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Acoustic competition in the gulf toadfish Opsanus beta: Acoustic tagging

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Acoustic competition in the gulf toadfish *Opsanus beta*: Acoustic tagging

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Nesting male gulf toadfish *Opsanus beta* produce a boatwhistle advertisement call used in male–male competition and to attract females and an agonistic grunt call. The grunt is a short-duration pulsatile call, and the boatwhistle is a complex call typically consisting of zero to three introductory grunts, a long tonal boop note, and zero to three shorter boops. The beginning of the boop note is also gruntlike. Anomalous boatwhistles contain a short-duration grunt embedded in the tonal portion of the boop or between an introductory grunt and the boop. Embedded grunts have sound-pressure levels and frequency spectra that correspond with those of recognized neighbors, suggesting that one fish is grunting during another's call, a phenomenon here termed acoustic tagging. Snaps of nearby pistol shrimp may also be tagged, and chains of tags involving more than two fish occur. The stimulus to tag is a relatively intense sound with a rapid rise time, and tags are generally produced within 100 ms of a trigger stimulus. Time between the trigger and the tag decreases with increased trigger amplitude. Tagging is distinct from increased calling in response to natural calls or stimulatory playbacks since calls rarely overlap other calls or playbacks. Tagging is not generally reciprocal between fish, suggesting parallels to dominance displays. © *2002 Acoustical Society of America.* [DOI: 10.1121/1.1466865]

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I. INTRODUCTION

Toadfish produce sounds by contracting extremely fast muscles on the sides of a heart-shaped swimbladder.[1–3] As originally shown by Skoglund,[3] the muscle contraction rate generates the fundamental frequency of their sounds. Toadfish of both sexes in the subfamily *Batrachoidinae* produce short pulsatile grunts in agonistic situations,[4–7] and nesting males produce a long-tonal boatwhistle advertisement call[6,8,9] that functions in male–male competition and in female choice.[5,10–12] Males increase their calling rate in response to calls or playbacks of nearby males,[10–12] and females have been attracted to playbacks in pen tests.[12] The boatwhistle begins with a gruntlike component before exhibiting a clear fundamental frequency with harmonics. *Opsanus tau* and *Haplobatrachus didactylus* produce a boatwhistle of a single note,[8,9] but the gulf toadfish *Opsanus beta* produces a more complex call.[6,13] Its boatwhistle [Fig. 3(a)] includes from zero to three introductory grunt pulses followed by a long tonal boop note and up to three shorter boops.[13] Males call occasionally and irregularly during the day and increase their calling rates around sunset.[13,14] Calling males remain in nests for extended periods,[5,12] which has allowed us to separate the calls of individual fish by their sound parameters.[13]

Fine[15] recorded anomalous boatwhistles of *Opsanus tau* that contained a grunt embedded within the tonal portion of the call. We examined this phenomenon in the gulf toadfish *Opsanus beta* living in a canal in the Florida Keys and present evidence that it is caused by a second fish grunting during the call, i.e., acoustic tagging.

II. METHODS

Boatwhistles were recorded from a hydrophone installation placed on the bottom of a bayside canal at Plantation Key, Islamorada, FL. We listened to over 300 hours of underwater sound in 2000 (sounds were heard from January 9 to April 4) and over 200 hours in 2001 (28 December 2000 to 4 May 2001). Most attention was devoted to the crepuscular period, when calling rate increases, although recordings were made at various times. We present detailed data (quantification of all grunts and boatwhistles) from a typical 2-h twilight recording from 12 March 2000. Additional qualitative and quantitative observations from other recordings indicate these results are typical until near the end of the mating season (see Sec. III).

The hydrophone was at approximately 3 m depth and about 3 m from the sea wall. The canal is about 26 m wide and 230 m long and leads out to Florida Bay. The sea wall is made of coquina block and extends down about 2 m. The bottom of the canal is coral covered by silt and vegetation. The hydrophone installation remained fixed in the water during the course of the study. Since *Opsanus tau* boatwhistles attenuate rapidly with distance in shallow water,[16] we tested the hypothesis that acoustic interactions and tagging are restricted to nearby fish by making several additional stereo recordings utilizing a second hydrophone positioned along the sea wall 4 m to the left of the first one. Although two hydrophones are insufficient to localize a position, marked changes in level between the two channels would suggest that it is unlikely for fish to communicate over long distances.

