Review

Weakfish sonic muscle: influence of size, temperature and season

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Summary

The influence of temperature, size and season on the sounds produced by the sonic muscles of the weakfish *Cynoscion regalis* are categorized and used to formulate a hypothesis about the mechanism of sound generation by the sonic muscle and swimbladder. Sounds produced by male weakfish occur at the time and location of spawning and have been observed in courtship in captivity. Each call includes a series of 6–10 sound pulses, and each pulse expresses a damped, 2–3 cycle acoustic waveform generated by single simultaneous twitches of the bilateral sonic muscles. The sonic muscles triple in mass during the spawning season, and this hypertrophy is initiated by rising testosterone levels that trigger increases in myofibrillar and sarcoplasmic cross-sectional area of sonic muscle fibers. In response to increasing temperature, sound pressure level (SPL), dominant frequency and repetition rate increase, and pulse duration decreases. Likewise, SPL and pulse duration increase and dominant frequency decreases with fish size. Changes in acoustic parameters with fish size suggest the possibility that drumming sounds act as an 'honest' signal of male fitness during courtship. These parameters also correlate with seasonally increasing sonic muscle mass. We hypothesize that sonic muscle twitch duration rather than the resonant frequency of the swimbladder determines dominant frequency. The brief (3.5 ms), rapidly decaying acoustic pulses reflect a low-Q, broadly tuned resonator, suggesting that dominant frequency is determined by the forced response of the swimbladder to sonic muscle contractions. The changing dominant frequency with temperature in fish of the same size further suggests that frequency is not determined by the natural frequency of the bladder because temperature is unlikely to affect resonance. Finally, dominant frequency correlates with pulse duration (reflecting muscle twitch duration), and the inverse of the period of the second cycle of acoustic energy approximates the recorded frequency. This paper demonstrates for the first time that the dominant frequency of a fish sound produced by a single muscle twitch is apparently determined by the velocity of the muscle twitch rather than the natural frequency of the swimbladder.

Key words: sound production, reproductive behaviour, dominant frequency, sound pressure level, pulse duration, repetition rate, muscle hypertrophy, testosterone, swimbladder, acoustics, secondary sexual character, weakfish, *Cynoscion regalis*.

Introduction

The weakfish *Cynoscion regalis* is a member of the sciaenid family, also known as the drumfishes. Sound production has been associated with this family of teleosts since before the turn of the century (Smith, 1905; Tower, 1908) and has often been linked with reproductive behavior (Fish and Mowbray, 1970; Mok and Gilmore, 1983; Saucier and Baltz, 1993; Connaughton and Taylor, 1995a). Sciaenids produce sound through the use of highly specialized sonic muscles (Tavolga, 1964; Fish and Mowbray, 1970). Contraction and relaxation of the sonic muscles cause rapid movements of the swimbladder resulting in sound production. Sonic muscles may be either intrinsic to the swimbladder, as in toadfish, midshipman fish and searobins amongst others, or extrinsic, as in sciaenids and

a number of other families (Tavolga, 1964). The sonic muscles of the weakfish are present only in the males (Tower, 1908; Fish and Mowbray, 1970) and run the length of the body cavity in close association with, but not directly attached to, the swimbladder (Fig. 1) (Ono and Poss, 1982). The sonic muscles originate on hypaxial abdominal muscle and insert on an aponeurosis attached to the swimbladder dorsally. Sonic muscle fibers are oriented dorsoventrally (Tower, 1908; Hill et al., 1987).

