a long-term effect on just the striped bass. Striped bass and cod tended to

swim around the tank in a circle when no lobster was present in the tank (Fig. 5B,D). However, after several experiences with the sounds produced by a vibrating lobster, striped bass subsequently avoided them (Fig. 5A,C). As a result, the amount of time the striped bass spent within 0.5 m of the lobsters (if they came closer than 0.5 m the lobsters would make sounds) tended to decrease during the course of a trial. For example, when a sound-producing lobster was in the tank the three striped bass spent 3.79% of the time within 0.5 m of the lobster, whereas when no lobsters were present they spent >10% of the time within the same area of the tank.

This long-term change in behavior was not apparent in the cod. Cod continued to approach lobsters even after lobsters produced sounds and, as a result, lobsters produced more sounds per 30 min in the presence of cod than in the presence of striped bass (which explains the data shown in Fig. 2). We should note that our findings concerning the long-term change in the behavior of the striped bass are only based on the responses of three striped bass and therefore additional studies are recommended in order to confirm these data.

DISCUSSION

Although it is known that American lobsters are capable of detecting sounds (Fish, 1966) and producing sounds (Henninger and Watson, 2005), the adaptive significance of sound production in this species

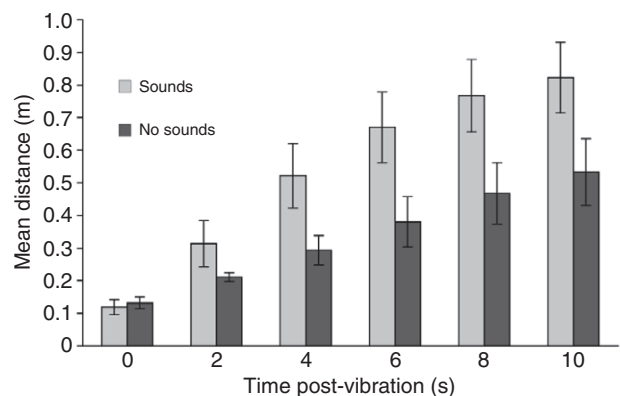


Fig. 4. Mean distance a cod swam after an interaction with either a lobster that produced a sound ($N=5$) or a lobster that did not produce a sound (control; $N=5$). Distances between the fish and the lobster were measured every 2 s, for 10 s, starting from time zero, when a sound was produced. For control trials, using a lobster that did not produce sounds, time zero was assigned to the time when a cod came within 0.3 m of the lobster (the ‘area of influence’). Cod swam significantly further away following a sound event at time intervals of 4, 6 and 8 s, but not at 2 and 10 s.

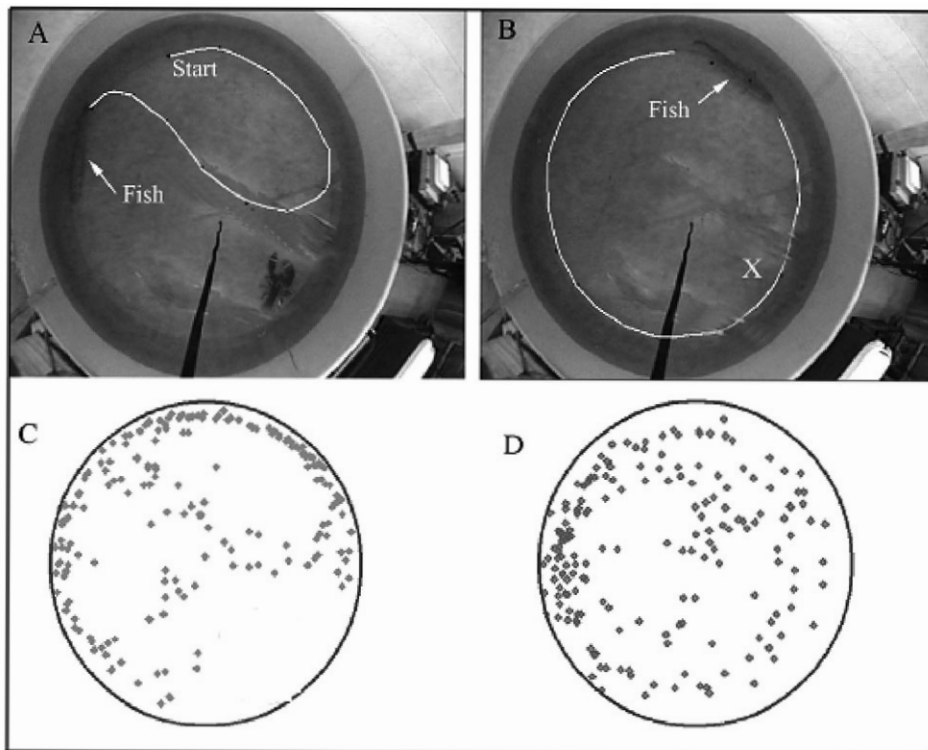


Fig. 5. The pattern of swimming expressed by a striped bass in the presence and absence of a lobster. (A) The path of a fish during a 1 min period, showing how it avoided the lobster. Points were obtained every 10 s. (B) Comparable data obtained when a lobster was not present, illustrating the normal circling pattern of swimming. The position where lobsters were normally placed is indicated by an X. (C) The distribution of points during a full 30 min trial with a lobster present. Points were obtained every 10 s. (D) The distribution of fish positions when no lobster was present. To view actual videos go to: www.lobsters.unh.edu.