The ceramic piezoelectric hydrophone and ac amplifier (designed and constructed by Robert F. Thorson) were battery powered and built with low-noise components. The

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sounds were transmitted to a receiver via a Wavecom Sr, 2.4-GHz microwave transmission link, demodulated, and then stored digitally on the hard disk of a CTX FC3A300 computer and archived on CD. The hydrophone and amplifier were sensitive from 14 Hz (3-dB down point) to nearly 20 kHz. Most energy in toadfish calls is below 1 KHz,[9] and *Opsanus tau* hears to about 800 Hz.[17]

Boatwhistles were analyzed using a sampling rate of 11 020 Hz with SPECTRA-PLUS PROFESSIONAL version 4.0 software on the CTX FC3A300 computer. Because fish were of unknown distance from the hydrophone, sound-pressure levels were determined in dB relative to full scale on the monitor, and frequency spectra were determined using a 1024-point fast Fourier transform with a Hanning window.

As in previous work,[13] we identified boatwhistles of individual callers by a combination of their signal level, frequency spectra boop number, and duration. Grunts were also sufficiently stereotyped that we attempted to separate individuals similarly by a combination of frequency and amplitude on their frequency spectra (Figs. 1 and 2). For this analysis we obtained one representative frequency spectrum for each of the four fish weekly for 9 weeks. Since fish 4 did not call for 2 of these weeks, it was represented with seven spectra. Amplitude values were obtained from each spectrum at 50-Hz intervals and averaged for each fish. Data were analyzed with a two-way analysis of variance (ANOVA) with frequency and fish number as the two factors. Grunts were also separated into clusters by plotting the peak frequency against the amplitude at that frequency.

For analysis of tagging, each grunt was individually identified as coming from one of four nearby fish by determining its frequency spectrum and comparing it with representative templates from the individual fish. Latencies to tag, i.e., time from a sound (grunt or gruntlike portion of a boatwhistle) to grunt tag were measured in milliseconds using the oscilloscope display in the analysis software. In cases with multiple potential tag triggers (i.e., two separate grunts before a boatwhistle and the beginning gruntlike portion of the boatwhistle), we considered any tag occurring later than the shortest tag latency recorded from that fish to be triggered by that sound (see Sec. III for further clarification).

In order to demonstrate that tags are in fact triggered by an acoustic stimulus rather than being a random occurrence, we examined every grunt produced by fish 1 during the 2-h recording on 12 March 2000 and measured the time from the preceding stimulus that could have triggered the grunt. This interval could potentially vary from a small number of milliseconds to many seconds or even minutes. A histogram of this data (equivalent to a time-interval histogram in neurophysiology) will indicate whether grunts occur randomly in time or are tied to a specific stimulus.

