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EFFECTS OF FISH SIZE AND TEMPERATURE ON WEAKFISH DISTURBANCE CALLS: IMPLICATIONS FOR THE MECHANISM OF SOUND GENERATION

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Summary

To categorize variation in disturbance calls of the weakfish *Cynoscion regalis* and to understand their generation, we recorded sounds produced by different-sized fish, and by similar-sized fish at different temperatures, as well as muscle electromyograms. Single, simultaneous twitches of the bilateral sonic muscles produce a single sound pulse consisting of a two- to three-cycle acoustic waveform. Typical disturbance calls at 18 °C consist of trains of 2–15 pulses with a sound pressure level (SPL) of 74 dB re 20 μPa at 10 cm, a peak frequency of 540 Hz, a repetition rate of 20 Hz and a pulse duration of 3.5 ms. The pulse duration suggests an incredibly short twitch time. Sound pressure level (SPL) and pulse duration increase and dominant frequency decreases in larger fish, whereas SPL, repetition rate and dominant frequency increase and pulse duration decreases with increasing temperature. The dominant frequency is inversely related to pulse duration and appears to be determined by the duration of muscle contraction. We suggest that the lower dominant frequency of larger fish is caused by a longer pulse (=longer muscle twitch) and not by the lower resonant frequency of a larger swimbladder.

Key words: sound production, bioacoustics, frequency, amplitude, pulse duration, sonic muscle, swimbladder, acoustic communication, weakfish, *Cynoscion regalis.*

Introduction

Teleost fishes utilize a number of different mechanisms for sound production, including stridulation of bony structures and contraction of sonic muscles attached to the swimbladder that cause it to vibrate (Tavolga, 1971; Demski et al., 1973). For long-duration calls produced by swimbladder mechanisms, such as the boatwhistle advertisement call of the oyster toadfish *Opsanus tau* and the plainfin midshipman *Porichthys notatus*, it has long been known that the muscle contraction rate determines the fundamental frequency of the sound (Skoglund, 1961; Cohen and Winn, 1967; Bass and Baker, 1991). That is, a boatwhistle with a fundamental frequency of 200 Hz is generated by simultaneous 200 cycle s^{-1} contractions of paired sonic muscles intrinsic to the swimbladder. However, most fish sounds are of short duration and pulse-like in nature (Winn, 1964; Fine et al., 1977) and are therefore likely to be generated by a small number of muscle contractions or even a single twitch. Frequency generation in sounds evoked by a single contraction has not been investigated. Although one might presume the spectrum of such sounds to be determined by bladder acoustics, i.e. the resonant frequency of the swimbladder (Harris, 1964; Van Bergeijk, 1964), we report that the frequency spectrum in weakfish disturbance calls appears to be determined by the rapid twitch time of the sonic muscles. Further, we suggest that this mechanism of sound generation provides the selective force for the evolution of sonic muscles specialized for speed.

Sciaenid fishes produce sound primarily during the spawning season (Fish and Cummings, 1972; Takemura et al., 1978; Mok and Gilmore, 1983; Saucier and Baltz, 1993; Connaughton and Taylor, 1995b). Seasonal sound production has been shown to play a role in the courtship behavior of *Corvina nigra* (Dijkgraaf, 1947), the red drum *Sciaenops ocellatus* (Guest and Lasswell, 1978) and the weakfish *Cynoscion regalis* (Connaughton and Taylor, 1996). Although representative sonagrams for a number of sciaenid species have been published (Fish and Mowbray, 1970), detailed descriptions of sound parameters and variation due to fish size or environmental conditions (temperature) have not been published for any sciaenid species. This absence is particularly striking since there is considerable similarity among the calls of different species (e.g. weakfish and Atlantic croaker *Micropogonias undulatus*; Fish and Mowbray, 1970) and because these sounds are being used to describe the location and timing of spawning populations (Mok and Gilmore, 1983; Saucier and Baltz, 1993; Connaughton and Taylor, 1995b).

As in most sciaenid species, male weakfish possess sonic muscles that are absent from the female (Smith, 1905; Tower, 1908; Chao, 1978; Hill et al., 1987). The bilaterally paired muscles lie on the inner body wall adjacent to, but not directly attached to, the swimbladder and extend nearly the entire length of the body cavity. The sonic muscle fibers run dorsoventrally, originating on an aponeurotic sheet that extends over the dorsal surface of the swimbladder, and extend down to the hypaxial muscles. The muscles are separated from the lateral body wall musculature by connective tissue (Ono and Poss, 1982). In the weakfish, the condition of these muscles is as seasonal as their use, with the muscles hypertrophying early in the spring spawning season and atrophying markedly late in the summer in response to changes in blood androgen levels (Connaughton and Taylor, 1994, 1995a). Sound amplitude mirrors this pattern, becoming more intense when the muscle is hypertrophied and decreasing in amplitude coincident with muscle atrophy (Connaughton et al., 1997). The detailed role of the sonic muscles and swimbladder in sound generation is not well understood and has not been critically examined since Tower (1908).

The purpose of the present study was to describe the disturbance call (a call made voluntarily when the fish is handled out of the water) of the weakfish, including quantitative effects of temperature and fish size on acoustic parameters, to gain insight into sound generation, and to examine the scope of variability likely to be encountered by investigators examining natural spawning populations. To help understand the role of sonic muscle contraction in generating the acoustic waveform, we recorded muscle action potentials (an electromyogram or EMG) from a representative individual. To avoid the difficulties associated with making acoustic recordings in an enclosed aquatic environment (Tavolga, 1962; Parvulescu, 1964; Schneider, 1967), sounds were recorded in air. This allowed absolute sound pressure level (SPL) to be determined at a standard distance and also eliminated tank effects such as echoes and resonance, which might complicate measurements of SPL, dominant frequency and duration.

