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SPAWNING SOUNDS OF THE DAMSELFISH, *DASCYLLUS ALBISELLA* (POMACENTRIDAE), AND RELATIONSHIP TO MALE SIZE

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SPAWNING SOUNDS OF THE DAMSELFISH, *DASCYLLUS ALBISELLA* (POMACENTRIDAE), AND RELATIONSHIP TO MALE SIZE

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ABSTRACT

Synchronous audio-video recordings were made of free-living *Dascyllus albisella* on coral reefs at Johnston Atoll, Central Pacific Ocean. Males produced distinct and consistent sounds during courtship and mating. The courtship sound is a well-known feature of pomacentrid behavior, and is produced during the signal jump. Male *D. albisella* also produced a mating sound, which has not been previously described for any other pomacentrid. The mating sound is produced as the male quivers during spawning. The courtship sound differed from the mating sound by having a greater number of pulses (6 ± 4 vs. 3 ± 1 , mean \pm SD) and a longer duration (262 ± 57 vs. 127 ± 45 msec). The courtship sounds of larger males were lower in frequency than those of smaller males ($r^2=0.64$, power regression). The median dominant frequency of small males (20 to 40 g) was 390 Hz ($n=12$ males), compared to 334 Hz ($n=7$ males) for large males (40 to 60 g).

Key words: sound production, damselfish, Pomacentridae, *Dascyllus albisella*, spawning.

INTRODUCTION

Males of many fishes, including pomacentrids, produce sounds during courtship. The simplest information that may be contained in the acoustic signals are the male's location, readiness to spawn, and body size. In this study we examined the courtship calls of *Dascyllus albisella* (Pomacentridae) to define within- and between-individual variation in pulse content and dominant frequency. We also discovered that *D. albisella* produced another pulsed sound that was associated with the mating act. The details of these acoustic signals were examined to determine if they were distinct and definable according to behavioral context, and whether any features of the courtship call were related to male size.

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A basic principle of underwater physics is that larger swimbladders resonate at lower frequencies than smaller swimbladders (Clay and Medwin 1977, Urick 1983. Spanier (1970) hypothesized that sounds produced by the domino damselfish *Dascyllus trimaculatus* (Pomacentridae) were generated by pharyngeal jaw grating and resonance through the swimbladder. In sonic fishes, the association between swimbladder size and resonance frequency may provide females with a reliable signal of male size. Body size is an important variable affecting the reproductive success of males in many fishes (Perrone 1978, Noonan 1983, McKaye 1986, Myrberg et al 1986, Hert 1990, Wootton 1990, Bisazza and Marin 1991, but see Petersen 1995). There is some evidence that among sonic teleosts (except, perhaps, for those species with highly specialized sonic muscles on the swimbladder) larger fish produce lower frequency sounds than smaller fish (Myrberg et al. 1965 Demski et al. 1973, Fine et al. 1977, Rowland 1978, Myrberg and Riggio 1985). To date this has been rigorously tested only for the bicolor damselfish, *Stegastes partitus* (Pomacentridae) (Myrberg et al. 1993). We hypothesize that frequency is a morphologically determined signal related to swimbladder and body size, and therefore should be evident among many species.

METHODS

Study site

Johnston Atoll is a coral reef ecosystem in the Central Pacific Ocean (16° 44' N, 169° 31' W). Recordings were made of free-living fish in the lagoon during May 1991 and April 1994. Sea water temperatures in the lagoon ranged from 26.0 to 26.8°C in May 1991, and 25.1 to 26.6° C in April 1994. Water depth was between 4-6 m.

Acoustic-video recording

Synchronous audio-video recordings were made underwater using a SONY model V-9 8mm video camera coupled to a hydrophone. The hydrophone had a frequency range of 10 to 3000 Hz and a sensitivity at 10 psi of -162 dBV/mPa + 2dB (BioAcoustics, Box 594, Woods Hole, MA).

Audio-video recordings of courting and mating *Dascyllus albisella* were made while using SCUBA with controlled breathing to avoid excessive regulator and bubble noise. The hydrophone was generally placed between 0.5-1.0 m of the fish, while the diver was positioned 3 to 5 m away operating the video camera. The hydrophone was attached to the video camera by a 5 m long cable and manipulated on a sound

boom (a 2.5 m pole) that rested on the bottom. The hydrophone was located at the end of the boom with 40 cm of free cable, and buoyed so it that floated freely in the water column. After recording, fish were collected by spear and measured and weighed while fresh. Histological analysis of the gonads of the 9 males recorded in May 1991 confirmed that each specimen was a mature male.