Fish sonic muscles are adapted for speed and are considered to be the fastest-contracting vertebrate skeletal muscles (Rome and Lindstedt, 1998). The sonic muscles of the squirrelfish (*Holocentrus* sp.) and midshipman (*Porichthyes notatus*) can
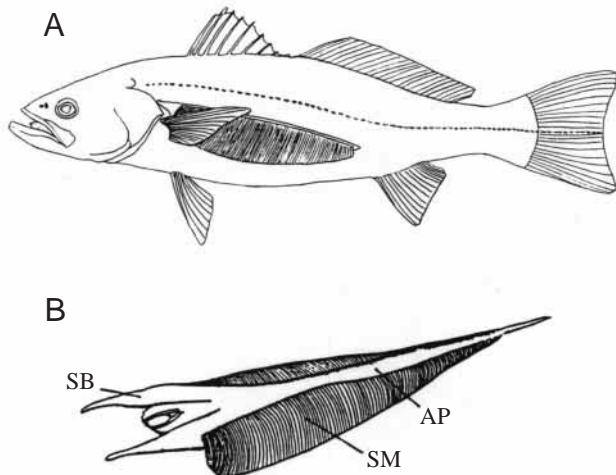
Fig. 1. (A) An illustration of the location of the sonic muscle in the weakfish *Cynoscion regalis* (modified from an illustration by H. L. Todd in Goode, 1884). (B) An oblique view of the swimbladder and associated sonic muscles; SM, sonic muscle; SB, lateral horn of the swimbladder; AP, aponeurosis overlying the dorsal surface of the swimbladder (modified from Ono and Poss, 1982). The swimbladder of a weakfish is approximately one-third of the total length of the fish, which ranged from 25 to 36 cm in our experiments. Figures taken from Connaughton et al. (1997).
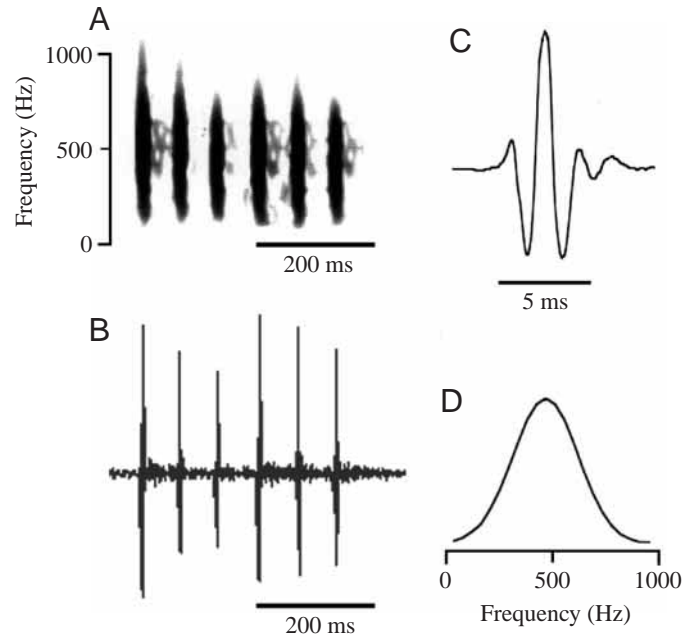

Fig. 2. Sonogram (A) and oscillogram (B) of a typical weakfish disturbance call consisting of a series of individual pulses of sound. Expanded oscillogram (C) of a single pulse consisting of 2–3 cycles of acoustic energy. Spectrum (D) of the pulse in C, demonstrating a dominant frequency of 480 Hz. Figures taken from Connaughton et al. (1997).

contract at over 100 Hz (Gainer et al., 1965; Cohen and Winn, 1967), and the toadfish (*Opsanus tau*) sonic muscle can contract at over 400 Hz without reaching tetany (Skoglund, 1961; Rome et al., 1996; Fine et al., 2001). The fibers of toadfish sonic muscles express a number of structural, biochemical and biophysical adaptations for speed, including an unusual radial morphology (Fawcett and Revel, 1961; Fine et al., 1993; Loesser et al., 1997), multiple innervation (Gainer and Klancher, 1965; Hirsch et al., 1998), the positioning of the triads over the A/I boundary (Fawcett and Revel, 1961), a large volume of sarcoplasmic reticulum (Franzini-Armstrong and Nunzi, 1983; Appelt et al., 1991) with a huge Ca^{2+} capacity (Feher et al., 1998), the fastest Ca^{2+} spike known in a vertebrate muscle and extremely rapid cross-bridge detachment (Rome et al., 1996, 1999). Weakfish sonic muscle fibers share similar radial morphology and multiple innervation, as well as expressing well-developed folding of the postsynaptic membrane, not reported in other fishes (Ono and Poss, 1982).