Materials and methods

Capture and holding of fish

Weakfish *Cynoscion regalis* (Bloch & Schneider) were captured using hook and line in the early spring from the Delaware Bay, near Lewes, DE, USA. All fish were maintained under natural photoperiod and fed live mummichogs (*Fundulus heteroclitus*) *ad libitum*. Fish used to determine the effects of total length on acoustic parameters were maintained in a 4500 l circular enclosure at 18 °C. Fish used to examine the effects of temperature on acoustic parameters were maintained in a 1500 l circular enclosure at temperatures that were changed from 18 °C to 23 °C to 12 °C and back to 18 °C during the course of the experiment.

Electromyogram recording

Simultaneous sound and EMG recordings were made in air from a single adult male weakfish (total length 31 cm) maintained under cold conditions for approximately 8 hours (10 °C) to prolong survival time out of the water. The acoustic signal was amplified (Hydrophonics, Ferndale, WA, USA), sent to an analog-digital oscilloscope (MacLab/4, AD Instruments, Inc., Milford, MA, USA) and analyzed on a Macintosh computer using Scope software (version 3.2.8, AD Instruments, Inc.). Two 28 gauge wires (Vector, P178-1), stripped of insulation and hooked at one end after being inserted through a single 18 gauge needle, were placed in the sonic muscle through the hypaxial musculature. The needle was pulled back after placing the electrodes, which remained hooked in the sonic muscle tissue. The recorded compound muscle action potentials were passed through a DAM 50 differential amplifier (World Precision Instruments, New Haven, CT, USA) and into the MacLab/4 oscilloscope. The specimen drummed voluntarily during all trials. Electrodes were also placed in the epaxial musculature dorsal to the lateral line as a control. After recording, the fish was deeply anesthetized in MS222 (500 mg l^{-1}), and electrode placement in the sonic muscle was checked by dissection. The electrodes were observed to be positioned 1 mm into the sonic muscle (total thickness approximately 4 mm) and approximately 1 mm apart.

Recording procedures

Sound production by fish maintained in the laboratory was recorded in air with a Realistic Pressure Zone Microphone (Radio Shack, Tandy Corp., Fort Worth, TX, USA; range 20 Hz to 18 kHz) and an Aiwa HS-J470 stereo cassette-recorder. Each specimen was held 10 cm from the microphone for less than 1 min. for several bouts of drumming. An 80 dB calibration tone, measured with a Realistic Sound Level Meter (Radio Shack), was recorded at the microphone for measurement of absolute SPL.

Sound recording experiments: effects of body length and temperature

We examined the effects of specimen total length (TL) and temperature on the characteristics of drumming sounds. The effect of fish TL on acoustic variables was determined by recording from 11 weakfish ranging in TL from 25 to 36 cm and held at 18 °C. The effect of temperature on acoustic variables was examined by recording sounds produced by eight similarly sized fish (28–31 cm TL) at three temperatures. Temperature changes took place over 3–4 days, and the fish were allowed to acclimate to each temperature for a minimum of 4 days after it had been reached. Recordings were made at 18, 23 and 12 °C and then again at 18 °C to determine whether health or other variables (such as seasonally changing sonic muscle mass) had altered the responses of the fish over the 28 day experiment.

Recordings were analyzed on a Macintosh 6500/250 personal computer using Canary bioacoustic software (version 1.2, Cornell University, Laboratory of Ornithology). We recorded drumming bursts or trains, which consist of a series of sound pulses. A pulse consists of 2–3 cycles of acoustic energy. Sounds were analyzed for SPL, repetition rate within a train (number of pulses per second expressed in Hz), pulse duration and dominant frequency, which represents the most intense frequency (in Hz) of the individual sound pulses. All variables were measured for the ten most intense pulses from each fish, except for repetition rate, which was determined for all recorded trains. Pulse duration indicates the entire duration of the acoustic waveform clearly discernible above the background noise and always included 2–3 cycles of acoustic energy. Measurement was terminated at the zero crossing of the final cycle. The durations of the first and second cycles of acoustic energy were also measured independently for each pulse.

Statistical analyses

Least-square linear regressions were used to examine changes in all acoustic variables across total length or temperature and variations in dominant frequency across pulse duration. The data used in these analyses were mean values of 10 pulses for each fish. Data recorded during the initial and final recordings at 18 °C in the temperature experiment were compared by *t*-test, then pooled for linear regression analyses. A *P* level of 0.05 was used for all analyses (Zar, 1984). Results are expressed as means ±1 S.D.

Results

Electromyogram recordings

Simultaneous sound and EMG recordings of sonic muscle activity revealed a single action potential prior to each multi-cycle acoustic waveform (Fig. 1B). The amplitude of the evoked sound pulses varied considerably compared with the amplitude of the compound action potentials (Fig. 1A), indicating that the EMGs were recorded from a limited portion of the entire muscle. EMGs were recorded from one of the bilateral pair of sonic muscles, and there was always a single action potential preceding each sound pulse (Fig. 1A, *N*=212), indicating simultaneous rather than alternate contraction of the bilateral sonic muscles. When electrodes were placed, as a control, in the epaxial musculature dorsal to the lateral line, no action potentials were recorded during sound production.

Action potential duration (Fig. 1B), measured from the initiation of depolarization to the point where repolarization crossed the zero line, was 2.1±0.2 ms (mean ± S.D., *N*=20). This was followed by a waveform of opposite polarity that varied in duration from 5.8 to 11.5 ms (mean 8.9±1.8 ms) for a total duration that ranged from 7.9 to 13.6 ms. The time between the initiation of the action potential and the initiation of the sound pulse averaged 2.2±0.4 ms (Fig. 1B). The interval from the time of maximum depolarization of the action potential to the initiation of the sound pulse averaged 1.0±0.4 ms. These values do not take into consideration the speed of sound travelling from the muscle to the microphone 10 cm away, which would reduce the delay by approximately 0.3 ms.