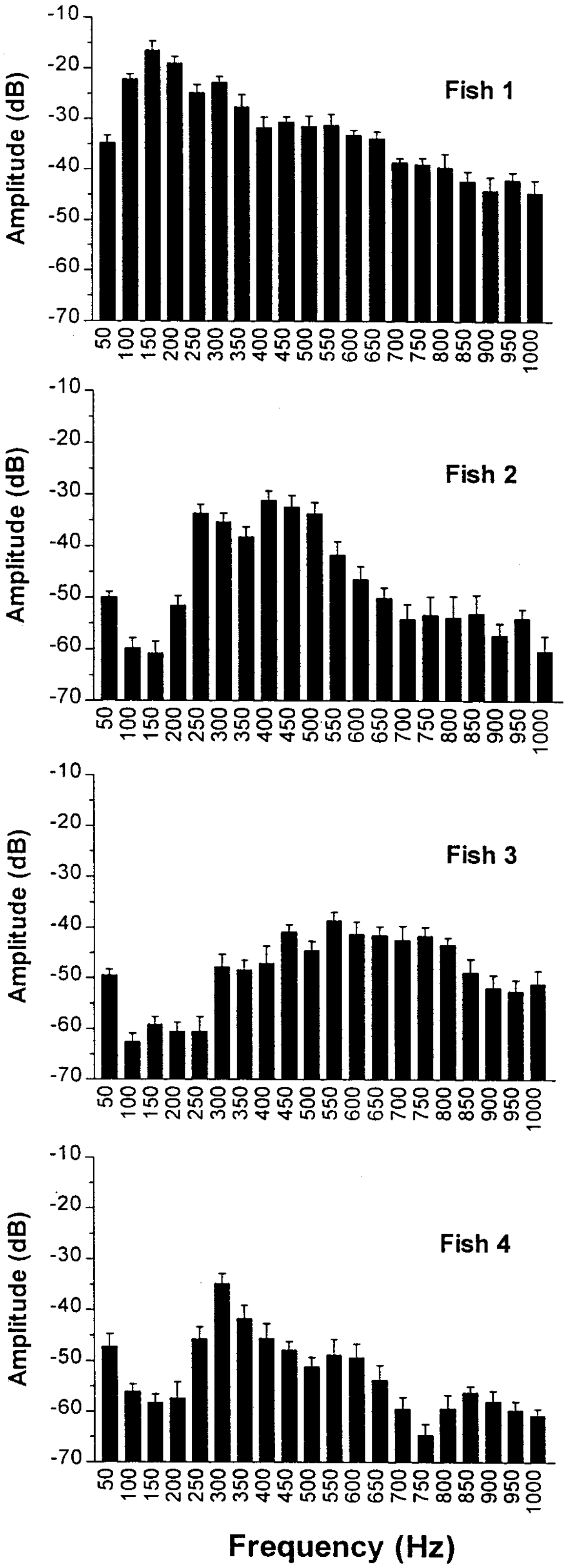

FIG. 1. Mean amplitude ± s.d. at 50-Hz intervals determined from frequency spectra of individual grunts obtained weekly over the course of 9 weeks for fish 1–4. $N=7$ for fish 4 who did not call during two of the recordings. Spectra were determined with a 1024-point fast Fourier transform and a Hanning window.

III. RESULTS

A. Individual identification

Four fish (fish 1–4) remained close enough to the hydrophone to be recognized repeatedly. Grunt frequency spectra are relatively stable for weeks, and differences in sound amplitude with frequency vary among fish and support separations based on boatwhistle parameters (Figs. 1 and 2). Comparison of the frequency spectra by fish number and frequency with two-way ANOVA is highly significant. There is a significant interaction accounting for approximately

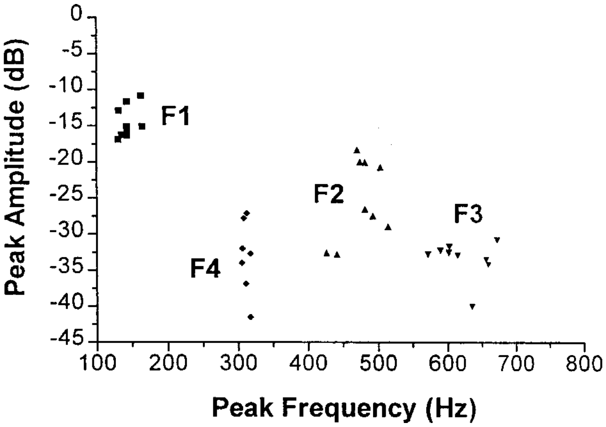

FIG. 2. Plot of peak amplitude in dB against the frequency of peak amplitude for individual grunt spectra of all four fish (separate symbols). Data points represent a single grunt per week recorded on 9 separate weeks. $N=7$ for fish 4 who did not call during two of the recordings.

