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Disruptive communication: stealth signaling in the toadfish

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ABSTRACT

Male oyster toadfish, *Opsanus tau*, produce long duration (250 to 650 ms) sexual advertisement calls or 'boatwhistles' during the breeding season. When males are in close proximity, the fishes alternate the production of boatwhistles with other males to avoid call overlap. However, males can also produce a number of different sounds, including a single, short duration pulse or 'grunt' (~100 ms). The vocalizations of competing males were recorded *in situ* with multiple hydrophones to examine intraspecific interactions. These short grunts were emitted almost exclusively during the boatwhistle of a conspecific male. The fundamental frequency (or pulse repetition rate) of the boatwhistles were modified by this disruptive grunt, 'jamming' the signal and decreasing its frequency. The disruptive grunt specifically targeted the second stage or tonal portion of the boatwhistle, believed to be the primary acoustic attractant for females, and its brevity and precision may allow its emitter to remain undetectable. While the acoustic repertoire of teleost fishes may be less diverse compared with terrestrial species, the disruptive grunts indicate fish have the capacity for complex acoustic interactions.

KEY WORDS: Acoustics, Intraspecific communication, Fish vocalization, Batrachoid

INTRODUCTION

Acoustic advertisement signals have evolved in many taxa and are best known among arthropods, anurans and birds. Patterns can range from intense signaling during daily or seasonal intervals to synchronous or alternating interactions with precisely timed vocalizations between neighboring individuals. In populations that alternate signals, males often adjust the timing of calls to avoid overlap, but as the density of callers increases, some overlap may be unavoidable (Greenfield, 1994). However, specific attempts at signal jamming, in which a conspecific sends an acoustic signal during the vocalizations of another signaler, especially using an acoustic signal that differs temporally and spectrally in fundamental frequency from the advertisement signal, appear to be rare.

Batrachoidid fishes (toadfish and midshipman) produce sounds through contractions of sexually dimorphic sonic muscles attached to the swimbladder, and are some of the best-studied vocal fishes (for reviews, see Bass and McKibben, 2003; Amorim, 2006). Acoustic communication plays a vital role in the natural history of the oyster toadfish, *Opsanus tau* (Linnaeus). At the start of the breeding season, male toadfish establish nests under hard substrate from which they produce advertisement boatwhistles (Fish, 1972; Gray and Winn, 1961; Gudger, 1910). Once attracted, females will

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attach eggs to the nest where the male fertilizes them. Males remain in the nest to guard the developing young until they are free-swimming, and may continue to attract additional females (Mensinger et al., 2003).

Only sexually mature male toadfish produce the advertisement boatwhistle, which consists of a brief irregular initial grunt followed by an extended period of regular pulsing (Edds-Walton et al., 2002). However, both male and female toadfish can produce shorter broadband grunts (Fish, 1954; Gray and Winn, 1961). Postulated to be agonistic in nature, toadfish grunts have been described as non-harmonic pulsed sounds that are produced by both males and females throughout the year (Fish, 1954; Gray and Winn, 1961; Winn, 1972). Many soniferous species produce several different types of agonistic sounds that may provide specific behavioral information (Ladich, 1997). Recent experiments have determined that *O. tau* can produce several types of grunts including single and double grunts as well as grunt trains. Spontaneous grunts are relatively rare, averaging less than 0.1 fish[−1] h^{−1} during the summer outside of the spawning season (Maruska and Mensinger, 2009). However, during the breeding season, grunt production by individual males can exceed 200 grunts fish[−1] h^{−1}, with the vast majority consisting of single, ~100 ms pulses emitted during a conspecific's boatwhistle. Previous investigations in the congener *Opsanus beta* (Gulf toadfish) characterized these grunts as 'acoustical tagging', but reported that predominantly one fish was responsible for the grunts, and reciprocal tagging was mostly absent. The grunts were also considered too short to mask or jam the boatwhistle (Thorson and Fine, 2002), and it was suggested *O. beta* avoids call overlap by making simpler and shorter calls (Fine and Thorson, 2008). Additionally, studies of chorusing behavior of the Lusitanian toadfish (*Halobatrachus didactylus*) did not report grunt generation during boatwhistle production (Jordão et al., 2012).

The present study, using multiple hydrophones, showed that grunts were emitted often by males during a congener's boatwhistle, and it was hypothesized that these grunts were emitted specifically to disrupt the fundamental frequency of the boatwhistle. The experiments examined the effect of these grunts on the boatwhistle to determine their potential in signal perception by female fish.

