





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Fishing with sound: Insights into the plainfin midshipman's reproductive ecology from field acoustic playbacks

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Abstract: The long-duration advertisement “hums” produced by type I male plainfin midshipman fish (*Porichthys notatus*) are tonal signals consisting of a fundamental frequency and multiple harmonics. Using acoustic playback of synthetic, hum-like stimuli under natural conditions, we found that the fundamental frequency is likely required for females’ final entry into a type I male’s nest, whereas higher harmonics may play a limited role. We found no evidence of phonotaxis in type I and type II males. Additionally, the observed decrease in body size of captured individuals over the breeding season suggests that larger individuals migrate earlier to spawning sites. © 2026 Author(s). All article content, except where otherwise noted, is licensed under a Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

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1. Introduction

All fishes examined to date can detect sound, and approximately 1000 species are known to actively produce sounds, many of which play critical roles in social communication.¹ Most fish sounds that have been recorded are short, on the order of a few milliseconds to seconds.² However, the plainfin midshipman (*Porichthys notatus*) and possibly the Atlantic midshipman (*Porichthys plectrodon*)³ appear to be exceptions. Type I, or “singing,” male plainfin midshipman produce long-duration hums that can last nearly two hours.⁴ To the best of our knowledge, these hums represent the longest known uninterrupted vocalizations in the animal kingdom.

The plainfin midshipman spends most of the year in deeper offshore waters at depths of up to 300 m, but migrates to rocky intertidal habitats along the west coast of North America from late April through September to breed.⁵ Early in the breeding season, type I, or “singing” males construct nests under rocks and produce hums to attract females. After arriving at a nest, females engage in courtship interactions with the resident type I male and then deposit eggs on the nest roof.⁶ Type I males then provide sole parental care, guarding and fanning eggs until the larvae hatch and disperse. In contrast, type II or “sneaker males” do not produce hums or construct nests; they attempt to fertilize eggs by sneak spawning.⁶ Hums exhibit a highly periodic temporal structure and clear harmonic periodicity in the frequency domain, with the fundamental frequency typically ranging from approximately 70 to 120 Hz, depending on water temperature⁶ and the male’s body condition⁴ [Figs. 1(a) and 1(b)].

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Acoustic playback experiments conducted in both captive settings and natural environments have played a crucial role in uncovering the functions of vocalizations in several fish species, including their roles in courtship and agonistic encounters (reviewed in Ref. 7). In the plainfin midshipman as well, acoustic playback experiments were used to identify the mating hum and determine its active components. Females perform phonotaxis in large outdoor tanks,⁸ suggesting that they localize the nests of calling males using the hum in the wild. The fundamental frequency alone is sufficient to attract females, and adding a second harmonic does not increase the hum’s attractiveness in captive settings.⁹ This indicates that the fundamental frequency is the primary active component of the call, with higher harmonics playing a limited role in female attraction.

However, it remains unclear whether the fundamental frequency is necessary when higher harmonics are present or whether the overall harmonic structure, i.e., acoustic energy concentrated at integer multiples of the fundamental frequency, is essential for attracting females. Additionally, behavioral playback studies suggest that type I and type II males may also perform phonotaxis, although this has not yet been confirmed in the natural environment.⁹

To determine whether the attraction of females to hums observed in captive environments also occurs in the wild, and whether type I and type II males perform phonotaxis, synthetic hum-like stimuli modeled after the hums of type I male midshipman⁴ were broadcast from underwater speakers housed within modified shrimp traps. Additionally, two and three choice experiments were conducted to assess whether the fundamental frequency is necessary for attracting females in the presence of higher harmonic frequencies and to evaluate the importance of harmonic structure in determining the attractiveness of the hum.

In several fish species, such as the Atlantic herring (*Clupea harengus*)¹⁰ and capelin (*Mallotus villosus*),¹¹ larger individuals mature earlier and arrive at spawning grounds before smaller individuals, likely because they reach reproductive maturity sooner. We also quantified the sizes of individuals captured in the acoustic trapping experiments to test whether similar trends occur in the plainfin midshipman.