is unknown. In other lobster species, and a wide variety of other animals, acoustic signals are often used to deter predators. In this study we demonstrated that the close proximity of a potential fish predator, or fake fish of a similar size, significantly increased the probability that a lobster would produce carapace vibrations and associated sound pulses. In addition, in response to these sounds, both cod and striped bass immediately moved away from the lobsters and, at least in the case of striped bass, avoided further approaches after experiencing several of these acoustic signals. Therefore, it seems likely that some American lobsters may use acoustic signals to deter potential fish predators. However, further studies are necessary in order to determine whether lobster sounds actually reduce the likelihood that lobsters will be attacked and eaten by predatory fish. For these studies it would be necessary to use larger fish, and smaller lobsters, so that the fish would be capable of successfully attacking and consuming the lobsters.

According to our measurements, and those obtained in two previous studies (Fish, 1966; Henninger and Watson, 2005), the sounds produced by lobsters have a frequency of ~ 180 Hz and an intensity of 118 dB. A sound of this frequency and amplitude in the ocean will travel quite a long distance, quite fast, because of the incompressible nature of water vs air (Bone and Moore, 2008). However, because of the high background noise in the ocean, it is unlikely that signals of this frequency and magnitude would be effective, as sounds, at any significant distance (more than a few meters) from the source (Patek et al., 2009).

Sounds in water create two types of stimuli, due to both the pressure component of the signal and particle displacement (Popper and Fay, 1993; Bone and Moore, 2008). The particle displacement component does not propagate as far as the pressure wave and so, in the 'near field', the particle displacement component of the signal is proportionally much larger than when further away in the 'far field'. It is likely that the entire tank used in this study received a portion of the near-field component, and most of the far-field component, of the sounds produced by the lobsters. As a result, it

is impossible at this time to determine which component of the signal was most responsible for causing fish to move away from sound-producing lobsters. However, for the following reasons, our working hypothesis is that fish are primarily responding to the particle displacement (near-field) component of the sounds produced by American lobsters when they vibrate their dorsal carapace. First, these sounds were mostly produced when the fish were within 0.5 m of the lobster and when the fish were this close they appeared to perceive the sounds as an aversive stimulus. In contrast, on the few occasions when lobsters produced sounds when fish were on the other side of the tank, they did not appear to respond. Second, based on the measurements and calculations made by Patek and colleagues (Patek et al., 2009) with spiny lobsters, sounds of this nature would likely be obscured by ambient noise within about 1–2 m of the source. Finally, with few exceptions, aquatic species tend to be more sensitive to the particle displacement component of sounds (Mooney et al., 2010). Therefore, it seems reasonable to assume that the carapace vibrations produced by American lobsters evolved to function in the near field, to deter predators, rather than in the far field, for some type of long distance communication.

Interestingly, lobsters also occasionally produced sounds in response to other lobsters. Our previous work (Henninger and Watson, 2005), as well as studies with other marine invertebrates [Norway lobster (Goodall et al., 1990); shrimp (Lovell et al., 2005); squid (Mooney et al., 2010); crayfish (Monteclaro et al., 2010)], indicates that a number of species are capable of detecting sounds over a frequency range that encompasses the 180 Hz carapace vibrations produced by American lobsters. Moreover, it appears that in most of these cases, species are detecting the particle displacement component of the sound using either statocysts (Mooney et al., 2010) or sensory elements on their antennules (Monteclaro et al., 2010). However, in this study, and in our previous studies (Henninger and Watson, 2005), there was no clear response of other lobsters to these sounds. Therefore, while we cannot rule out the possibility that the lobsters produce sounds as a form of intra-species communication,

especially given their ability to detect sounds in this frequency range, our current data only support the hypothesis that the sounds produced by American lobsters mostly serve as a near-field signal to deter fish predators.

In our previous study, 7.5% of the lobsters surveyed vibrated when grasped, and when we surveyed all the potential subjects for the present study we also noted that only a small percentage of them vibrated when handled. The purpose of this study was to determine whether lobsters would produce sounds in response to potential predators and, if they did, assess the response of the fish to the sounds. We were not attempting, in this study, to determine how often this behavior might occur in a natural population of lobsters. Therefore, we purposely selected lobsters that exhibited a high probability of responding for use in these experiments and the data presented in this paper are probably not a reflection of how often lobsters in their natural habitat produce sounds.