Acoustic analysis of sounds

Each sound was classified according to the behavior of the male producing the sound as seen on the video. Acoustic analyses used the signal processing hardware and software package SIGNAL (Engineering Design, Belmont, MA). The acoustic signal was processed through a digital filter (Frequency Devices, Model 9002) that attenuated frequencies above 2 kHz (after verifying that the dominant energy in the signals was below 1 kHz), before being converted to a digital signal at a sampling rate of 5000 Hz. Dominant frequency was analyzed using 325 recordings from 19 males (mean = 17 sounds/fish, range = 5–44). Other analyses of courtship sounds used 393 calls from 25 males (6 males were not collected) (mean = 15 calls/fish, range = 4–44). Measurements of the number of pulses in a sound and its duration were made from the oscillogram. Pulse period was calculated by dividing the call duration in milliseconds by the number of pulses minus one in that call. The dominant frequency of a call was calculated by averaging the dominant frequencies of the pulses comprising the call. Since the sounds produced by *D. albisella* are broad-band, energy is spread among several frequencies and not concentrated at one frequency as in tonal sounds. To calculate the dominant frequency of a sound, each pulse within a multiple-pulse sound was isolated, and its power spectrum was derived by a 32k-point fast Fourier transform (FFT). The power spectrum displays the distribution of energy in the signal as a function of frequency. The dominant frequency of a pulse was calculated from the power spectrum by measuring 3 dBVolts (re 1 V) down from the peak frequency, and averaging the lowest and highest frequencies at that amplitude. By determining the dominant frequency of a pulse using this “3dB down” technique, the average of the energy distribution is better represented than by the frequency that has the highest peak energy (R. Fricke, M.I.T., Cambridge, MA, pers. comm.). Because the signal lengths of the pulses were about 50 ms, the frequency resolution bandwidth is approximately 20 Hz (Papoulis 1984).

Statistical analyses used StatWorks (Cricket Software, Philadelphia, PA) and SYSTAT (Systat Inc, Evanston, IL). P-values for regression analyses test the null hypothesis that the slope is zero ($H_0: \beta = 0$). For comparison of correlation coefficients (r) the 95% confidence

intervals for the linear regression and power regressions were calculated using Fisher's z-transformation (Zar 1984).

We are following the nomenclature of Allen (1991) in the naming of the pomacentridae: *Stegastes partitus* synonyms are *Pomacentrus partitus* and *Eupomacentrus partitus*.

RESULTS

Courtship and mating sounds

Males produced the courtship call while performing the "signal jump" or "dip", in which a male rises in the water column and then rapidly swims down while producing the pulsed courtship sound (described by Myrberg (1972) for *Stegastes partitus*) (Figure 1a). In addition to the courtship sound, males also produced a mating sound. This mating sound (Figure 1b) was accompanied by a "mating quiver", a lateral quivering of the body that began at the head and progressed posteriorly. Analysis of videos of six males performing this behavior revealed that it occurred at the beginning of mating bouts as a female moved to the nest site, and during what we presumed to be egg laying. The male apparently fertilized the eggs while fanning the nest surface both during and after egg laying. The mating quiver did not occur during apparent male fertilization behavior.

The number of pulses of the courtship calls ($n = 393$ by 25 males) correlated with the call duration ($r = 0.841$, $p < 0.001$), indicating that the courtship calls had a relatively constant pulse period. Coefficients of variation were calculated for courtship calls using the median values of the call characteristics for each male (frequency CV = 10%, number of pulses CV = 10%, call duration CV = 12%, pulse period CV = 9%).

Two-way ANOVA analyses were used to test for differences in call characteristics (number of pulses, call duration, and pulse period) between courtship calls and mating sounds using call type ($n = 2$) and individual males ($n = 6$) as factors. The analysis of pulse period excluded sounds with only one pulse. The sound made during the mating quiver had a longer pulse period (mean \pm SD = 63 ± 11 msec/pulse) than the courtship call (mean \pm SD = 57 ± 5 msec/pulse), was of shorter duration (mean \pm SD = 127 ± 45 msec vs. mean \pm SD = 262 ± 57 msec), and contained fewer pulses (mean \pm SD = 3 ± 1 vs. mean \pm SD = 6 ± 4) (Figure 2). All of these differences were highly significant ($p < 0.001$). However, there was a significant interaction between call type and individual male for pulse period, thus the difference in pulse period of courtship and mating sounds cannot be considered statistically significant.