RESULTS

Several male toadfish quickly took up residence in the artificial shelters and began vocalizing with 48 h of placement. Two intense calling periods in late spring were selected for analysis, featuring two males (2006) that generated ~8000 calls and 4200 grunts over 12 h (sunset to 3 h post-sunrise), and three males (2004) that produced ~1600 calls and 500 grunts over 10 h (sunset to sunrise). Call production was typical of toadfish throughout the breeding season, with males alternating boatwhistles and less than 0.5% of calls showing temporal overlap. Vocalizations were detectable at all hydrophone locations (Fig. 1). The boatwhistles were characterized by an initial brief irregular grunt (phase I) followed by an extended
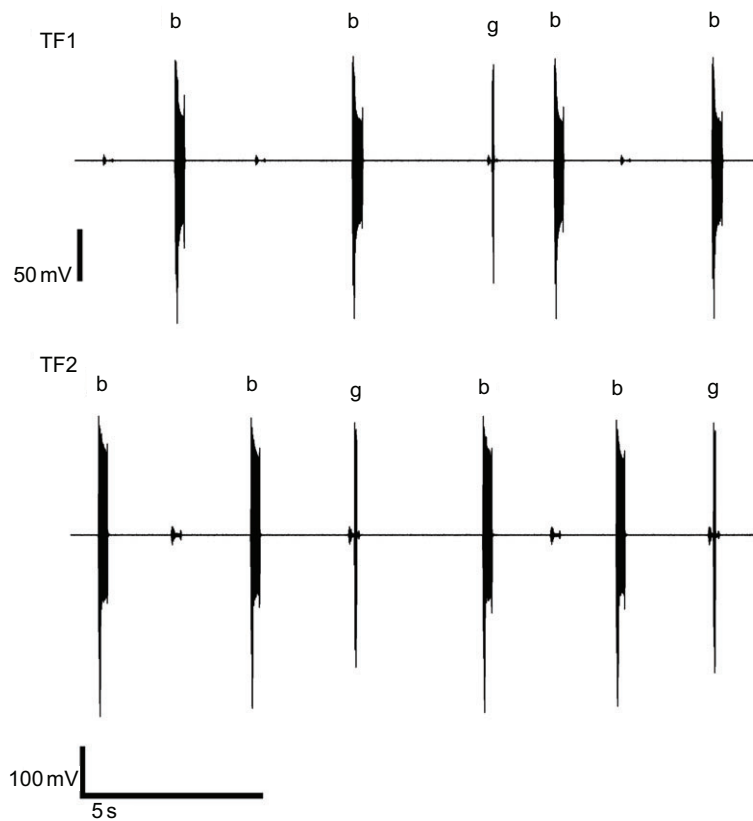
Fig. 1. Oscillograms of vocalizations from two different male toadfish (TF1 and TF2) from hydrophones placed near the entrance of each nest. The top (TF1) and bottom (TF2) traces display the amplitude from each hydrophone and were recorded simultaneously. Labels indicate boatwhistles (b) or grunts (g) produced by the toadfish identified in each trace. The small blips on each trace represent the arrival of the competitor's boatwhistle at the other toadfish's location.

period of regular pulsing (phase II). The average hourly duration of the boatwhistles ranged between 267 and 638 ms while grunts ranged between 78 and 116 ms (Fig. 1).

The fundamental frequency (FF) of phase II or the tonal portion of the boatwhistle was distinct for each toadfish, with the highest frequencies emitted at sunset and gradually decreasing as the pond cooled ~2 to 3°C throughout the night. The mean FF (per hour) of the boatwhistle ranged from 150 to 178 Hz in 2004 and 172 to 204 Hz in 2006, with the overall (entire calling period) average of the boatwhistles ranging from 155 to 170 Hz (2004) and 189 to 192 Hz (2006). Mean hourly call duration ranged between 267 and 638 ms and increased throughout the night, with individual overall averages (entire calling period) ranging from 332 to 467 ms (Table 1).

Although various types of grunts were emitted infrequently throughout the summer, grunts emitted by one male during the boatwhistle of another male were especially common during each spawning season (Fig. 1, Fig. 2F), and were characterized as disruptive grunts. For the toadfish pair analyzed in 2006, 38% of the calls from toadfish 1 (TF1; N=4592) and 51% from TF2 (N=3427) were disrupted by the other's grunt. In 2004, during the interactions of three toadfish (TF3, TF4 and TF5), 12 to 44% of an individual's

calls (N=110–931) were disrupted. Of the ~4700 grunts that were analyzed during the two calling periods in 2004 and 2006, 88% were generated and concluded during a detectable boatwhistle. The disruptive grunts ranged in median duration from 78 to 116 ms with FF ranging from 80 to 90 Hz, while grunts not emitted during a boatwhistle were significantly longer (Mann–Whitney, P=0.001), with median durations of 100 to 183 ms and significantly higher FF ranging from 110 to 130 Hz (Mann–Whitney, P<0.01).