2. Methods

2.1 Acoustic stimuli

Using custom MATLAB code (MathWorks, Natick, MA), synthetic versions of four stimuli were generated: (1) a synthesized replication of a typical male advertisement call (hereafter referred to as a “hum” for brevity) with a fundamental frequency denoted as f_0 throughout the article [Figs. 1(c) and 1(d)]; (2) diminished f_0 hum, similar to the natural hum but with reduced energy at f_0 relative to higher harmonics, such that the root mean square sound pressure level (SPL) of the second harmonic, f_1 , exceeded that of f_0 by 20–39.2 dB re. 1 μ Pa [Figs. 1(e) and 1(f)]; (3) subharmonic hum, a sound with peak energy at f_0 but with a fundamental frequency one-third that of the hum (i.e., $f_0/3$) [Figs. 1(g) and 1(h)]; and (4) a hum-like buzz, a sound with peak energy at f_0 but altered spectro-temporal structure. The hum-like buzz had acoustic energy concentrated at irregularly spaced frequencies, with an average spacing between frequencies being $\sim 1/5$ to $1/6$ that of a hum, resulting in reduced periodicity [Figs. 1(i) and 1(j)]. Because f_0 varies systemically with water temperature,⁶ we scaled f_0 and harmonics proportionally to measured temperature for the hum, diminished f_0 hum, and subharmonic hum stimuli. For the hum-like buzz, the peak frequency f_0 also increased proportionally with temperature, while changes in the other spectral components were more complex. For a detailed description of acoustic stimulus generation and the experimental procedure, see the Experimental Protocol in the [supplementary material](#).

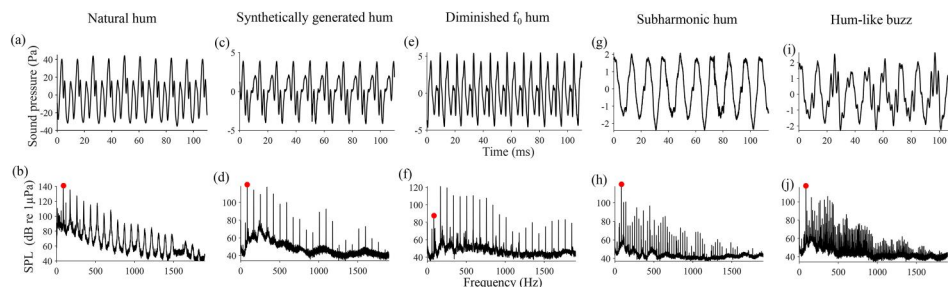


Fig. 1. Temporal waveforms and power spectra of a laboratory recording of a representative natural hum (a), (b) and field recordings of the synthetic acoustic stimuli used in the acoustic trapping experiments (c)–(j). Panels (a) and (b) show the waveform and corresponding power spectra of a naturally recorded type I male advertisement hum. Panels (c)–(j) present the waveforms and power spectra for each synthetic stimulus used in the field experiments: (c), (d) full spectrum synthetic hum (referred to as a “hum” throughout the manuscript for brevity); (e), (f) diminished- f_0 hum; (g), (h) subharmonic hum; and (i), (j) hum-like buzz. Refer to Sec. 2 for detailed descriptions of the acoustic stimuli. Power spectra were computed using the Welch method, employing a Hanning window equal to ten times the 44.1 kHz sampling frequency and 50% segment overlap, yielding a frequency resolution of 0.1 Hz. The fundamental frequency (f_0) of the hum, present in all stimuli, is marked with a red dot on each power spectrum. For panels (c)–(j), f_0 is approximately 84.1 Hz, corresponding to a temperature of 13 °C (see the [supplementary material](#) for additional details).