Sound recording experiments: effects of body length and temperature

Disturbance calls evoked by removing fish from the water had a median of three pulses, and ranged from one to more than 20 pulses. A voluntary train of pulses recorded in the field (Connaughton and Taylor, 1994) or during spawning in the laboratory (Connaughton and Taylor, 1996) had a median of six pulses, and a range of 4–10 pulses, but disturbance and unsolicited calls were otherwise similar (Fig. 2). While pulses in a given train were typically of similar SPL, variations in pulse SPL of up to 9 dB were noted within a train, in both evoked and voluntary sounds (see Fig. 1A, top recording). Several trains of drumming were typically produced by the fish during handling. The oscillogram of recorded sound pulses consisted of 2–3 cycles of acoustic energy, with the third cycle often greatly attenuated. In most recordings, the second cycle had the greatest amplitude (Fig. 3, center recordings). A typical disturbance call for a fish of 28–31 cm total length, recorded at 18 °C, included a train of 2–15 pulses with a sound pressure level (SPL) of 74 dB (re 20 μPa at 10 cm), a peak frequency of 540 Hz, a repetition rate of 20.2 Hz and a pulse duration of 3.5 ms.

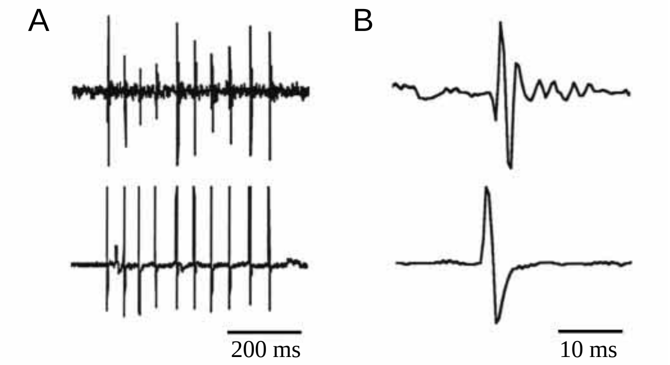


Fig. 1. Simultaneously recorded sounds (upper recordings) and electromyograms (lower recordings) from weakfish sonic muscle. Recordings from (A) a train of pulses and (B) a single expanded pulse.

The clearest changes in acoustic characteristics with fish size were increased SPL (notable both in the intensity of the sonagram and the amplitude of the waveform) and decreased frequency (Fig. 3). SPL and pulse duration both increased significantly with increasing TL (Fig. 4A,C; Table 1), whereas dominant frequency decreased significantly (Figs 3, 4D). Repetition rate did not change significantly with TL (Fig. 4B). Across a range of 11 cm of total length (25–36 cm), SPL increased by 9.7 dB from 65.6 to 75.3 dB, pulse duration increased by 0.6 ms from 3.3 to 3.9 ms and dominant frequency decreased by 91 Hz from 560 to 479 Hz.

SPL, repetition rate and dominant frequency increased significantly with increasing temperature (Fig. 5A,B,D; Table 1), and pulse duration decreased significantly (Fig. 5C). Over the range of temperatures from 12 to 23 °C, the call of 28–31 cm fish ranged in SPL from a mean of 69.6 to 75.5 dB, in repetition rate from 13.4 to 24.3 Hz and in dominant frequency from 494 to 554 Hz. Pulse duration decreased from 3.7 to 3.4 ms.

The mean SPL of initial (21 June) and final (19 July) recordings at 18 °C decreased by 3.1 dB (*P*=0.05). None of the

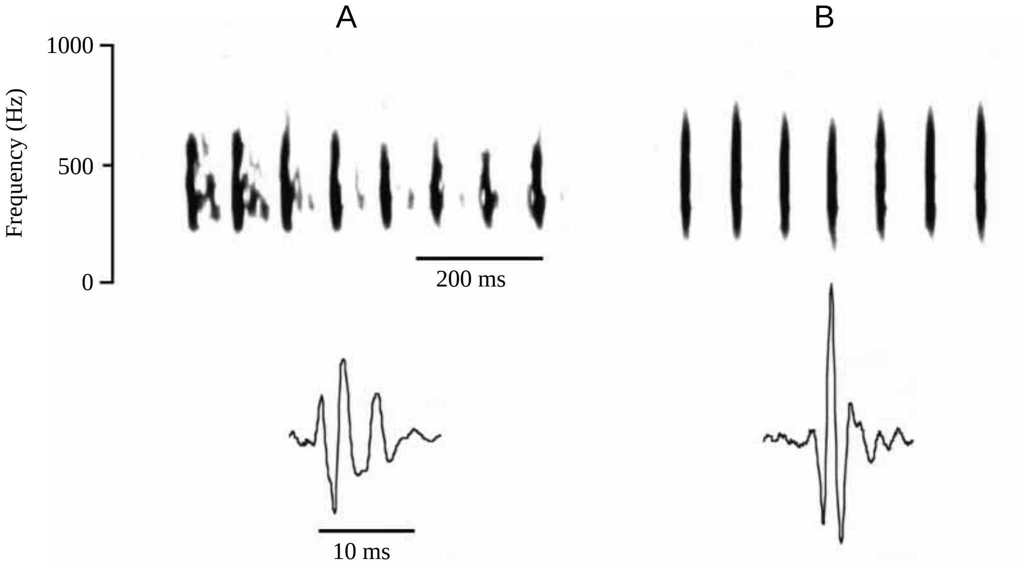
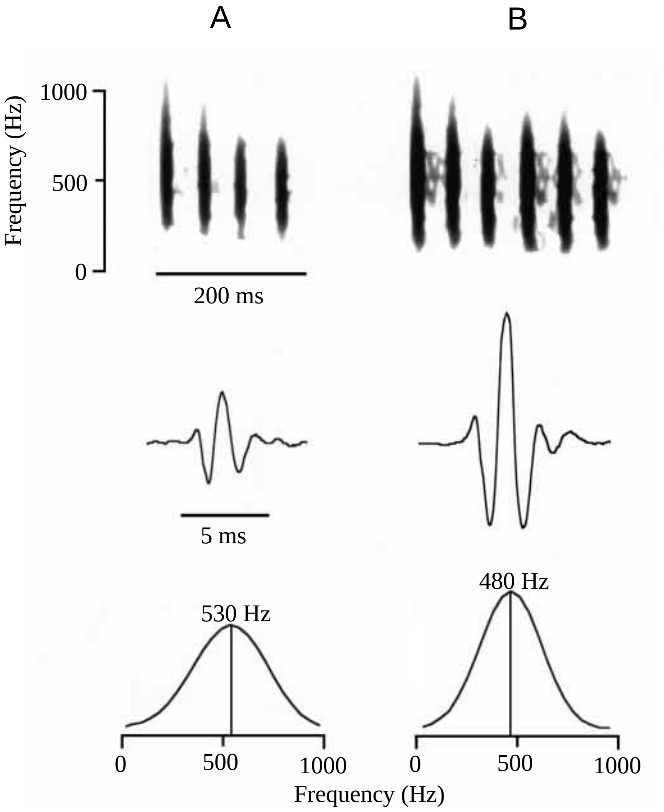