In this paper, we review our research on weakfish sonic muscles and their use in sound production. We have three goals. First, we will characterize the sounds produced by the weakfish, their periodicity (seasonality) and behavioral role. Second, we will describe seasonal hypertrophy and atrophy of the muscle, including its endocrine basis and the morphological changes occurring in the muscle. Finally, we will describe the influence of size, temperature and season (i.e. muscle mass) on the acoustic parameters of weakfish disturbance calls. We use these data to formulate a hypothesis for the mechanism of sound generation in weakfish.

Sound production and spawning

Weakfish sonic muscles produce staccato bursts of 6–10 pulses of sound (Fig. 2) (Fish and Mowbray, 1970; Connaughton and Taylor, 1996a). Although various acoustic parameters vary with temperature and fish size, a typical call for a fish 28–31 cm in total length at 18 °C includes a sound pressure level (SPL) of 74 dB (re 20 µPa at 10 cm in air, see below), a dominant frequency of 540 Hz, a pulse repetition rate of 20.2 Hz and a pulse duration of 3.5 ms (Connaughton et al., 2000). Each sound pulse is generated by single but simultaneous contractions of the bilateral sonic muscles, and the waveform consists of 2–3 cycles of sound, the second of which is the most intense (Connaughton et al., 2000).

Field and laboratory studies indicate a close link between male drumming behavior and reproductive activity. In Delaware Bay, weakfish form spawning aggregations in shallow, in-shore waters during May, June and July (Taylor and Villoso, 1994; Connaughton and Taylor, 1995a). Hydrophone recordings in Delaware Bay indicate that drumming activity is always more intense in-shore than in deeper, offshore waters. Drumming is also strongly seasonal, increasing abruptly to near peak levels in mid-May and waning in late July (Connaughton and Taylor, 1995a). Reproductive data, including male and female gonad condition, male plasma androgen levels, sperm motility and the percentage of males running ripe (producing milt when handled), indicate that spawning activity for this population peaks during the period of maximal drumming activity (Connaughton and Taylor, 1995a). Drumming activity

also exhibits a diel periodicity, peaking in the early evening (Connaughton and Taylor, 1995a) when weakfish spawning activity is at its maximum, as indicated by the percentage of hydrated eggs in the ovaries and back-calculation of time of fertilization from collected larvae (Taylor and Villoso, 1994).

Positive identification of the sounds recorded in the field and the role of these sounds in courtship were examined in captive weakfish (Connaughton and Taylor, 1996a). The calls of captive, spawning weakfish were identical to the sounds recorded in the field. Audio and video recordings of captive weakfish indicate that the rate of calling by the male does not increase as the spawning event approaches. Drumming may begin before or after the first spawning event and continues for several hours after the last one of the evening, but it is maintained at a relatively constant rate until the behavior ceases. In addition, drumming ceases prior to spawning and is apparently not involved in the timing of gamete release in weakfish (Connaughton and Taylor, 1996a) or in two other sciaenids, red drum *Sciaenops ocellatus* (Guest and Lasswell, 1978) and Atlantic croaker *Micropogonias undulatus* (M. A. Connaughton and M. L. Lunn, unpublished data). Male courtship drumming therefore probably functions to attract a female, although this could not be experimentally determined in the small tanks used for these studies. The high turbidity of the inshore waters in which these fish reproduce (Biggs et al., 1983), the evening spawning habit (Taylor and Villoso, 1994; Connaughton and Taylor, 1995a) and the absence of external sexual dimorphism that might serve as visual cues support this hypothesis. Drumming may also act as a rallying call for the formation of spawning aggregations, as has been suggested for haddock *Melanogrammus aeglefinus* (Templeman and Hodder, 1958). As pair spawning was observed in captivity, drumming may play a role in mate selection. Variation in acoustic signals with fish size (Connaughton et al., 1997, 2000) could also provide females with a basis for choice among several calling males (see below).