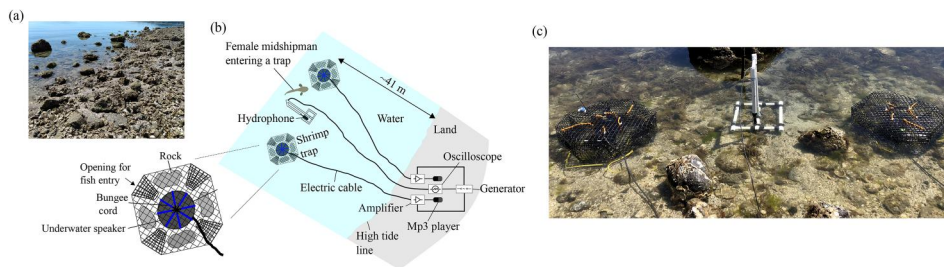


Fig. 2. (a) Representative view of the rocky intertidal breeding habitat of the plainfin midshipman (*Porichthys notatus*) at Seal Rock, Brinnon, WA. This site provides natural nesting cavities used by males during the reproductive season and is characterized by tide-dependent submersion. (b) Schematic illustration of the experimental setup, highlighting the shrimp trap that housed a submerged underwater speaker. The speaker was used to broadcast acoustic stimuli mimicking male advertisement calls during behavioral trials. (c) Photograph of the field deployment, showing the experimental setup during the incoming tide as water levels rise to submerge both the traps and the hydrophone positioned to monitor acoustic playback.

2.2 Experimental setup

The main components employed in the experiments are listed in Table S1 in the [supplementary material](#). Experiments were conducted in the rocky intertidal zone at Seal Rock, Brinnon, WA, an established plainfin midshipman breeding site [Fig. 2(a)]. The experiments included four experimental comparisons: (1) hum vs silent control, (2) diminished f_0 hum vs silent control, (3) hum vs subharmonic hum, and (4) hum vs hum-like buzz vs silent control. Experiments 1–3 were conducted in 2021, and experiment 4 was conducted in 2022. The dates of each experiment are listed in Table S2 in the [supplementary material](#).

The experimental layout is illustrated in Figs. 2(b) and 2(c). For experiments 1–3, two octagonal shrimp traps (dimensions: 61 cm \times 61 cm \times 21.6 cm; Seattle Marine and Fishing Supply Co., Seattle, WA) were positioned roughly parallel to the shoreline, 41 m offshore from the high tide line. Each trap featured four funnel-shaped openings and an underwater speaker (Lubell AQ339; Clark Synthesis, Littleton, CO) suspended from the top center via bungee cords, approximately 10–12 cm above the ground. Trap positions were fine-tuned to ensure that the centers of the two speakers were 2 m apart, exceeding the distance at which plainfin midshipman have been shown to discriminate between two sound sources.⁹ An HTI-96-min hydrophone (sensitivity: -164.2 dB re 1 V/ μ Pa; frequency response: 2 Hz–30 kHz; High Tech Inc., Long Beach, MS) was positioned equidistant (1 m away) from each speaker.

For experiment 4, speaker traps were positioned 4 m apart, and a third trap, positioned midway between the two traps, served as a silent control. The silent trap contained a speaker-like disk, meant to resemble the contents of the two active traps. Additionally, to improve capture rates of the traps as deployed in experiments 1–3, traps were now covered with fine wire mesh with one-way flaps on the entrances to prevent escape (see Fig. S2 in the [supplementary material](#)).

Playback equipment consisted of MP3 players (RUIZU, Shenzhen, China) feeding an amplifier (Bosch Plena PLE-1P120-US; Bosch Security Systems Inc., Fairport, NY), with output monitored via an oscilloscope (TDS 1002; Tektronix, Beaverton, OR). Stimuli were stored in temperature-specific 5-min files (10–25 $^{\circ}$ C in 0.5 $^{\circ}$ C increments) and looped overnight. The SPL was standardized to 127 dB re 1 μ Pa (1 m from source), a level previously shown to attract female plainfin midshipman.¹² A hydrophone was also connected to an oscilloscope to monitor playback sound levels. Electronic equipment was powered by a gasoline-fueled generator (Sportsman 4000/3500-Watt; Buffalo Corporation, O’Fallon, MO).