The three hydrophones allowed triangulation of toadfish position, and calculation of the transit time required for the boatwhistles to reach other calling males. The toadfish remained in approximately the same position throughout the night, and the transit time for boatwhistles to reach other nests ranged from 3 to 8 ms. Although amplitude attenuated with distance, the spectral characteristics of the signal were maintained upon reaching the competitor's location (Fig. 3). In all cases, the grunt amplitude at its origin was greater than the arriving boatwhistle amplitude. The tonal, second stage of the boatwhistle comprised 70 to 80% (77.3±0.3%, N=251) of total call duration. The vast majority of disruptive grunts were initiated and terminated within the tonal portion of a boatwhistle.

Fig. 3 tracks a typical boatwhistle from its origin, through the center of the habitats, and to its competitor's nest. Although the

Table 1. Toadfish vocalizations

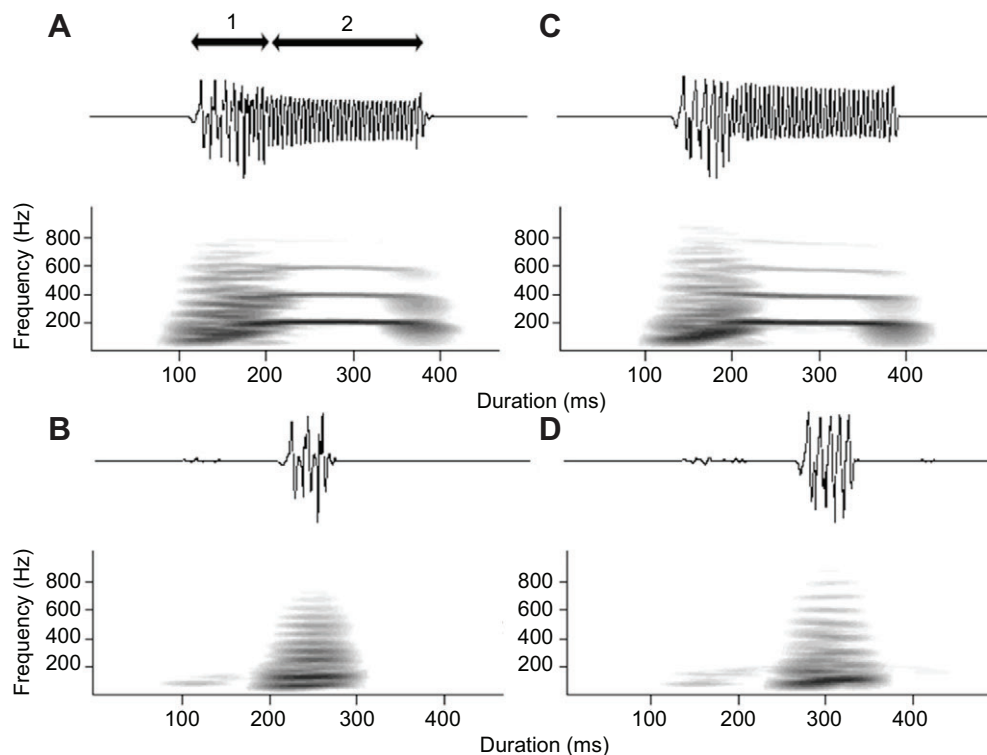| Toadfish	Boatwhistles h^{-1}	Boatwhistle duration (ms)	Boatwhistle fundamental frequency (Hz)
TF1	412.8±41.4 (32–596)	398.2 ±21.2 (351–638)	192.5±0.7 (172.3–198.7)
TF2	307.1±32.9 (30–406)	331.6±13.3 (267–324)	189.0±0.2 (168.2–203.9)
TF3	79.3±19.8 (14–166)	385.3± 6.8 (385–415)	155.2±0.1 (149.7–163.1)
TF4	116.3±26.3 (20–312)	403.0±7.2 (359–435)	158.2±0.1 (151.8–162.9)
TF5	23.5±9.2 (3–78)	467.0±6.7 (434–492)	169.7±0.6 (161.3–177.5)

Data are means ± 1 s.e. (range).

Fig. 2. Oscillograms (top) and sonograms (bottom) of representative vocalizations from two different male toadfish (TF1 and TF2), illustrating the temporal and frequency difference between males. All sounds were recorded at the nest of the vocalizing male. (A) TF1 boatwhistle. Arrow 1 indicates the first part of the boatwhistle and arrow 2 the second, tonal segment. (B) Disruptive grunt of TF1 emitted during TF2 boatwhistle. (C) TF2 boatwhistle. (D) Disruptive grunt of TF2 emitted during TF1 boatwhistle.

boatwhistle amplitude was attenuated as it traveled from its origin, the FF (185 Hz) was maintained between nests (Fig. 3A–C). The effect of a competitor's grunt on the boatwhistle is illustrated in Fig. 3D,F, with the disruptive grunt dominating the acoustic spectrum both at its origin and at the midpoint between the two nests where the female would presumptively be located, lowering the dominant frequency to 88 Hz. Examination of boatwhistles that had an embedded disruptive grunt demonstrated that the FF of the tonal portion of the call was significantly altered (Mann–Whitney rank sum test, P=0.002; Fig. 3E).