Seasonal cycles in the sonic muscle

Merriner (1976) noted that the sonic muscle of the weakfish changes color and thickness seasonally. Indeed, the sonic muscle triples in mass as the spawning season approaches and remains hypertrophied until after the spawning season, when it atrophies (Connaughton and Taylor, 1994). A similar seasonal increase in sonic muscle mass has been observed in male haddock (Templeman and Hodder, 1958) and has recently been noted in male Atlantic croaker (S. Modla, M. L. Lunn and M. A. Connaughton, unpublished data). In weakfish, this hypertrophy is the result of increasing muscle thickness since muscle width and length do not change seasonally (Connaughton and Taylor, 1994). Sonic muscle hypertrophy is driven by elevated androgen levels, which are triggered by photoperiod and temperature cues that initiate sexual recrudescence (Connaughton and Taylor, 1994, 1996b). The sonic muscle also responds directly to exogenous testosterone and remains hypertrophied as long as testosterone is available (Connaughton and Taylor, 1995b).

Sonic muscle hypertrophy results from increases in fiber cross-sectional area. Fiber diameter averages 40 μm during the spawning season and 23 μm during the off-season (Connaughton et al., 1997). Both the contractile cylinder (myofibrils and sarcoplasmic reticulum) and the peripheral sarcoplasm increase in size. The late-summer atrophy of the muscle reflects decreasing contractile cylinder size and the virtual disappearance of the peripheral sarcoplasm in conjunction with a significant decrease in muscle protein content. Ono and Poss (1982) observed a fiber diameter of 29.6 μm in specimens collected in late August, after sonic muscle atrophy had begun. Muscle glycogen and lipid content decrease precipitously during early June as these energy stores are used, but muscle mass, protein content and fiber cross-sectional area do not decrease until later in the summer as androgen levels decrease (Connaughton and Taylor, 1994, 1995a; Connaughton et al., 1997).

Variation in call characteristics: influence of temperature, size and season

The impact of temperature, fish size and sonic muscle mass on the acoustic characteristics of drumming sounds (Table 1) were examined using in-air recordings of weakfish disturbance calls. Recordings were made in air to alleviate the problems associated with the acoustics of small tanks (Parvulescu, 1964) and to allow absolute SPL to be determined by recording at a known distance from the microphone, which can be difficult with a free-swimming fish. We recognize that the SPL values measured here will not be equivalent to those from recordings made at the same distance in water because of the density of the medium; however, SPL values in this study are internally consistent. Disturbance calls are similar to those of aquatic recordings made in the field or during captive spawning, apart from expressing a wider range in the number of pulses (Connaughton et al., 2000).

The effects of temperature on acoustic characteristics were determined by recording eight similarly sized fish (28–31 cm) at 18, 23 and 12 °C, and again at 18 °C (Connaughton et al., 2000). Temperature changes took place over 3–4 days, and fish were then allowed to acclimate to each temperature for a minimum of 4 days. Recordings were made twice at 18 °C to control for possible effects of on-going muscle atrophy on acoustic characteristics. Repetition rate increases with temperature as a result of its effect on the pulse pattern-generator circuits in the central nervous system (Demski et al., 1973). Over the temperature range 12–23 °C, mean repetition rate increased from 13.4 to 24.3 Hz. Similar changes in repetition rate with temperature have been noted in a number of sound-producing teleost species (Schneider, 1967; Fine, 1978; Bass and Baker, 1991). SPL also increases with temperature (from 69.6 to 79.5 dB), suggesting a faster twitch time in warmer muscle.