The experimental setup was typically assembled during daytime low tides within the timeframe \sim 0930–1500 h. In all experiments, nearby nests within roughly 3 m were cleared each day during the low tide to minimize the chance that females would visit a nearby calling type I male’s nest instead of entering the acoustic traps. Type I males calling beyond 3 m from either speaker are unlikely to be audible to females near the acoustic traps (see the Experimental Protocol in the [supplementary material](#)). During the acoustic trapping experiments, water depth always exceeded 2.4 m and likely reached 3–4 m at high tide (see Supplementary Experimental Protocol in the [supplementary material](#)).

2.3 Experimental procedure

Acoustic playback trials ran nightly from 2100–0600 h. Water temperature was measured every 3 h to the nearest 0.1 $^{\circ}$ C by casting a data logger (HOBO Pendant MX Water Temperature Data Logger, Bourne, MA) towards the fish traps’ location using a fishing rod and reel loaded with monofilament line. The sound file corresponding to the nearest 0.5 $^{\circ}$ C interval was then played on a loop. Each night constituted a single trial within a given experiment.

During the following morning low tide, traps were checked, and captured fish were categorized by sex and morph type and measured for standard length (SL) and mass. In experiments 1–3, one of the two traps (left or right) was randomly selected each night to broadcast one of the two acoustic stimuli used in the experiment. In experiment 4, the

hum or hum-like buzz was randomly broadcast each night from either the left or right trap, while the center trap remained silent.

2.4 Statistical analyses

For experiments 1–3, nightly differences in the number of captured females and type I males between paired traps were evaluated using the Wilcoxon signed-rank test.¹³ For experiment 4, a Friedman test was used to evaluate the effect of stimulus type on female capture rates,¹⁴ with Conover *post hoc* tests for pairwise comparisons when significant.¹⁵

Spearman’s rank correlation coefficients (r_s) were calculated between body size (mass and SL) and breeding season day (relative to May 11, 2021) to test for seasonal size shifts. A *t*-test was used to determine whether r_s differed significantly from zero ($\alpha = 0.05$).¹⁶ Wilcoxon signed-rank tests were performed in MATLAB; all other statistical analyses were conducted using JASP.¹⁷

3. Results

3.1 Attraction of female and male plainfin midshipman to hum-like acoustic stimuli

In a series of field playback experiments, we quantified the phonotactic responses of reproductive female and male plainfin midshipman to synthetically generated hum-like stimuli. In the hum vs silent control experiment, traps broadcasting a synthetic hum captured significantly more females overnight than paired silent traps (Wilcoxon signed-rank test, $n = 8$ nights, $p < 0.01$) [Fig. 3(a)]. This result confirms that a synthetically generated hum effectively elicits phonotaxis in reproductive females.

In contrast, when the acoustic stimulus was altered such that the amplitude of the fundamental frequency was reduced relative to its higher harmonics (diminished f_0 hum vs silent control), female capture rates did not significantly differ between traps (Wilcoxon signed-rank test, $n = 7$, $p > 0.05$) [Fig. 3(b)]. This suggests that the fundamental frequency plays a critical role in mediating female attraction. Mean overnight trap counts decreased from 5.25 in traps broadcasting the hum in the hum vs silent experiments to 1.71 in traps broadcasting the diminished f_0 hum in the diminished f_0 hum vs silent experiments. Thus, attenuating the fundamental frequency markedly reduced the hum’s attractiveness.

In the hum vs subharmonic hum experiment, no significant difference in female captures was observed between traps (Wilcoxon signed-rank test, $n = 6$, $p > 0.05$) [Fig. 3(c)]. In contrast, the hum vs hum-like buzz vs silent control experiment revealed a significant effect of stimulus type on female capture rates (Friedman test, $n = 8$, $p < 0.01$). Both the hum and hum-like buzz traps captured significantly more females than the silent control traps (Conover *post hoc* test: $p < 0.05$ for both comparisons) [Fig. 3(d)], whereas female capture did not differ between the hum and hum-like buzz traps (Conover *post hoc* test: $p > 0.05$) [Fig. 3(d)]. Together, these results suggest that acoustic energy at the fundamental frequency of the hum is necessary for eliciting phonotaxis, whereas the precise harmonic structure of the hum, including acoustic energy concentrated at integer multiples of the hum’s fundamental frequency, may be less important for female attraction.