22.85% of the variance ($F_{57,600}=10.62, p<0.0001$). Because of the interaction, row and column effects are difficult to interpret and will be given here as approximations. Frequency accounts for approximately 18.45% of the total variance ($F_{19,600}=25.72, p<0.0001$), and fish number accounts for 36.06% of the variance ($F_{3,600}=318.42, p<0.0001$), the largest of the three factors. For our current purposes it is unnecessary to compare the amplitude values for the four fish individually at each of the 20 frequencies, but it is clear that there are major differences in the frequency spectra among these individuals. Likewise, plots of the peak dB level against frequency separate the four fish into clusters with no overlap in peak frequency (Fig. 2). Although there is no independent confirmation of fish identity in field recordings, our separation of individuals is reasonable and parsimonious.

B. Tagging

We recognize tagging in about a third of the boatwhistles emitted during the crepuscular period during the two winter–spring seasons. Tagging is absent (2000) or rare (2001) during daylight hours. Note that the tag by fish 1 of fish 2 [Figs. 3(b) and (c)] has both lower frequency components (sonogram) and greater amplitude (oscillogram) than the grunt or the gruntlike beginning of the boatwhistle of fish 2. Fish also tagged snaps of snapping shrimp (Fig. 4), and both snaps and toadfish calls could set off chains of multiple tagging [Fig. 4(c)]. During the recording session, fish 1 tagged boatwhistles of all the other fish (132 tags), concentrated on fish 2 (128 tags), and shrimp (42 tags), but was tagged itself only twice. Fish 2 tagged 251 times and was tagged 149 times. Fish 3 and 4 tagged 20 and 3 times, respectively, and were tagged 234 and 18 times. The number of boatwhistles produced by fish 1–4 is relatively similar (235, 372, 282, and 197, respectively), but the number of untagged calls is higher in fish 1 and 2 (233 and 220) than in fish 3 and 4 (48 and 179). The percentage of tagged calls for the four is 0.9%, 41%, 83%, and 9%, respectively. Fish 4 produced only three tags, but it was tagged only 18 times. The smaller number of tagging interactions involving fish 4 may relate to its location at a greater distance from the other fish, as suggested by the lower amplitude level evident in its frequency spectrum (Fig. 1). In early April 2001, toward the end of the mating season, three of the fish appeared to move from their original territories, causing their sound levels to change. Fish 1 ceased spontaneous calling on 24 April but continued to tag occasionally. At this time we encountered incidents of reciprocal tagging.

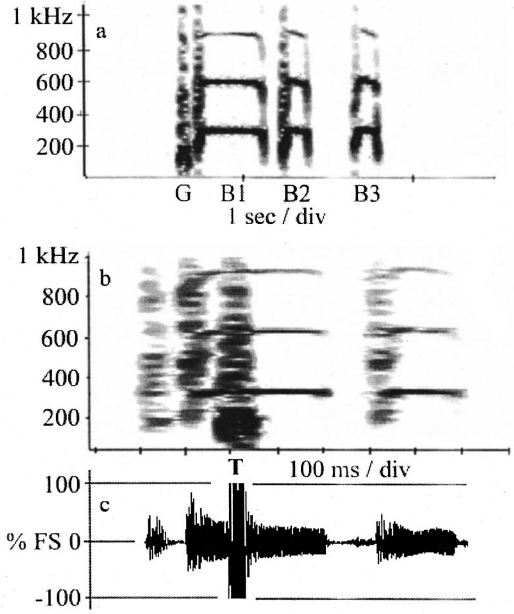

FIG. 3. Sounds of *Opsanus beta*. (a) Typical boatwhistle advertisement call with an initial grunt (G); a long tonal boop (B1) and two shorter boops (B2 and 3). (b) Sonogram and (c) Oscillogram of a boatwhistle produced by fish 2 that was tagged by fish 1. The T marks the tag, which has a greater amplitude and lower frequency energy than the call of fish 2.