The rate of Ca^{2+} uptake in toadfish sonic muscle sarcoplasmic reticulum increases at higher temperatures, which would support more rapid contraction (Feher et al.,

Table 1. *Influences of temperature, fish size and season (equivalent to changes in sonic muscle mass) on acoustic parameters of weakfish disturbance calls*

	Acoustic parameters			
Variable	Repetition rate of pulses within a call	Sound pressure level (amplitude)	Dominant frequency	Pulse duration
Increasing temperature	Increase	Increase	Increase	Decrease
Increasing total fish length	No change	Increase	Decrease	Increase
Increasing sonic muscle mass	No change	Increase	No change	Slight increase

All changes were significant ($\alpha=0.05$) as determined by linear regressions.
Data from Connaughton et al. (1997, 2000).

1998). As acoustic amplitude is proportional to volume velocity, which is the product of surface area and the movement velocity of the swimbladder surface (Bradbury and Vehrenkamp, 1998), SPL will increase with greater movement velocity generated by faster muscle twitches. Similarly, dominant frequency increases from 494 to 554 Hz across the 11 °C change in temperature. It is unlikely that this temperature range would change the resonant frequency of the swimbladder; the standard resonance equation for an oscillating bubble does not contain a temperature variable (Harris, 1964). Therefore, we argue that dominant frequency is determined by the forced response to muscle contraction rather by than the natural frequency of the swimbladder. Finally, pulse duration, which is inversely proportional to frequency, decreases with increasing temperature (from 3.7 to 3.4 ms), supporting the notion of faster twitches.

Eleven fish ranging in total length from 25 to 36 cm were recorded at 18 °C to examine the effect of fish size on acoustic parameters (Connaughton et al., 2000). Repetition rate does not change with fish size, indicating that the output of central pattern generators is independent of fish size. SPL increased by 9.7 dB, from 65.6 to 75.3 dB, across an 11 cm increase in total length. Increasing SPL with size may be attributed to increasing swimbladder size in larger fish (Hill et al., 1987). A larger swimbladder has a greater surface area, resulting in an increase in the volume velocity and, consequently, acoustic pressure. Dominant frequency decreases (from 560 to 479 Hz) and pulse duration increases (from 3.3 to 3.9 ms) with fish size. We argue against a resonance interpretation for the decrease in frequency because of the inverse relationship between pulse duration and dominant frequency (Fig. 3A,B); pulse duration

would not be affected by the natural frequency of the bladder. A scaling argument suggests that a larger muscle with longer fibers would take longer to complete a contraction, resulting in
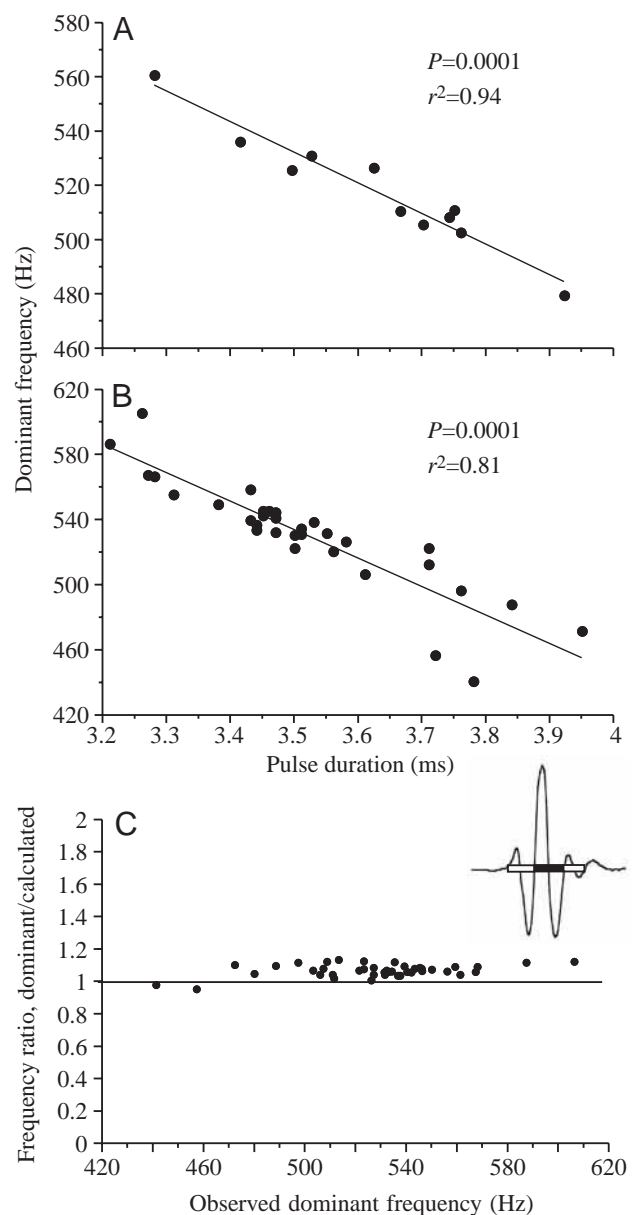