Across all four experiments, stimulus type did not influence capture rates of type I or type II males (Wilcoxon signed-rank test for experiments 1–3, Friedman test with Conover *post hoc* comparisons for experiment 4) (see Fig. S5 in the supplementary material), which were generally much lower than female capture rates (total females captured across experiments = 641, total type I males captured = 89, total type II males captures = 13).

Finally, there was no evidence that male presence affected female attraction or vice versa. For each experiment, the number of females captured per trap was uncorrelated with the number of type I males (Spearman’s rank correlations, $p > 0.05$ for all) (see Table S4 in the supplementary material). Likewise, no significant correlations were observed between female captures and type II male captures in the 2022 experiments (see Table S5 in the supplementary material). Together, these results indicate that female phonotaxis was driven solely by the acoustic characteristics of the stimuli,

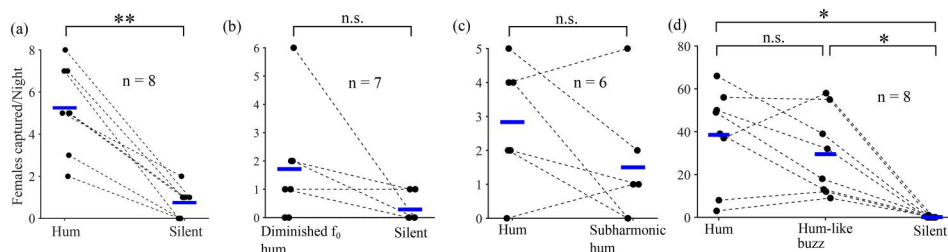


Fig. 3. Overnight capture results from four separate acoustic trapping experiments designed to assess the phonotactic attraction of reproductive female plainfin midshipman to different acoustic stimuli. Panels show the number of females captured under the following conditions: (a) hum versus silent control, (b) diminished f_0 hum versus silent control, (c) hum versus subharmonic hum, and (d) hum versus hum-like buzz versus silent control, allowing assessment of relative preference across multiple stimuli. Refer to the main text for detailed descriptions of the stimuli and the statistical analyses used to compare capture counts across experimental conditions. * and ** represent $p < 0.05$ and $p < 0.01$, respectively.

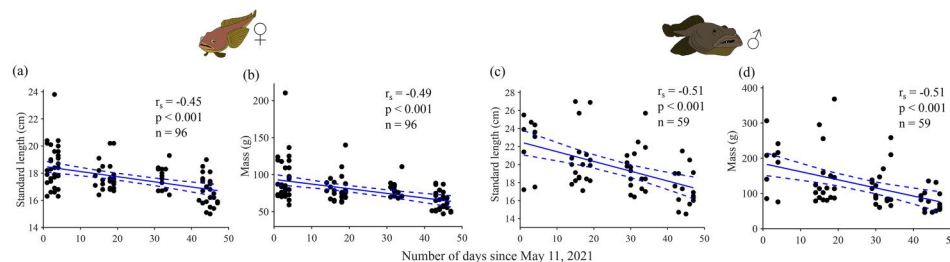


Fig. 4. Temporal patterns in body size metrics, SL and mass, of captured reproductive females and type I males across the 2021 breeding season, based on data from the first three acoustic trapping experiments (experiments 1–3, see Sec. 2 for details). Each data point represents an individual fish captured on a given night, with corresponding linear trend lines plotted over time. Panels display (a) SL of females, (b) mass of females, (c) SL of type I males, and (d) mass of type I males. Best-fit lines are shown with dotted lines representing the 95% confidence interval bands. Temporal associations were evaluated using Spearman’s rank correlation coefficient (r_s).

particularly the presence and amplitude of the fundamental frequency, and not by the presence of conspecific males in the traps.