Fig. 2. Sonagrams of recordings made at 12 °C from (A) a voluntarily calling fish in the field and (B) a restrained fish recorded out of water (a disturbance call). The upper recordings shows sonograms of entire calls and the lower recordings shows expanded oscillograms of individual pulses. Alternate pulses in the sonogram of the field recording are from a second fish calling in the background. The slightly greater pulse duration of the waveform in A results in a lower dominant frequency of this sound, 330 Hz, compared with 450 Hz for the pulse represented in B. This difference may be the result of the bottom temperature in the field being lower than the recorded surface temperature of 12 °C or because the fish in A (TL unknown as fish was unseen) may have been larger than that recorded in B (TL, 28.5 cm).

other parameters changed significantly. The initial and final values for each measured characteristic at 18 °C, including SPL, were therefore pooled for the regression analyses.



Frequency and pulse duration were inversely proportional in both experiments (Fig. 6; Table 1). Linear regression of frequency across pulse duration resulted in r^2 values of 94 % in the size experiment and 81 % in the temperature experiment. Pulse duration ranged from 3.3 to 3.9 ms across a decrease of 81.2 Hz in dominant frequency (from 560.9 to 479.7 Hz) in the size experiment and from 3.21 to 3.95 ms across a decrease of 165 Hz (from 606 to 441 Hz) in the temperature experiment.

To relate dominant frequency to pulse waveform, we independently calculated acoustic frequencies from the inverse of the duration of the first cycle of acoustic energy, the second cycle of acoustic energy and the total pulse duration [1/(duration×1000)]. Each of the three values was plotted against the dominant frequency determined from the power spectrum (Fig. 7A). We then divided the dominant frequency for each pulse by each of the calculated values and plotted the results (Fig. 7B). The dominant frequency for all recordings was most closely matched (expressed as values near to 1) by the inverse of the duration of the second cycle of acoustic energy, which was the longest and most intense component of the call.

Fig. 3. Sonagrams of pulse trains (upper recordings; frequency *versus* time), oscillograms of single pulses (middle recordings; amplitude *versus* time) and power spectra of single pulses (lower recordings; amplitude *versus* frequency) of disturbance drumming sounds recorded in air from restrained (A) 25 cm and (B) 35 cm weakfish at 18 °C. Note the increase in intensity of the sonagram and amplitude of the oscillograms indicating increasing sound pressure level with increasing fish size. Also note the decrease in frequency with increasing size.

Table 1. *Details of linear regression equations*

Variables (*x versus y*)	Slope, *m*	*y*-intercept, *b*	r^2	*P*
Total length *versus* sound pressure level	0.68	50.28	0.73	0.0005
Total length *versus* repetition rate	–0.08	21.85	0.04	0.26
Total length *versus* pulse duration	0.04	2.53	0.45	0.014
Total length *versus* dominant frequency	–3.93	636.70	0.38	0.026
Temperature *versus* sound pressure level	0.53	63.22	0.50	0.0001
Temperature *versus* repetition rate	1.00	1.78	0.85	0.0001
Temperature *versus* pulse duration	–0.03	3.34	0.27	0.0013
Temperature *versus* dominant frequency	5.47	434.03	0.39	0.0001
Pulse duration *versus* dominant frequency				
Size experiment	–112.9	927.5	0.94	0.0001
Temperature experiment	–174.7	1145.4	0.81	0.0001

Significance was determined at $P<0.05$. The linear regression equation is: $y=(mx)+b$.