The decision to tag is made rapidly (Fig. 5). Latencies

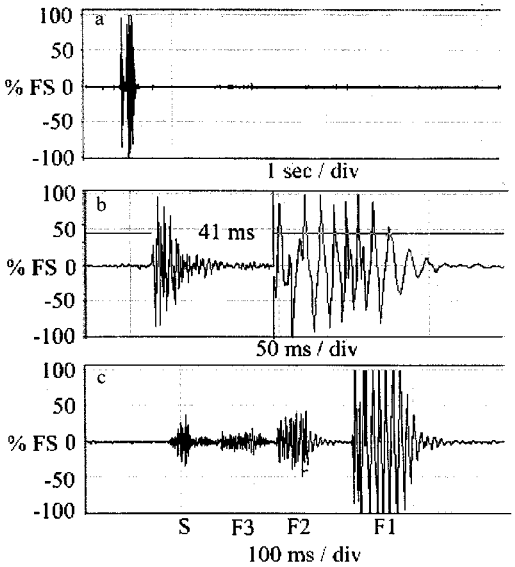

FIG. 4. Tags of shrimp snaps. (a) Oscillogram of a pistol shrimp snap tagged by fish 1 with a latency of 41 ms shown in real time. (b) Same selection expanded. (c) Chain of tags initiated by a shrimp snap that is tagged by fish 3. The fish 3 tag is then tagged by fish 2, who in turn is tagged by fish 1.

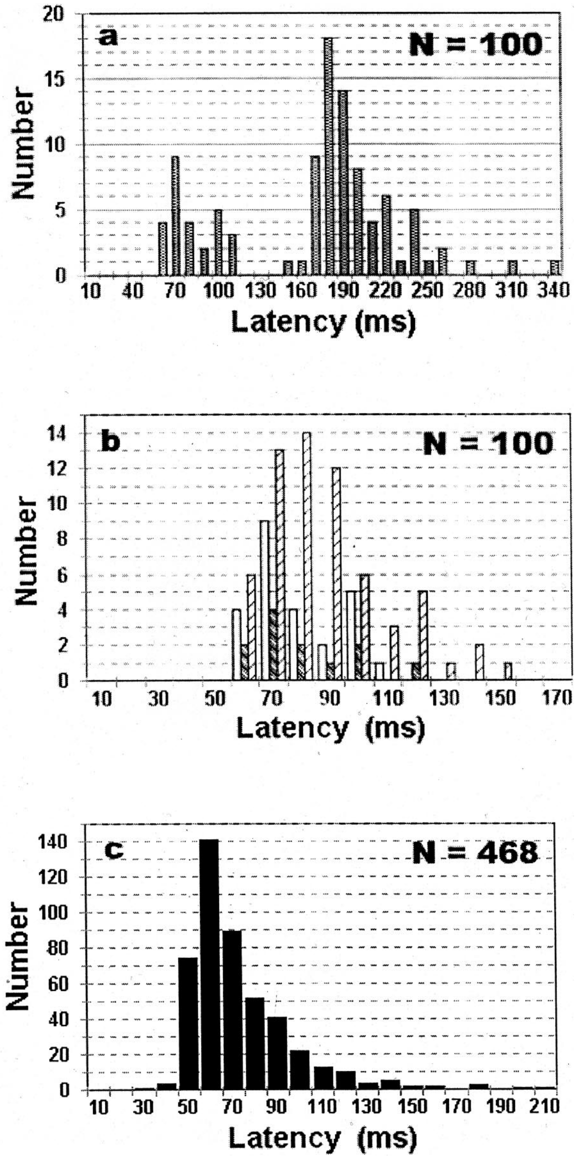

FIG. 5. Histogram of tag latencies on 12 March 2000. (a) Latency of fish 1 tags of fish 2 boatwhistles. (b) Latency of fish 1 tags after correction for triggering on grunt 1, grunt 2, or the initial gruntlike portion of the first boop. (c) Latency of all tags from the four fish after correcting for timing of trigger stimulus.