3.2 Temporal trends in body size of captured females and males over the breeding season

Experiments 1–3 were conducted intermittently across a 47 day period (May–July 2021), spanning multiple spring tide cycles and encompassing most of the reproductive season. Over this period, both SL and body mass of captured females and type I males showed significant decreases, with individuals captured later in the season being consistently smaller than those captured earlier.

To quantify this pattern, individual size was regressed against days since the onset of the experiment (May 11, 2021). For females ($n = 96$), both SL and mass were significantly negatively correlated with date (Spearman’s rank correlation, $r_s = -0.45$ and -0.49 , respectively; $p < 0.001$) [Figs. 4(a) and 4(b)]. Type I males showed an equivalent pattern, with both SL and mass negatively correlated with date ($n = 59$; $r_s = -0.51$ for both correlations, respectively; $p < 0.001$ for both) [Figs. 4(c) and 4(d)].

4. Discussion

In this study, we performed acoustic trapping experiments in the plainfin midshipman to gain bioacoustic insights into their reproductive ecology. By broadcasting synthetic versions of the advertisement hum produced by type I males, we successfully attracted reproductive females and identified the acoustic features necessary and sufficient to elicit phonotactic behavior. In addition, measurements of the size and weight of captured individuals revealed seasonal patterns in the timing of arrival to the breeding habitat.

Our results support and extend findings from previous laboratory findings by showing that the fundamental frequency of the male hum is the primary feature driving female attraction. Consistent with earlier work in controlled settings (e.g., Ref. 8), traps broadcasting a full-spectrum synthetic hum captured significantly more females than silent traps. In contrast, stimuli with reduced energy at f_0 were no more attractive than silent traps, although one trial deviated from this pattern [see Fig. 3(b)]. While it has been shown previously that the fundamental frequency is sufficient to elicit female phonotaxis,¹² our results, alongside previous work showing that playbacks containing only the second harmonic do not elicit phonotaxis,⁹ suggest that the fundamental frequency is also necessary for close-range localization and nest entry.

Earlier laboratory experiments reported no difference in female attraction between playbacks containing only the fundamental frequency and those containing both the fundamental and second harmonic.⁹ Taken together with our findings that the subharmonic hum and hum-like buzz are as attractive as a full-spectrum hum, this suggests that the harmonic or note-like structure of the hum may play a limited role in female attraction. As long as the stimulus contains peak energy at the hum’s fundamental frequency, it is attractive to females.

Because the fundamental frequency (~ 100 Hz) appears to be both necessary and sufficient for female phonotaxis, anthropogenic underwater sounds in this frequency range may be especially disruptive to reproductive success. Acoustic playback experiments have been used in both laboratory and field settings to investigate fish mating vocalizations.^{7,18} However, to the best of our knowledge, the specific “active frequency components” required to drive reproductive phonotaxis have been explicitly identified only in the plainfin midshipman. In other soniferous species that rely on phonotaxis for reproduction, some components of vocalizations may be non-functional byproducts of the sound production mechanism. In these species, identifying the frequency components essential for reproductive phonotaxis may be crucial for predicting which anthropogenic underwater sounds pose the greatest threat to reproductive ecology.

In contrast to females, neither type I nor type II males appeared to be attracted to any of the hum-like acoustic stimuli. Capture rates did not differ between stimulus and silent traps in any experiment, suggesting that males do not use the hum to locate rivals or nesting sites. These findings, therefore, support the interpretation that the advertisement

hum functions primarily as a mate-attraction signal rather than a cue for males to locate nest sites. This result contrasts with a previous laboratory study in which 37.5% of type I males and 13.6% of type II males approached a speaker broadcasting a pure tone at the fundamental frequency.⁹ However, that study used a single speaker and did not include a silent control, raising the possibility that some males were simply investigating a speaker-shaped object. Additional work will be needed to resolve this discrepancy.