At the current time we cannot explain why so few lobsters make sounds when handled. During previous studies designed to determine the underlying mechanisms of sound production in American lobsters it appeared that all lobsters have the capacity to make sounds (Henninger and Watson, 2005). Therefore, it is likely that most lobsters did not make sounds when handled either because the stimulus was not sufficient to elicit sound production or because, as a result of the stress of captivity, they had habituated to being disturbed. However, these explanations do not account for the fact that our 'control' lobsters, which were held under the same conditions as our sound-producing lobsters, rarely made sounds when exposed to fish, while the lobsters that had a propensity for making sounds produced vibrations during >70% of their encounters with fish. Clearly, further studies are necessary to determine why some lobsters produce sounds and some do not in response to an aversive stimulus, and why some lobsters spontaneously produce sounds when alone and not disturbed, and some never spontaneously produce sounds (at least in our experience). Perhaps, now that we have determined that large fish are good natural triggers for sound production, such studies will be more feasible. For example, it would be interesting to determine the percentage of randomly selected lobsters that produce sounds when approached by a large fish in comparison to the number that vibrate in response to being handled.

While it was not surprising to find that American lobsters produce sounds in response to the approach of potential fish predators, it was interesting that fish responded so clearly to the sounds. The aversive responses of fish had two components. The first component was an immediate turn, following by swimming away from the lobster. The second component, expressed only by the striped bass, was a tendency to avoid lobsters after experiencing several acoustic events. Rather than continuously circling the tank, striped bass altered their swimming pattern and repeatedly avoided moving close enough (<0.5 m) to stimulate the production of sounds by lobsters. Thus, while these findings are only based on data from three fish, it appears that producing sounds might serve to keep predators away over the long term as well as the short term.

While striped bass appeared to learn to stay away from lobsters, cod did not. There could be several reasons for this differential response. First, there could be differences in the hearing abilities of the two species of fish. Unfortunately, at present, we have a fair understanding of the hearing abilities of only 100 of the ~27,000 species of fish (Popper et al., 2003). Although both cod and striped bass belong to the group of teleosts known as 'hearing generalists', to our knowledge there is no specific information about the sensitivity and hearing threshold of striped bass so it is hard to compare their hearing abilities with those of cod. If, for the present,

we assume that the two species of fish have similar hearing abilities, then some other factor must cause cod to repeatedly approach sound-producing lobsters, while striped bass tend to avoid them after a few encounters. Our working hypothesis is that the cod used in this study were farm-raised from birth, so they had little experience interacting with any other marine animals, while the striped bass were captured in the Great Bay estuary and it is likely that they had considerable experience interacting with lobsters and other invertebrates. As a result of these previous interactions they may have already learned that interactions with some lobsters can be aversive, because of either sound production or direct contact, or both. To test this hypothesis we plan to repeat this study using wild cod. The results of such a study might also help determine whether lobster sounds serve as aposematic signals, reducing further attacks [see Staaterman et al. (Staaterman et al., 2010) for a good discussion of the possible roles of spiny lobster sounds]. At least for striped bass, this appears to be a possibility, based on their reluctance to approach sound-producing lobsters after several encounters.

Scientists have been investigating the role of acoustic signals in animals ranging from insects to whales for many years and a great deal is known about their role in attracting mates, announcing territories and maintaining communication within a group. It is interesting that, despite a plethora of reports concerning the production of sounds by a variety of crustaceans and other marine invertebrates, there is a great deal left to learn about the function of these sounds in their natural habitat (Budelmann, 1992). In this paper, and several other recent papers, the role of these sounds as antipredator signals is beginning to be revealed. However, it is still not clear whether lobsters can also hear these sounds, how potential fish and invertebrate predators detect these sounds, and how often and under what circumstances lobsters make sounds in their natural habitat. Hopefully, progress in these areas will proceed as rapidly as it has in many terrestrial species.

ACKNOWLEDGEMENTS

We are grateful for the assistance provided by Dean Elder in the animal care facility where the experiments were carried out and the cooperation of the people at Island Seafood in Elliot, ME, when we needed to search through their supply of lobsters for appropriate subjects. Several graduate and undergraduate students participated in aspects of this study and we would like to express our appreciation to Tom Langley, Jeff Caron, Jason Goldstein and Jesse Krauss for their help. Finally, we are grateful for the comments and suggestions made by Dr Sheila Patek on a draft of this manuscript, and the two anonymous reviewers who provided suggestions that significantly improved this version of the manuscript. This project was funded, in part, through grants to W.H.W. from NOAA (Sea Grant) and the USDA (Hatch).

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