from the recording are as short as 41 ms for a pistol shrimp snap, which has a faster rise time than a toadfish grunt, and 53 ms for a grunt tagged by fish 1. Longest latencies are approximately a third of a second. The latency histogram of fish 1 tagging fish 2 is bimodal, with the first peak between 53–110 ms and a pause of over 43 ms before the start of the second mode [Fig. 5(a)]. Fish 2 sometimes produced two grunts before the gruntlike beginning of the boop. Using these three events as possible triggers, we estimate the latency by counting any tag occurring ⩾53 ms (the latency of the shortest tagged grunt) as evoked by that trigger. With this correction almost all tags occur within the first time mode [Fig. 5(b)]. There are 25 tags after the first grunt, 12 after the second, and 63 after the gruntlike beginning of the boop. Similarly, earliest latencies to tag shrimp snaps and calls of other fish, respectively, are 43 and 44 ms for fish 2. 48 and 64 ms for fish 3, and 56 ms for fish 4 to tag a grunt (it did not tag shrimp snaps in this recording). After correcting for the trigger, latencies from all fish are similar, and average 68.7 ±23.7 ms (s.d.) [Fig. 5(c)].

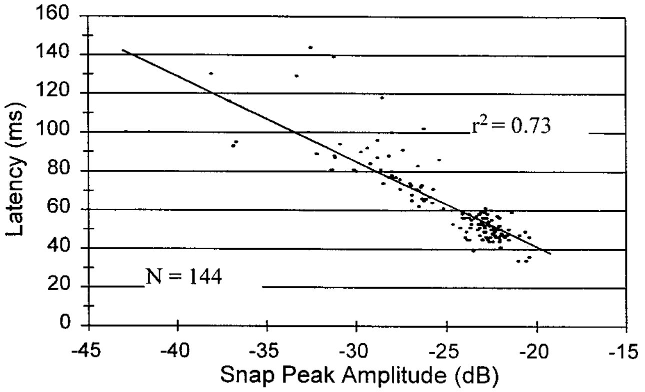

FIG. 6. Relationship of latency to peak amplitude for 144 shrimp snaps tagged by fish 1 on 21 March 2000. The regression equation is latency $=-46.13-4.36$ dB.

The trigger to tag is a relatively intense sound with a rapid rise time, a feature shared by toadfish grunts and shrimp snaps. Toadfish tend to tag more snaps when there are few boatwhistles (i.e., early in the crepuscular period before the toadfish increase their calling rate or on days with little calling). From a session with few calls (21 March 2000), we measured latencies of fish 1 to tag 144 shrimp snaps (Fig. 6). Snap amplitudes vary by over 20 dB, suggesting shrimp are in different positions relative to the hydrophone and therefore the focal fish. There is a linear relationship ($r^2=0.73$) between latency and amplitude so that latencies range from 34 to 144 ms for snaps ranging from −21 to −43 dB). Residuals from the regression line increase for weaker snaps, likely because the hydrophone was not immediately next to the fish.

Measurement of the intervals between each grunt produced by fish 1 and the preceding sound (i.e., potential trigger) in the 2-h recording indicate that tags occur immediately after a trigger stimulus and not randomly in time (Fig. 7). Of 178 grunts, 168 occur within 150 ms of a toadfish sound or a shrimp snap. Time intervals vary between 32 and 1630 ms, and the median interval is 73 ms. With 178 grunts in 2 h and

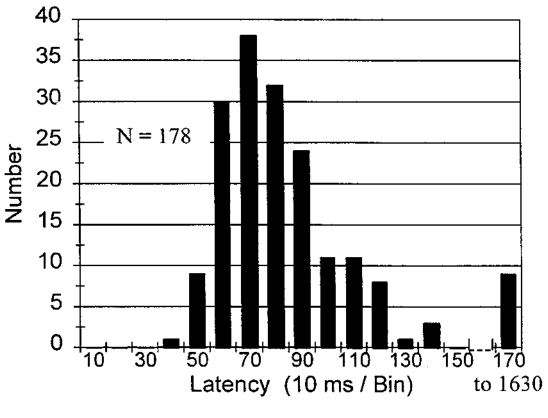

FIG. 7. Histogram of intervals between the preceding sound (grunt or snap) and all 178 grunts produced by fish 1 in 2-h recording on 12 March 2000.