The median delay between the boatwhistle arriving at the competitor's nest and grunt initiation varied between 130 and 180 ms. Fig. 4 shows the timing of grunt initiation relative to the boatwhistle phase. As the boatwhistle durations fluctuated throughout the night, the initiation of the grunt also changed. However, the grunts were consistently initiated during the early phase II of the boatwhistle, indicating that the disrupting male was responsive to the call components and was not emitting the grunt reflexively (linear regression, P=0.004; Fig. 5).

DISCUSSION

The pond used in the experiment provided a quasi-natural environment to monitor male toadfish interactions. The males initiated vocalizations very quickly after being transported to the pond, and call parameters closely resembled field observations (Edds-Walton et al., 2002). Although females were not present during the calling periods reported in this study, several gravid females were added in early June each year and at least three males per year successfully spawned. Thus the toadfish adapted quickly to the pond and exhibited natural behavior.

As most of the vocalizations transpired during the night, it was not possible to visually confirm the position of the fish throughout the calling periods. However, the same habitats were occupied the afternoon preceding and the morning following the experiments.

Additionally, amplitude and frequency of the calls remained consistent over the course of the night, with only gradual changes observed because of decreased temperatures. Furthermore, approximately every 10 min, fish position was determined by triangulation of the time differential for sound arrival at the three hydrophones. Based on this evidence, there is a high probability that the recordings were from the same fish that remained in the same position throughout the course of the calling period.

The present study showed that short grunts of specific frequency and duration were emitted almost exclusively during the boatwhistle of a conspecific male. The fundamental frequency of the boatwhistle was modified by this disruptive grunt, 'jamming' the signal and decreasing the frequency. The disruptive counterpulse specifically targeted the tonal portion of the boatwhistle, and its brevity and precision may allow its emitter to remain undetectable.

The main end organ for hearing in teleost fishes is the saccule, and primary saccular afferents in the toadfish are broadly tuned with best frequencies below 150 Hz and can be placed into two groups with respect to characteristic frequency: 74 to 88 Hz and 140 Hz (Edds-Walton et al., 1999; Fay and Edds-Walton, 1997). Thus toadfish have the capacity to detect the low frequency grunts (80 to 90 Hz) and higher frequency boatwhistles (range 150 to 204 Hz), and have the auditory sensitivity to discriminate between disrupted and nondisrupted calls.