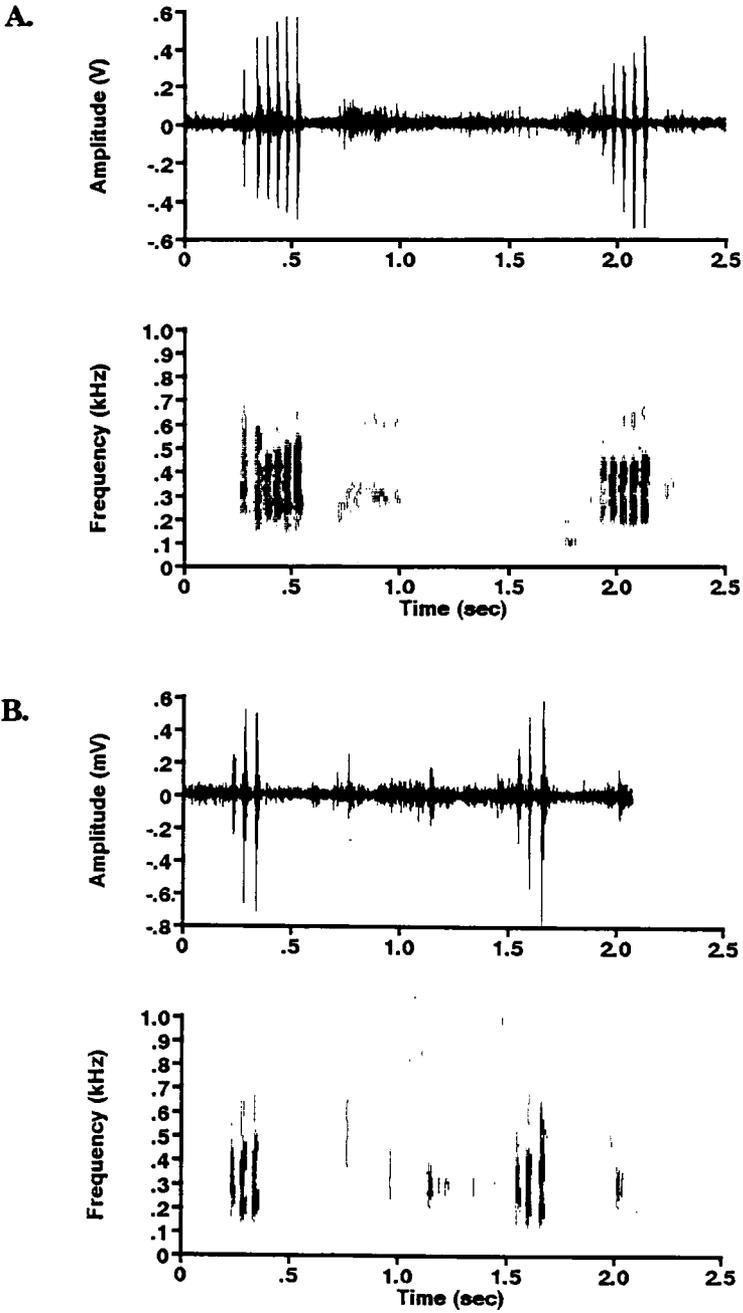


Figure 1. A. Oscillogram (top) and spectrogram (bottom) of two courtship calls produced by one male *Dascyllus albisella*. B. Oscillogram and spectrogram of sounds produced during two mating quivers by the same individual as Figure 1a.