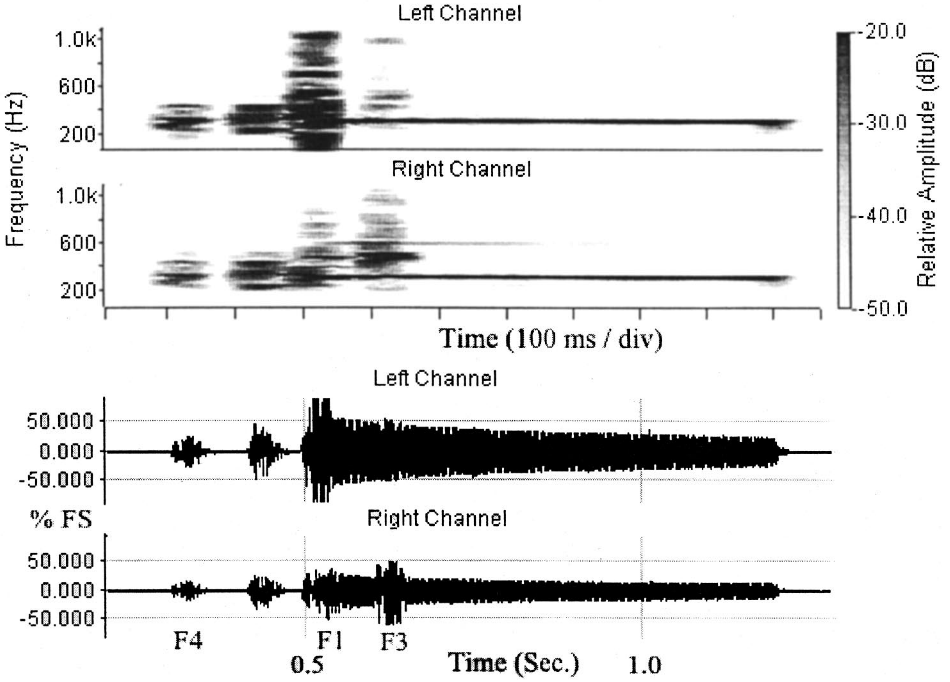

FIG. 8. Sonographs and oscillographs of two channel recordings (hydrophones 4 m apart) of two grunts and a long boop produced by fish 4 on 24 April 2001. The second grunt of fish 4 is tagged by fish 1 and is in turn tagged by fish 3. Note the disparity in sound amplitude, particularly for the tags produced by fish 1 and 3.

a time interval of 150 ms (a conservative value that includes 94% of the grunts by fish 1), the sum of all grunt intervals is 26.7 s out of 7200 s ($120\,\text{min}\times 60\,\text{s/min}$). Dividing the number of grunts into the session duration indicates that grunts would occur at an average of 40-s intervals if produced randomly. Clearly, these grunts (our tags) are triggered by an acoustic stimulus and are not a random occurrence.

Late season recording with two hydrophones (after three of the fish had moved from their original positions) indicates that fish 1, 2, and 4 were closer to hydrophone 1, and fish 3 was closer to hydrophone 2; representative differences in sound levels between the hydrophones for the four fish were 3, 4, 9, and 16 dB. Figure 8 illustrates a two-hydrophone recording of a chain of tags in which the second grunt of fish 4 is tagged by fish 1, who in turn is tagged by fish 3. The grunts of fish 4 are, respectively, 4.5 and 3.3 dB greater on hydrophone 1, and the tag by fish 1 is 9.6 dB greater on hydrophone 1. Fish 3, however, whose tag would not be recognized above the boatwhistle on the oscillogram from hydrophone 1, is at least 0.7 dB greater than the boatwhistle on hydrophone 2. A peak dB measurement of the highest amplitude of the most prominent frequency in the tag, which removes the background level of the boatwhistle, is 6.5 dB higher on hydrophone 2.