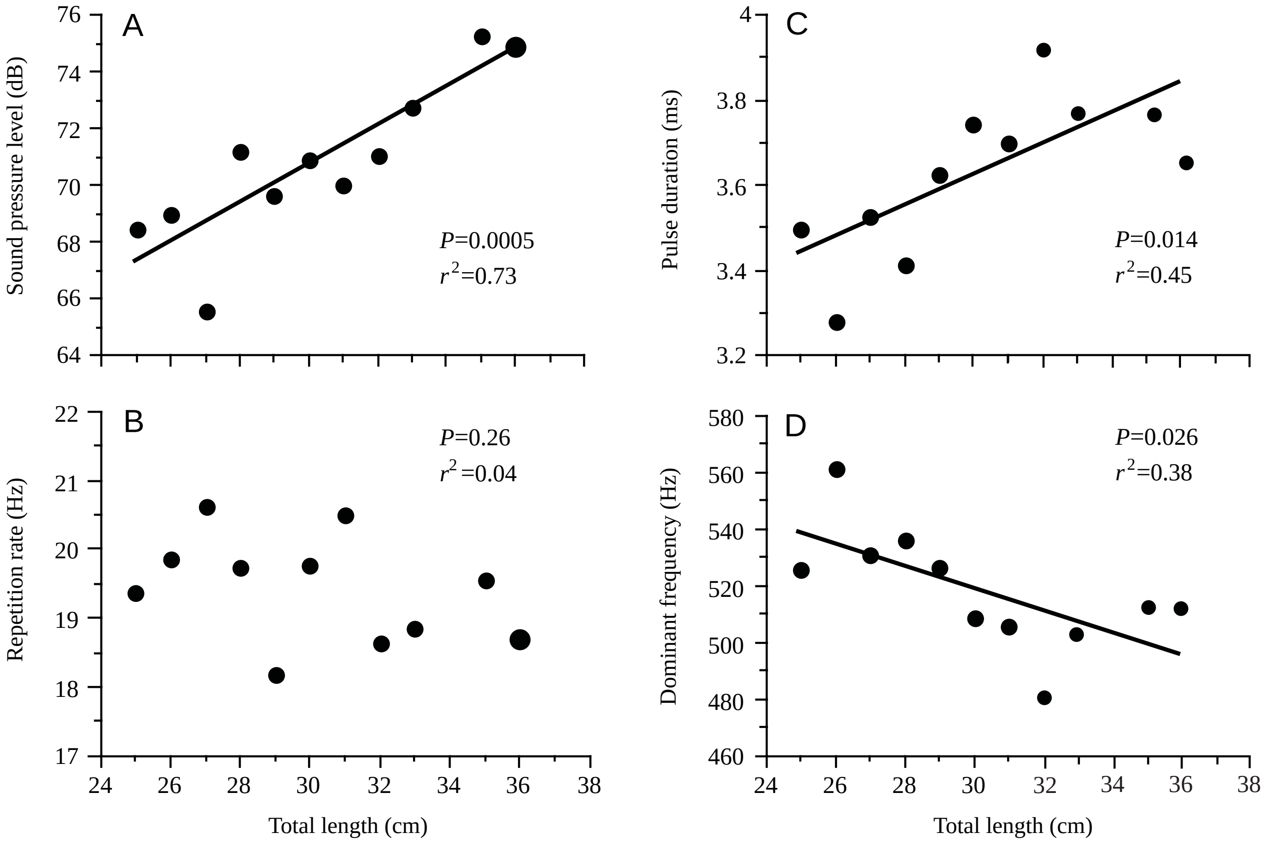


Fig. 4. Influence of fish size on disturbance calls. Linear regressions of (A) sound pressure level, (B) repetition rate, (C) pulse duration and (D) dominant frequency against total length. Fish ranged from 25 to 36 cm in total length (N=11) and all recordings were made at 18 °C. For regression equations, see Table 1.

Discussion

Sounds from sciaenid fishes have been associated with the mating season since early in the century (Smith, 1905) and are now being used routinely to monitor spawning populations in the field (Mok and Gilmore, 1983; Saucier and Baltz, 1993; Connaughton and Taylor, 1995b). Despite a number of ongoing local programs and fisheries recommendations for conducting ‘hydrophonic surveys’ to determine the location and timing of spawning activity (Klein, 1997), a detailed study of call parameters likely to be encountered during an acoustic census has not been published for a single species in the family. This omission has the potential to cause identification problems at sites where more than one species might be calling.