Jamming of a conspecific's acoustic signal requires detection, integration, response and disruption of an active vocalization. Furthermore, stealth signaling requires that the disruptive signal be initiated and completed prior to the cessation of the original call. Toadfish calls can vary between region and season, with fundamental frequencies often peaking and call duration decreasing in mid-summer (Fine, 1978; Fine et al., 1977). As toadfish calls in the Cape Cod population rarely exceeded 500 ms, a finite window existed for the jammer to detect and respond to the call, especially if the goal was to initiate and complete the grunt before the tonal
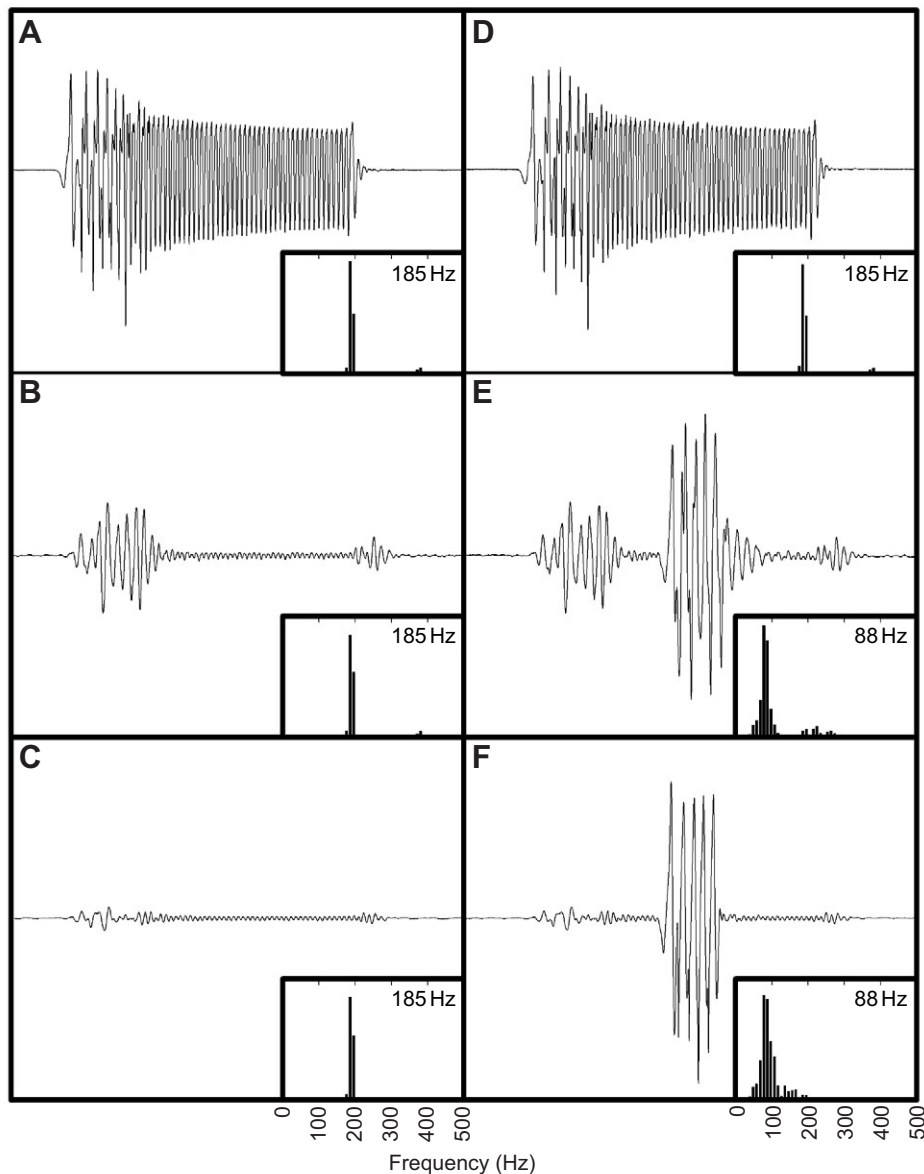
Fig. 3. Reciprocal calling and disruptive grunts. Each panel shows an oscillogram of toadfish vocalizations, with the insets containing a fast Fourier transform (Hamming window) of each vocalization with the dominant frequency indicated inside each box. (A–C) A toadfish boatwhistle from three hydrophone locations (see Fig. 6) as it travels across the circle of habitats. (A) Toadfish 1 (TF1) boatwhistle recorded from hydrophone A (HA) located near TF1 habitat; (B) TF1 boatwhistle recorded from hydrophone B (HB) positioned in the center of the toadfish habitats; (C) TF1 boatwhistle record from hydrophone C (HC) located near TF2 habitat. (D–F) The convergence of a TF1 boatwhistle and a subsequent TF2 disruptive grunt. (D) TF1 boatwhistle at HA; (E) TF2 grunt and TF1 boatwhistle at HB; (F) TF2 disruptive grunt recorded at HC near TF2 habitat.

portion of the call ceased. In the case of a 400 ms boatwhistle (divided into a 75 ms phase I and a 325 ms phase II) and 100 ms grunt, the jammer had less than 300 ms to detect the boatwhistle and initiate and complete the grunt. However, as grunts were initiated 100 to 200 ms following detection, the time required to make a decision to disrupt a congeneric grunt was probably much quicker. The grunt appeared to be deliberate and not reflexive, as grunt delays increased with longer boatwhistles, and there was considerable variability in grunt delays during the course of the evening. The delay was not an intrinsic property of sonic muscle as toadfish inter-grunt intervals range as low as 50 ms, and the half-widths of twitch tension for toadfish sonic muscle are less than 10 ms (Rome et al., 1996), indicating that toadfish have the capacity for quicker responses. Rather, the grunts appeared to be a deliberate mechanism to target the tonal portion of the boatwhistle of conspecifics.

Although male toadfish have the capability of producing long duration grunts (~250 ms), doublet grunts and grunt trains (Maruska and Mensinger, 2009), only single, short grunts were generated during boatwhistles. The duration of the disruptive grunts indicates that these sounds may have evolved to allow the disrupter to jam the call and remain undetected. It is unlikely that the caller could detect grunts during boatwhistle production as the amplitude of the caller's boatwhistle was consistently greater than grunt amplitude at the caller's nest, and spectral analysis was unable to detect any change in the FF of the boatwhistle at its origin. While it is possible that the toadfish has an adaptive filter or mechanism to cancel self-generated noise (Montgomery and Bodznick, 1994), efferent activation by the vocal motor system, as found in the plainfin midshipman (*Porichthys notatus*), could modulate auditory sensitivity to self-generated sounds and maintain sensitivity to ongoing external sounds (Weeg et al., 2005) and may also prevent toadfish from detecting other sounds during the call. Reverberations and echoes of the boatwhistle within the nest would further complicate noise filtering. Additionally, there was no change in calling rate in response to the grunts, suggesting that the calling males were unaware of the jamming.