Fig. 3. Relationship between dominant frequency and pulse duration for (A) fish ranging from 25 to 36 cm in total length (recorded at 18 °C, $N=11$) and (B) fish recorded at 12, 18 and 23 °C (28–31 cm in total length, $N=8$). (C) A plot of dominant frequency divided by a frequency calculated from the period of the second cycle of acoustic energy (shaded bar in inset). Frequency was calculated as [1000/(the duration of the second cycle of acoustic energy)]. Note that the dominant frequency is closely matched (expressed as values near to 1) by the inverse of the duration of the second cycle of acoustic energy. Figures modified from Connaughton et al. (2000).

both a longer pulse duration and a lower acoustic frequency in larger fish (Hill, 1950; Wainwright and Barton, 1995).

The influence of season on call characteristics reflects the seasonal hypertrophy/atrophy cycle of the muscle. SPL increases by 6 dB (a doubling of acoustic pressure) (Bradbury and Vehrenkamp, 1998) from 59.8 to 65.7 dB with the seasonal tripling in sonic muscle mass. Pulse duration also decreases slightly, although there is no significant change in dominant frequency or repetition rate (Connaughton et al., 1997). Acoustic pressure is proportional to volume velocity and, as there is no indication that swimbladder size varies seasonally, it is likely that the increased SPL with muscle mass is due to faster movement of the sonic muscle, which is supported by the slight decrease in pulse duration with increasing muscle mass. Although seasonal changes in muscle fiber morphology include increases in both myofibrillar and sarcoplasmic area, the mechanism relating the effect of increased muscle mass on SPL to pulse duration has not been examined.

Mechanisms of sound generation

The fundamental frequency of long-duration sounds produced by multiple contractions in toadfish and midshipman is determined by sonic muscle contraction rate (Skoglund, 1961; Cohen and Winn, 1967). However, since weakfish sound pulses are generated by a single muscle twitch, it is possible that the natural frequency of the swimbladder determines the dominant frequency of these sounds. This assumption is consistent with the low dominant frequencies observed in larger fish because a larger swimbladder, functioning as an underwater bubble, would resonate at a lower frequency (Harris, 1964; Van Bergeijk, 1964). We argue that dominant frequency is determined by the velocity of the swimbladder driven by the sonic muscle rather than by the natural frequency of the swimbladder. The acoustic waveform of weakfish pulses decays rapidly, and the sound spectrum contains energy with a wide bandwidth (Fig. 4). These are characteristics of a low-Q, broadly tuned resonator (the quality factor Q is a measure of the sharpness of tuning) (Bradbury and Vehrenkamp, 1998) responding to contractions of the sonic muscle rather than the natural frequency of the swimbladder. It has been understood for some time that the swimbladder is highly damped (Weston, 1967; Sand and Hawkins, 1973), but the low Q value was attributed to damping by the surrounding tissues rather being than a property of the swimbladder itself. Fine et al. (2001) have recently demonstrated, by driving the sonic muscle across a range of frequencies, that the toadfish swimbladder is a low-Q resonator that will produce any frequency of sound imparted by the sonic muscle. We argue a similar case for the weakfish. A larger fish will take more time to contract a longer muscle (Hill, 1950; Wainwright and Barton, 1995), resulting in decreased dominant frequency.