Drumming behavior in weakfish has been correlated with

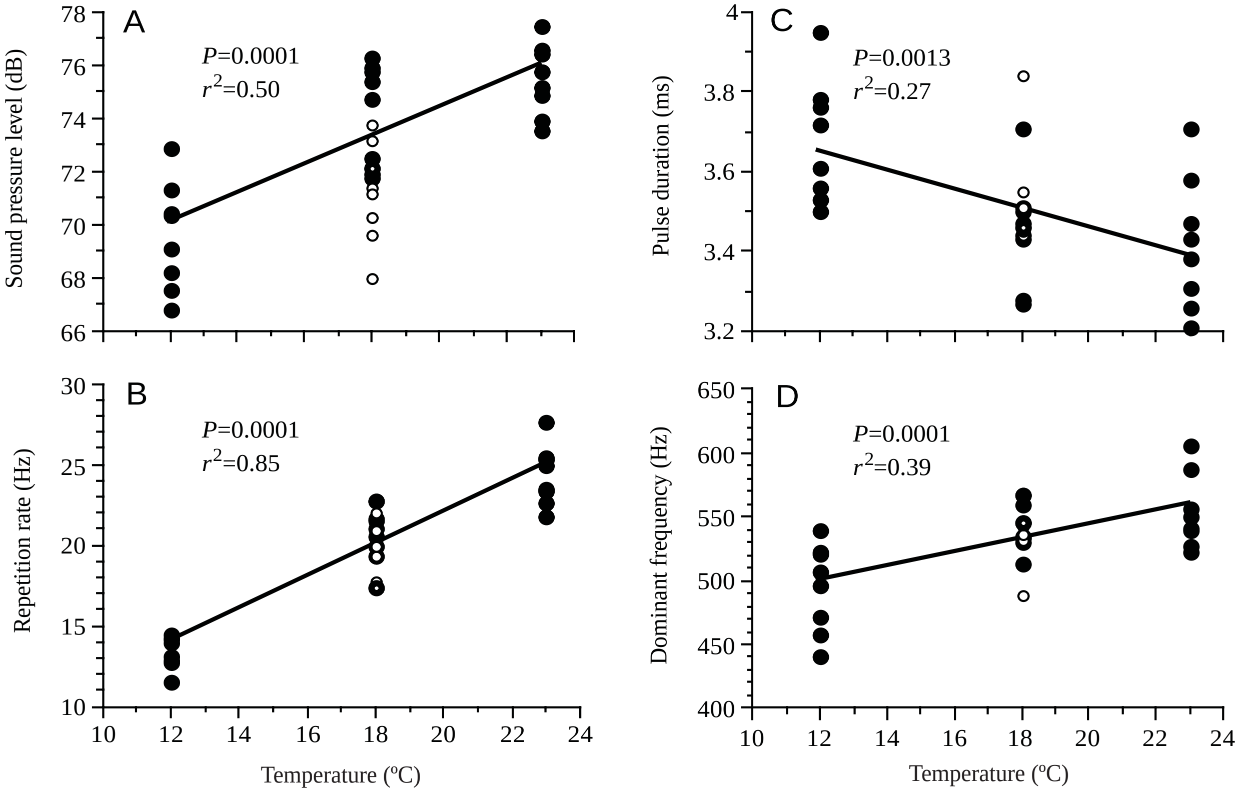


Fig. 5. Influence of temperature on disturbance calls. Linear regressions of (A) sound pressure level, (B) repetition rate, (C) pulse duration and (D) dominant frequency against temperature. Fish (*N*=8), ranging in total length from 28 to 31 cm, were recorded at 18, 23 and 12 °C and then again at 18 °C after a minimum of 4 days of acclimation at each temperature. Filled circles represent the data from the initial recording at 18 °C and open circles represent the final recording. All 18 °C data were pooled for linear regression analysis. For regression equations, see Table 1.

spawning in the field (Connaughton and Taylor, 1994) and observed in courting fish in captivity (Connaughton and Taylor, 1996). The weakfish disturbance calls recorded in this study were similar to the voluntary calls recorded in the field during the spawning season (Fig. 2). Weakfish do not naturally produce the drumming call outside the spawning season (Connaughton and Taylor, 1995b), nor do they produce these sounds if startled in captivity (when chased with a net, M. Connaughton, personal observation). Together, these observations indicate that the acoustic repertoire of the weakfish is surprisingly undifferentiated, and that the courting and disturbance calls may be essentially the same call.

The current study describes a suite of acoustic characteristics for disturbance calls from weakfish of varying size and encompassing the range of temperatures (15–24 °C) that would be encountered during a spawning season in Delaware Bay (Connaughton and Taylor, 1994). Age/length determinations of Delaware Bay weakfish indicate that the 25–36 cm TL fish recorded in this study were 2–3 years of age (Seagraves, 1981). The variation in call parameters with fish size suggests that acoustic parameters may be valuable to fisheries biologists as a non-invasive tool for gathering size and age data on males in spawning populations, although considerably more research will be necessary for us to learn to extract such data accurately from field recordings.

Call variation

Disturbance calls vary with fish size and temperature. Amplitude (SPL) increased by 9.7 dB with an 11 cm increase in fish size in this study. Pulse duration, averaging approximately 3.6 ms, increases by 0.6 ms over this range of fish size; therefore, longer muscles, presumably with longer fibers, are taking longer to complete a twitch in larger fish. Data on the scaling of motion with size in fishes and other animals indicate slower movements in larger animals, implying that the rate of muscle shortening per sarcomere decreases with increasing body size (Hill, 1950; Wainwright and Barton, 1995). Dominant frequency, which is inversely related to pulse duration, decreases by almost 100 Hz with an 11 cm increase in fish size.

The sonic muscle in the oyster toadfish *Opsanus tau*, often considered the fastest vertebrate muscle, can complete an electrically stimulated twitch in approximately 10 ms (Skoglund, 1961; Rome et al., 1996). The sound generated by such a twitch is also approximately 10 ms in duration. In this context, the duration of a weakfish sonic muscle twitch is probably less than half that of the toadfish, an incredibly rapid event, although this requires direct measurement.

Since weakfish spawn at night (Ferraro, 1980; Taylor and Villoso, 1994; Connaughton and Taylor, 1995b), when visibility is low, acoustic parameters of drumming sounds

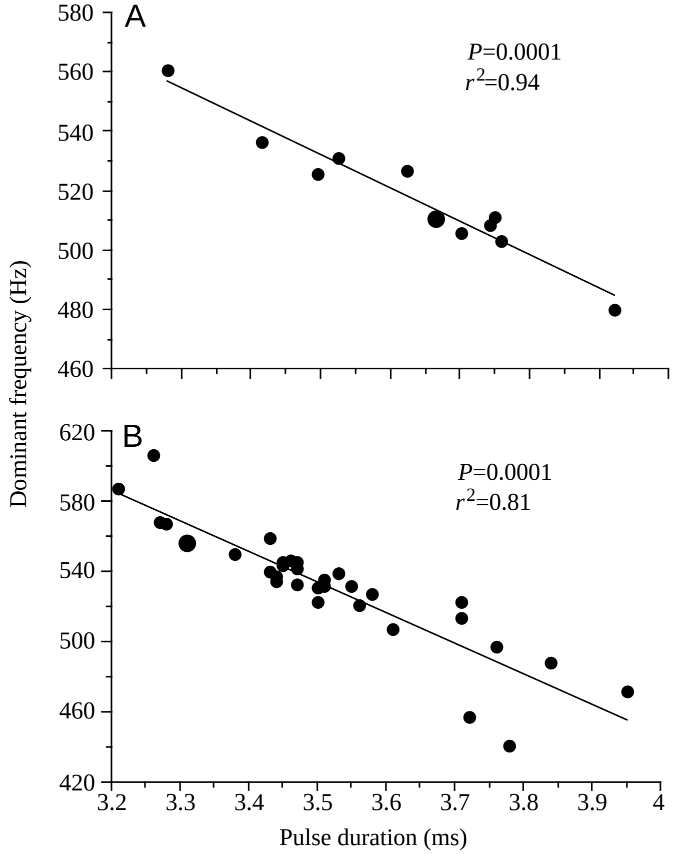


Fig. 6. Relationship between dominant frequency and pulse duration for (A) fish ranging from 25 to 36 cm in total length (size experiment, recorded at 18 °C; *N*=11) and (B) fish recorded at 12, 18 and 23 °C (temperature experiment; 28–31 cm in total length, *N*=8). For regression equations, see Table 1.