Toadfish male calling can be mediated by sound playback experiments (Fish, 1954; Fish, 1972; Jordão et al., 2012), and free-swimming female oyster toadfish will swim towards boatwhistles
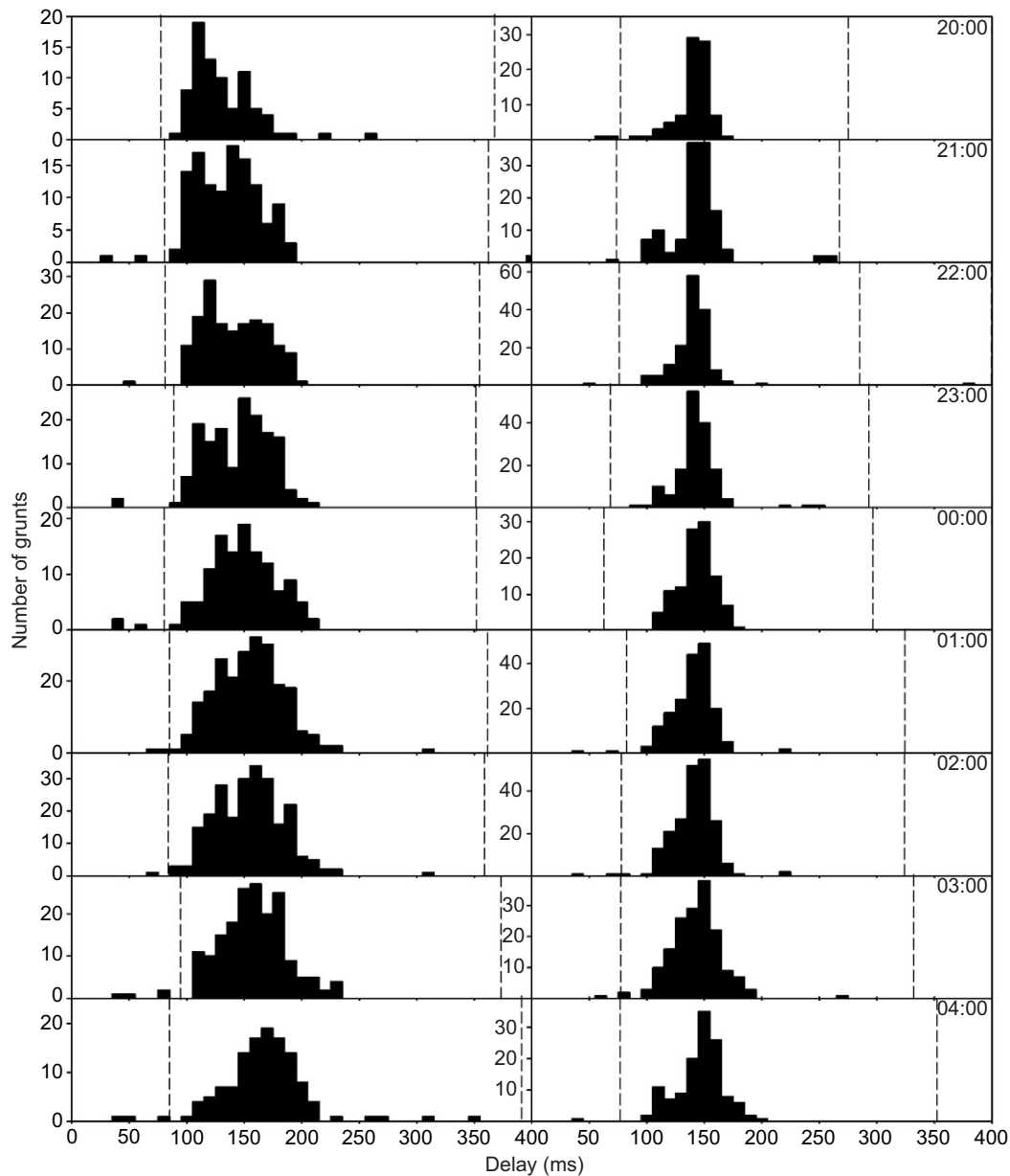
Fig. 4. Plots of the number of disruptive grunts versus the time (ms) for the grunting toadfish to respond to the arrival of a boatwhistle for two reciprocally calling male toadfish (TF1, left; TF2, right). Each panel represents a 1 h period, with the time of day indicated in the upper right. Time 0 represents the arrival of the boatwhistle at the other male's nest. The dashed vertical lines represent the median time of initiation and termination of the tonal segment of the other male's call during each hour. Grunt number is binned in 10 ms increments.