The variation in dominant frequency with temperature also indicates that sonic muscle twitch speed, and not the natural frequency of the bladder, determines acoustic frequency because only the former will vary with temperature (Harris, 1964). Finally, there is a tight inverse relationship between
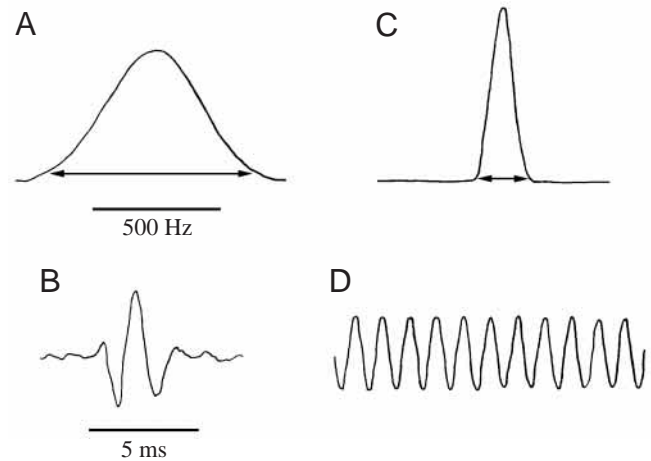

Fig. 4. Frequency and time-domain responses of low- and high-Q resonators. Acoustic data from a single weakfish pulse (A,B) express a wide bandwidth (arrows in A) and short duration (B, total duration less than 5 ms), typical of a low-Q, broadly tuned resonator. Acoustic data from a 440 Hz tuning fork (C,D) express a narrow bandwidth (arrows in C) and a long duration (D, total duration more than 10 s), common to a high-Q, tuned resonator (after Bradbury and Vehrenkamp, 1998). The time scales in C and D are the same as those in A and B.

pulse duration and dominant frequency across a wide range of temperatures and fish sizes. Indeed, the inverse of the second cycle of acoustic energy (with the greatest amplitude) matches the dominant frequency almost perfectly (Fig. 3C). These data support the hypothesis that acoustic frequency is determined by the velocity of the sonic muscle twitch rather than by the natural frequency of the swimbladder, i.e. we are extending established results on fish sounds produced by trains of muscle contractions to ones produced by a single twitch.

Concluding remarks

What are the implications of the mechanism of sound generation and the resultant variation in sound on the ecology and behavior of weakfish? The yearly cycle in condition of the sonic muscle reflects its seasonal use and its importance in reproductive behavior. One of the effects of the seasonal hypertrophy of the sonic muscle is an increase in SPL, and a more intense signal will be heard at a greater distance, presumably by a larger number of potential mates. Temperature influences a number of acoustic variables, but it will not have a strong impact on behavior if the responses of the females express temperature-coupling, as seen in frogs and insects (Gerhardt, 1978; Doherty, 1985), or even if they do not because all males will be calling at approximately the same temperature. However, the variability of acoustic parameters with fish size might have important repercussions on behavior. A larger male can produce a signal of greater SPL, which might attract a female from a greater distance. Finally, the lower-frequency and more intense sounds produced by a larger male might act as an 'honest' signal (Sargent et al., 1998) of male fitness and serve as a basis for female choice.

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