IV. DISCUSSION

The finding that gulf toadfish can grunt (tag) during the boatwhistle of another solves the riddle of boatwhistles recorded with embedded grunts in the oyster toadfish (*Opsanus tau*).[15] Latencies were not measured in the earlier study, but they appear to be longer in *O. tau* than *O. beta*, perhaps because the *O. tau* call is simpler, typically without preceding grunts that could cue the tagging fish. Gulf toadfish tag calls of nearby fish and snapping shrimp, and generally ignore less intense calls of toadfish located at a greater distance. The stimulus to tag appears to be an intense sound with a rapid rise time, and the decision to tag is usually made within 100 ms. The shrimp snap is an intense signal with a shorter rise time than the toadfish grunt [Fig. 4(b)], and the shortest latency was faster for a snap than for a toadfish grunt. Most of the energy in the shrimp snap is above the audible frequency range of toadfish (about 800 Hz in *Opsanus tau*),[17] but the snap's lower frequency components will be audible to the toadfish. We suggest that snaps are tagged because they mimic characteristics that stimulate the toadfish and not because of interspecific communication. Observations that toadfish tag shrimp snaps more frequently at times with few toadfish calls suggest an ability to discriminate snaps from grunts, a remarkable feat considering the short latency for a decision.

Since we cannot localize the position of the calling fish with two hydrophones, comparison of levels of sounds of the tagging and tagged fish are not clearly meaningful. However, a difference of as much as 16 dB between two hydrophones 4 m apart indicates rapid attenuation of these signals with distance in this shallow-water habitat. Further, a tag by fish 3 is almost completely masked in the oscillogram of the boop from hydrophone 1. Rapid attenuation of signals with distance in other toadfish[16,18] and a damselfish[19] likewise supports the notion that communication in *Opsanus beta* is restricted to short distances in shallow water.

Fish[10] apparently stimulated tagging experimentally in *Opsanus tau* without recognizing the phenomenon. Playbacks of boatwhistles or tone bursts at a rapid rate to calling toadfish will stimulate them to call faster,[11,12] but playbacks of continuous tones suppress calling.[10] Playbacks of two 6-s tone bursts with a silent interval between the bursts stimulate toadfish to produce a boatwhistle in the silent period. By shortening the interval between the bursts, Fish succeeded in getting toadfish to call with a ‘‘minimum auditory time’’ of 80 ms and more commonly response times of 120 to 140 ms. About 90% of the boatwhistles began in the silent interval even when the intervals were only 0.26–0.32 s long. These playbacks also evoked grunts (i.e., our tags), which Fish[10] interpreted as aborted boatwhistles. Grunts became increasingly common as the intervals shortened, and 521 of 535 grunts occurred in the first 100 ms of the second tone burst, with most occurring within 70 ms, approximately the same time as our average latency to tag. We suggest that it is highly unlikely for a fish to hear a neighbor's boatwhistle clearly over his own call, react to that boatwhistle (or tone-burst playback), and then somehow abort a call (stop the motor message already descending from the forebrain)[20,21] in such a short time window, presuming of course that it can stop it at all.

The rapid reaction time for tagging and placing a boatwhistle in the silent interval between tones is supported by intimate connections of the auditory and motor pathways in toadfish.[22,23] Routine electrical stimulation of the mating call in the forebrain but not lower centers[20,21] suggests that the decision to tag is made at higher centers rather than being a reflex.

We believe that tagging is an undescribed phenomenon in animal communication. It is quite different from a facilitated response to other callers or playbacks since toadfish boatwhistles rarely overlap in the field.[10,13] It is also different from phenomena like production of the ''co'' note of the coqui frog,[24] which is directed at males but is part of the normal advertisement call because a male toadfish places his tag as a response to occur during the call of a rival male.

Since data come from field recordings of unseen fish, we have no independent observations that explain its function. However, the absence of reciprocal calling over most of the mating season suggests that the tagging fish is expressing dominance over the fish it tags; reciprocal tagging toward the end of the mating season suggests that reversals of status are possible. Tagging does not appear to decrease the number of boatwhistles produced by the tagged fish. A tag is also too short to mask or jam the boatwhistle of the tagged fish. Because a grunt requires several muscle contractions, and a boatwhistle can require several hundred,[13] tags are energetically efficient compared to a boatwhistle. Occurrence of tagging primarily during the twilight peak of calling[13,14] suggests the hypothesis that at least some of the information in the call is directed at females who would be using the boatwhistle advertisement call to choose a mate[12,25,26] during this peak period.

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