In 2021, the order of the three acoustic trapping experiments was not randomized because trials could only be conducted during spring tide weeks, and sufficient sample sizes were needed for each experimental condition. Most trials comparing diminished f_0 hum vs silent controls were conducted after the hum vs silent control experiments (see Table S2 in the [supplementary material](#)). However, two hum vs silent control trials were conducted between nights of the diminished f_0 hum vs silent control trials. On those nights, an average of six females were captured in the stimulus traps, compared with an average of one female per night during the three adjacent nights of diminished f_0 hum vs silent control trials (see Sec. 3 and Table S6 in the [supplementary material](#)). This pattern makes it unlikely that any ordering effect influenced our conclusion that reducing the level of the fundamental frequency decreases the attractiveness of the hum to females.

Both females and type I males exhibited decreases in SL and mass over the course of the breeding season. Because females arrive at the intertidal zone, spawn, and then immediately return to deeper waters,¹⁹ our results suggest that larger females mature earlier and migrate sooner to the rocky intertidal habitat, consistent with patterns reported in other fishes that migrate to specific spawning grounds.^{10,11} A similar pattern may occur in type I males, although we cannot rule out the possibility that arrival time to the intertidal zone is independent of body size. An alternative explanation for the observed seasonal decrease in size is that larger type I males secure nest sites earlier, whereas smaller males without nests are more likely to enter the traps later in the season. Further research is needed to distinguish between these possibilities. Interestingly, a similar decrease in male size over the breeding season has been reported at artificial nest sites in wild populations of the Lusitanian toadfish (*Halobatrachus didactylus*),²⁰ suggesting that this pattern may be common within the Batrachoididae.

Notably, trap performance (as measured by numbers of captured fish) improved substantially in the second season of testing, likely due to design modifications such as the addition of internal netting and trap doors. This improvement is reflected in the marked increase in female captures in the second season of testing [see Fig. 3(d) vs Figs. 3(a)–(c)]. Similarly, the occasional capture of type II males in the second season but not the first likely reflects improved trap efficiency, as these individuals are generally smaller than females and may previously have escaped more easily. While increased fish abundance cannot be ruled out, trap refinement, and the resulting reduction in escape rate provide the more parsimonious explanation.

Limitations of the speaker system can constrain the generation of intended acoustic stimuli.⁷ In the Clark Synthesis AQ339 speaker used in our experiments, unintended acoustic clipping produced sounds that differed slightly from those originally designed (see [supplementary material](#) for details). However, the stimuli were of sufficient quality to allow testing of our hypotheses effectively in field playback experiments (Fig. 1).

Overall, our results demonstrate that acoustic trapping experiments in the field can provide an effective method to study the reproductive ecology of the plainfin midshipman. While concurrent presentation of non-acoustic stimuli is required to elicit attraction behaviors in many fishes,²¹ attraction on the basis of sound alone (i.e., pure phonotaxis) has now been demonstrated in at least ten species, including two shark species, and species belonging to four different orders of ray-finned fishes.⁷ Evidence for phonotactic behavior in a diverse range of species suggests that our methodology could be more widely adapted to test hypotheses related to acoustic communication in fishes. Acoustic trapping might also be leveraged for more applied purposes, e.g., in selected fisheries contexts for targeted capture of commercially important species or invasive species control with limited bycatch. Further work is required to evaluate the effectiveness of acoustic attraction and trapping methods in these extended contexts.

Supplementary Material

See the [supplementary material](#) for the detailed experimental protocol, descriptions of the main components used in the experiments, the dates of the trials, trap count data for type I and type II males, correlations between the number of females captured and the number of males in the traps, power spectra of ambient sound conditions at the study site, and the code used to generate the acoustic stimuli and to plot the acoustic waveforms and power spectra.

Acknowledgments

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Author Declarations

Conflict of Interest

The authors have no conflicts to disclose.

Ethics Approval

The field experimental and animal handling protocol was approved by the University of Washington's Institutional Animal Care and Use Committee (protocol 4079-06).

Data Availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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