could provide a valuable cue for female attraction and mate choice. Although untested, it is unlikely that a weakfish could perceive differences in pulse duration of less than 1 ms (Fay and Megala Simmons, 1999). However, variations in amplitude and frequency with fish size, which are likely to be perceived, suggest that weakfish acoustic pulses are an honest signal (Sargent et al., 1998) that could allow females to discriminate males on the basis of their size.

Repetition rate averages 19.4 Hz, ranging from 18.2 to 20.6 Hz over the size range we tested, and does not vary significantly with fish size. Unlike the other parameters related to movement of the sonic muscles and swimbladder, repetition rate is determined in the central nervous system (Demski et al., 1973). The output of the pattern-generating circuits stimulating the sonic muscles apparently remains relatively fixed developmentally, although it does change with temperature. Over a range of 11 °C, the mean repetition rate almost doubled from 13.4 to 24.3 Hz. Similar increases in repetition rate have been found in tigerfish *Therapon jarbua*, toadfish *Opsanus tau*, midshipman *Porichthys notatus*, long-horned sculpin *Myoxocephalus octodecimspinosus* and sea robin *Prionotus carolinus* (Schneider, 1967; Fine, 1978; Bass and Baker, 1991).

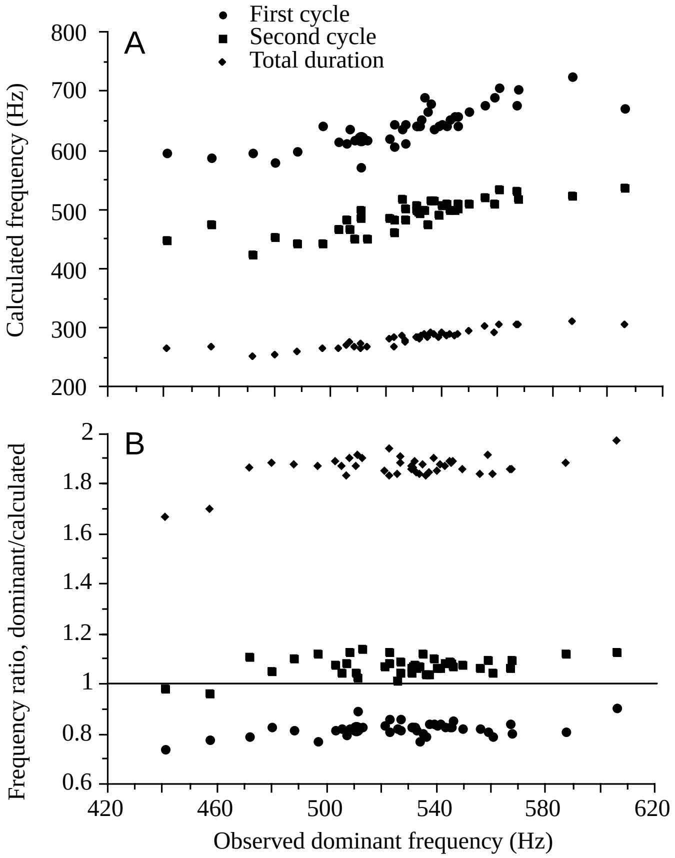


Fig. 7. (A) Calculated frequencies plotted against dominant frequency obtained from power spectra for individual pulses. These frequencies were calculated from the inverse of the duration of the first cycle of acoustic energy (circles), the duration of the second cycle of acoustic energy (squares) and the total pulse duration (diamonds) using the formula 1/(duration×1000). (B) A plot of the dominant frequency divided by each of the three calculated values. Note that the dominant frequency is most closely matched (expressed as values near to 1) by the inverse of the duration of the second cycle of acoustic energy.

Parameters associated with muscle contraction also changed significantly with temperature in weakfish. An increase in mean SPL of 5.9 dB and a decrease in mean pulse duration of 0.3 ms indicate that the muscles are taking less time to complete a twitch and contracting with a faster velocity at the highest temperature (see below). Feher et al. (1998) demonstrated faster re-uptake of Ca^{2+} at increased temperature by toadfish sarcoplasmic reticulum, which would support more rapid contraction of sonic muscles with increasing temperature.

The minor decrease in SPL of sounds produced by the same fish during the first and second trial at 18 °C, approximately a month apart, is probably due to decreased sonic muscle mass, which follows seasonal changes in plasma androgen levels (Connaughton and Taylor, 1995a). Muscle mass increases nearly threefold between the winter and the late spring spawning season and then decreases as the muscle atrophies following the spawning season (Connaughton and Taylor, 1994). SPL has been observed to decrease as the muscles atrophy (Connaughton et al., 1997).

Mechanism of sound generation

EMG data indicate that individual sound pulses are produced by single but simultaneous contractions of both sonic muscles, in agreement with Tower (1908), who recorded simultaneous mechanical contractions in weakfish sonic muscle. Simultaneous action potentials have been recorded from the bilateral sonic nerves of muscles in pigfish, oyster toadfish, midshipman and long-horned sculpin (Packard, 1960; Skoglund, 1961; Cohen and Winn, 1967; Bass and Baker, 1991). The study of Packard (1960) on the pigfish *Congiopodus leucopaecilus* demonstrated that occasional EMG failure was still accompanied by a sound pulse, indicating that the contralateral muscle normally contracted simultaneously with the one implanted with electrodes. In the present study, every sound pulse was accompanied by a single action potential recorded from one of the paired muscles. Alternate action potentials have been recorded from sonic motoneurons (Bass and Baker, 1991) and muscles (M. A. Connaughton, unpublished data) of the sea robin *Prionotus carolinus*, indicating alternate contraction of the sonic muscles.