(Fish, 1972) with the tonal part of the call the main determinant for female choice (Edds-Walton et al., 2002). Therefore, any jamming or disruptive signals should target this portion of the boatwhistle. In the current experiment, the middle hydrophone, situated between reciprocally calling males, served to record the signal a prospective female toadfish would encounter. Examination of disrupted calls (i.e. calls with an embedded grunt) demonstrated that the FF of the tonal portion of the call was decreased significantly. In the midshipman, females preferred vocalizations that were consistent with the expected frequency for ambient water temperature (Brantley and Bass, 1994). Because the boatwhistle and grunt temporally converged on the middle hydrophone, the embedded grunts lowered the median FF of the boatwhistle, presumably rendering the call less attractive to the female. A

previous study has shown that altering the FF of the boatwhistle frequencies and/or changing call duration altered toadfish behavior (Winn, 1972).

As low frequency sound can be rapidly attenuated in shallow water with soft sediment, the question remains, what is the distance at which female fish can detect boatwhistles? Male toadfish often nest in high densities (up to 10 to 12 m²) in estuaries near Woods Hole, MA, and produce loud [~140 dB re. 1 μPa (Tavalga, 1971)] boatwhistles with FFs ranging between 90 and 250 Hz depending on season and geographical location (Fine, 1978). Calls can propagate at least several meters underwater with distance influenced by toadfish size, water depth and substrate composition (Fine and Lenhardt, 1983). In the present study, calls were detected by hydrophones up to 5 m from toadfish nests,
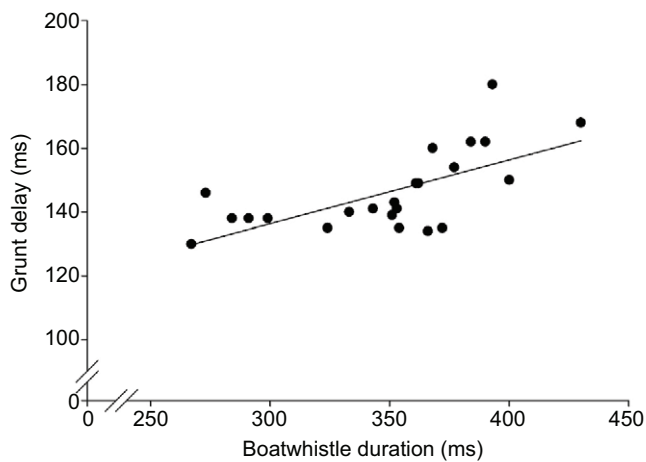
Fig. 5. Disruptive grunt delay as a function of boatwhistle duration. Time (ms) for grunting toadfish to respond to a boatwhistle is plotted versus the median hourly duration of the boatwhistle for reciprocally calling males. Each point represents the median hourly boatwhistle duration and grunt delay for a male. The data were collected from sunset through 11 consecutive hourly intervals. The line represents a linear regression through the data with the equation $y=76.41+0.1998x$, $r^2=0.44$, $P=0.002$.

although it remains to be determined at what range the females can detect the signal or what aspect of the signal influences mate choice.

Although male toadfish have the capability of producing long duration grunts (~250 ms), doublet grunts and grunt trains (Maruska and Mensinger, 2009), only single, short grunts were generated during spawning, and these were primarily in response to conspecific boatwhistles. The function of brief, stand-alone acoustic pulses in fish has remained unclear. The present study shows that toadfish have evolved a highly specialized signaling component for jamming the signals of conspecific males. Although vocal communication in fish has been characterized as limited and less diverse than in terrestrial animals (Amorim, 2006), oyster toadfish have the capacity for complex intraspecific vocal interactions.

MATERIALS AND METHODS

Recently captured toadfish from local Cape Cod collectors were obtained from the Marine Resources Center of the Marine Biological Laboratory,

Woods Hole, MA. Sexually mature male toadfish [N=6 (2004); N=10 (2006)] between 25 and 30 cm in standard length were transported to a 400 m^2×1 m (depth) artificial pond on the Quissett Campus of the Woods Hole Oceanographic Institute, Woods Hole, MA, in late May. A 4 mm thick pond liner was placed along the bottom and sides of the pond. The pond bottom was relatively flat; however, on three sides, the sides sloped steeply upward near the edge. The fourth side of the pond terminated into a vertical wall with a boardwalk that ran the length of this side and allowed observation of the fish. The pond was devoid of any structure that could be used for habitat except for a center pole anchored in concrete that provided support for the overhead netting that protected the toadfish from avian predation. The pool was continuously provided with salt water at ambient temperature (15 to 20°C) during the experiments.