Recent physiological/acoustic work on the mechanism of sound production in the oyster toadfish (M. L. Fine, K. Malloy, G. Mitchell and C. B. King, unpublished data) has caused us to re-evaluate the swimbladder as an acoustic source. That study evoked sounds by electrical stimulation of the sonic nerve and recorded movements of the swimbladder using a laser vibrometer and the accompanying sound using a microphone. Toadfish sounds ceased abruptly and did so before swimbladder movement ceased, suggesting that the swimbladder is a highly damped structure that does not resonate. In addition, sound output was related to the surface area of the swimbladder and to the velocity of swimbladder movement.

The toadfish boatwhistle advertisement call, produced by a series of rapid subtetanic contractions (Skoglund, 1961; M. L. Fine, K. Malloy, G. Mitchell and C. B. King, unpublished data), is quite different from the weakfish call. In the toadfish, the muscle contraction rate generates the fundamental frequency (Skoglund, 1961) irrespective of fish size (Fine, 1978; Waybright et al., 1990). The muscle contraction rate also determines the period of the waveform, so that a contraction frequency of 200 Hz would result in a sound with 5 ms between peaks. In a weakfish call, generated by a single twitch, one might expect sound frequency to be determined by a mechanism related to the size and acoustical properties of the swimbladder. This assumption is consistent with the lower dominant frequencies seen in larger fish. Classically, swimbladders have been compared with an underwater bubble as a sound source, and the resonant frequency of an underwater bubble is inversely proportional to its size (Harris, 1964; Van Bergeijk, 1964).

Even though the dominant frequency of sound produced by the weakfish decreases in large fish, which have been shown to have larger swimbladders (Hill et al., 1987), we argue against a resonance interpretation for a number of reasons. The waveform of acoustic pulses decays rapidly (Figs 1, 3), and a pulse of 3.5 ms is too short to come from a tuned (high-Q) resonator (Q is a quality factor; see Bennett-Clark, 1989; Bradbury and Vehrenkamp, 1998). Most tellingly, the change in dominant frequency in fish of the same size range recorded at different temperatures mandates an alternative explanation, since temperature is unlikely to exert such a great effect on resonance. Similarly, dominant frequency correlates with pulse duration (reflecting muscle twitch duration, Fig. 6), and pulse duration also increases with fish size (Fig. 4). Although correlation does not necessarily imply causality, note the tight scatter and high r^2 values (Table 1) when frequency is plotted against pulse duration, and compare this with regressions of the acoustic parameters against fish size and temperature that express considerable individual variation (Figs 4–6; Table 1). Further exploration of this correlation indicates that the period of the second cycle of acoustic energy (Fig. 7B), which has the greatest amplitude, is practically identical to the dominant frequency of the call. The minor difference between the calculated and observed frequency can be explained by the effect of the lower amplitude and shorter period of the first cycle, equivalent to a higher frequency of approximately 600 Hz (Fig. 7A), on the dominant frequency.

The effects of the swimbladder and sonic muscles on sound parameters in growing fish (acoustic scaling) will be determined by several factors. Acoustic pressure is proportional to volume velocity, the product of surface area and movement velocity (Bradbury and Vehrencamp, 1998). Therefore, increasing swimbladder size in larger fish (Hill et al., 1987) should increase sound amplitude. To understand the contributions of sonic muscle twitch duration and resulting swimbladder velocity, it is instructive to look at the analogy to running in a mouse and an elephant. The elephant can run faster, but its larger size causes it to take longer to complete a movement, again a scaling argument (Hill, 1950; Wainwright and Barton, 1995). Similarly, a larger weakfish should contract its sonic muscles with a faster velocity to produce sound of greater amplitude. However, it will take longer to complete a muscle twitch, resulting in a longer period in the acoustic waveform and therefore a lower dominant frequency. Similarly, higher temperatures speed up the velocity of motion and shorten the duration, resulting in greater sound amplitude and higher dominant frequency.

Despite the extensive literature on morphological and biochemical adaptations related to speed, no-one has formally considered the logic behind the functional adaptation of fast muscles to fish sound production. M. L. Fine, K. Malloy, G. Mitchell and C. B. King (unpublished data) found that extreme muscle speed is necessary to drive the swimbladder to produce intense sounds: again, the amplitude of toadfish sounds increases with the velocity of the swimbladder walls, and slow movements of the swimbladder fail to produce audible sound.

The sonic muscles of the weakfish and toadfish clearly have independent origins. Toadfish sonic muscles form in the occipital region (neck) embryonically and migrate to and secondarily attach to the swimbladder (Tracy, 1959, 1961; Galeo et al., 1987). These muscles are innervated by bilateral occipital nerves that also migrate down from the neck. Sciaenid sonic muscles are probably modified hypaxial (trunk) muscles that form during puberty on a dorsal tendon (aponeurosis) on top of the swimbladder (Hill et al., 1987), and they are serially innervated by true spinal nerves from a number of body segments (Ono and Poss, 1982). Despite their non-homologous origins, the fibers of both muscles have relatively similar but unusual radial morphologies that have been interpreted as adaptations for speed (Fawcett and Revel, 1961; Ono and Poss, 1982; Appelt et al., 1991; Loesser et al., 1997). We suggest that the necessity of producing sound with an inefficient, highly damped radiator has convergently led to the evolution of similarly specialized muscles in these two unrelated taxa and has culminated in the weakfish having the capacity to produce acoustic pulses as short as 3.5 ms in duration.

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