Artificial brick habitats were constructed of six bricks measuring 23.0×11.0×7.6 cm. Two bricks were placed on top of each other and placed parallel with another pair, with ~25 cm between the two stacks. Two additional bricks were placed at the back of the habitat to encourage the toadfish to face towards the front of the other habitats while still allowing water flow through the habitat. A 30×8 cm concrete slab was added to the top of the brick to serve as the habitat roof. Twelve brick habitats were added to the pond and arranged in a 2 m diameter circle, adjacent to the boardwalk side (Fig. 6). Thawed squid or baitfish was provided as food three times per week. All experiments conformed to institutional animal care protocols.

Three hydrophones (model TC4013, Teledyne Reson, Slangerup, Denmark; sensitivity −211 dB re. 1 V/µPa, frequency response 1 Hz to 170 kHz) were arrayed linearly, bisecting the circle, with two hydrophones placed peripherally, near the habitats, and the remaining hydrophone placed in the middle of the circle. Toadfish vocalizations were recorded continuously from sunset through sunrise from late May through mid-July with intermittent recordings conducted during the daytime hours. Two different groups of toadfish were monitored in 2004 and 2006.

Hydrophone output was amplified by a WPI amplifier (Sarasota, FL, USA) and recorded with an ADInstruments data acquisition system (Colorado Springs, CO, USA). Data were analyzed offline using Chart5 for Windows (ADInstruments) or Avisoft (Berlin, Germany) software. As most of the vocalizations transpired during the night, it was not possible to visually confirm the position of the fish throughout the calling periods. However, to ensure that the same fish were monitored throughout the experiment, call amplitudes and frequencies were analyzed continually. Furthermore, approximately every 10 min, the time differential in which the sound was detected by the three hydrophones was analyzed and the fish position was triangulated.

The duration, FF and calling interval of vocalizations were analyzed and frequency components were calculated with a 1024-point fast Fourier transform (Hamming window). Only the frequency of the second, tonal
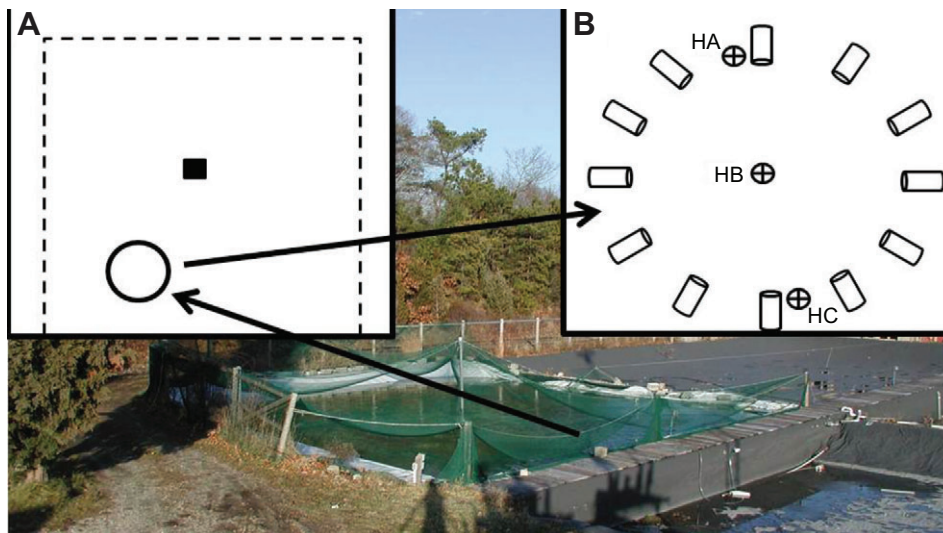

Fig. 6. Side view of outdoor pond housing the toadfish. The large net was draped over the pond to prevent avian predation. (A) Overview of the toadfish pond with the dashed line indicating the 1 m depth line. The solid square indicates base of support pole and the circle indicates the location of the habitats. (B) The 12 brick habitats were arrayed in a 2 m diameter circle. The crosshair symbols indicate approximate hydrophone (HA, HB and HC) location. Not to scale.

portion of the boatwhistle was calculated. All statistical analysis was performed with SigmaStat software (version 3.5, Systat Software, San Jose, CA, USA) and data were assessed with Kolmogorov–Smirnov normality tests. Non-parametric Mann–Whitney rank sum tests were used for data that failed the normality tests. The frequency of the boatwhistles and grunts gradually changed with decreasing water temperature throughout the night. Therefore, call duration and frequency were averaged in 1 h increments and mean hourly values were calculated for each fish. All data are reported as means ± 1 s.e. unless otherwise indicated.

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