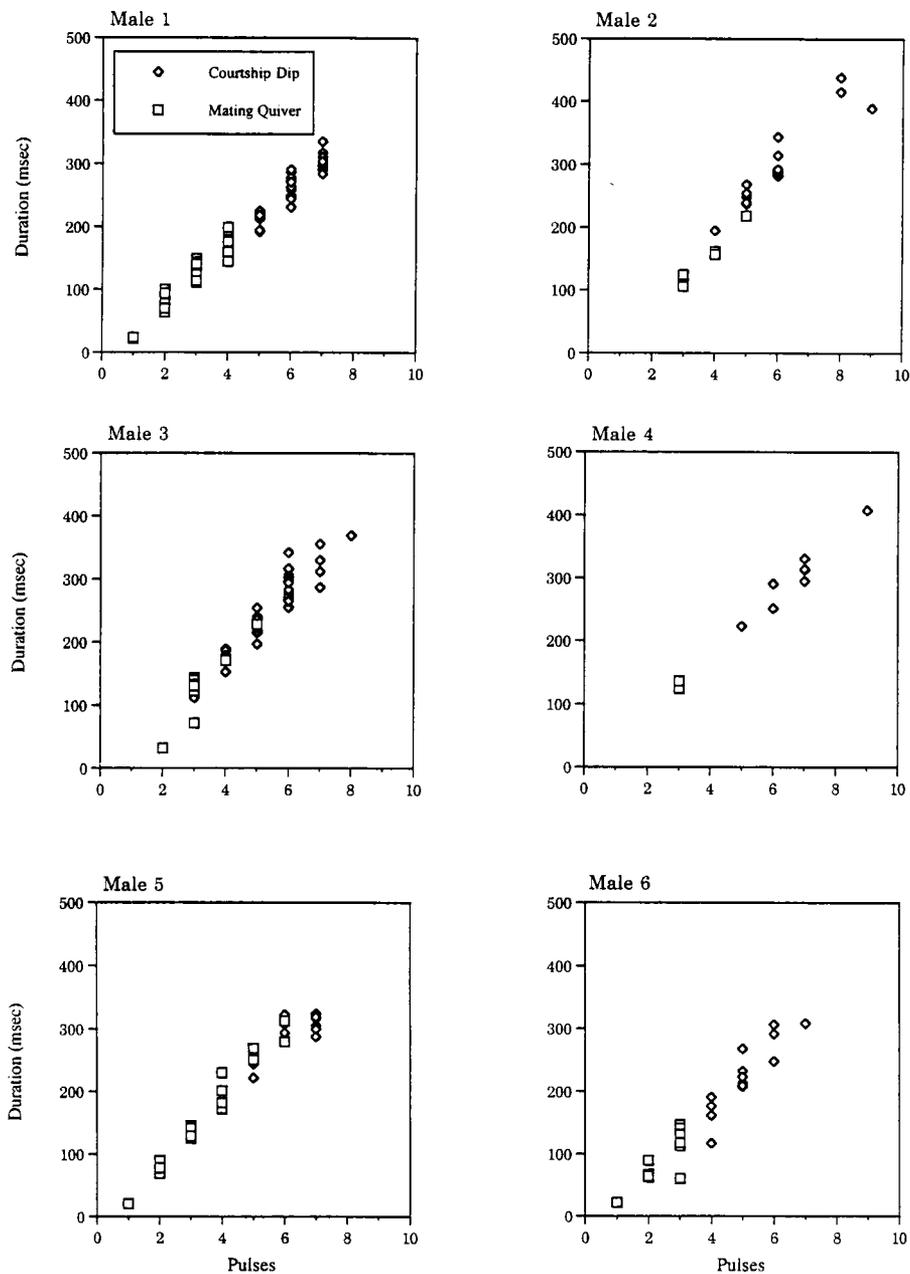


Figure 2. Comparison of number of pulses versus duration for the sounds produced during the courtship dip and mating quiver. Each of the graphs shows the data from one of six males.

Relationship of courtship call and male size

To determine if the size of the fish producing the courtship calls could explain any of the variation in the call characteristics, the weights of the fish were plotted against the median number of pulses ($r^2 = 0.147$, $p = 0.094$), duration ($r^2 = 0.248$, $p = 0.031$), and period ($r^2 = 0.096$, $p = 0.148$) (Figure 3). These analyses showed a positive slope indicating that the median number of pulses, call duration and pulse period increased with increasing size. However, the r^2 values were low, indicating that much of the variation was not explained by the weight of the fish. Only the regression of duration on size had a slope significantly different from zero.

To test the hypothesis that the dominant frequency correlates negatively with male size, the medians of the dominant frequencies of the courtship calls were plotted against the weight of the fish and linear and power regressions were performed (Figure 4). These regressions produced a negative slope ($r^2 = 0.590$, $p < 0.001$ linear, $r^2 = 0.639$, $p < 0.001$ power), indicating that larger fish produced lower frequency calls. The correlation coefficients were not significantly different at $\alpha = 0.05$ (95% confidence intervals for linear regression, $r = 0.694 \pm 0.213$; power regression, $r = 0.799 \pm 0.189$). Among these fish, the mean coefficient of variation of the dominant frequency of the courtship calls was $11\% \pm 1\%$ (mean \pm SD).

DISCUSSION

The two sounds produced by *Dascyllus albisella* during courtship and mating are distinct in the number of pulses and duration of the sound. There is a negative relationship between male size and the dominant frequency of the courtship call: larger males produced lower frequency calls.

Although there is a lack of strong experimental data, most evidence suggests that sound is important in reproductive behavior of sonic fishes and plays a role in species and size identification (Myrberg 1980a, 1980b, 1981, Hawkins and Myrberg 1983). Playbacks of male courtship sounds elicited responses by both male and female conspecific pomacentrids (Spanier 1979, Myrberg and Spires 1972, 1980, Myrberg et al. 1986). Species-specific recognition of sympatric pomacentrids (*Pomacentrus* spp.) was experimentally demonstrated to be based upon the number of pulses and pulse rate of a call (Myrberg and Spires 1972, Spanier 1979). *D. albisella*, in comparison with *Stegastes partitus*, has a longer pulse period (45 msec vs. 38 msec) and more pulses per call (6 vs. 3). Its call is more similar to the call of *Stegastes dorsopunicans* (41 msec period, and 6 pulses per call) (data from Spanier 1979).

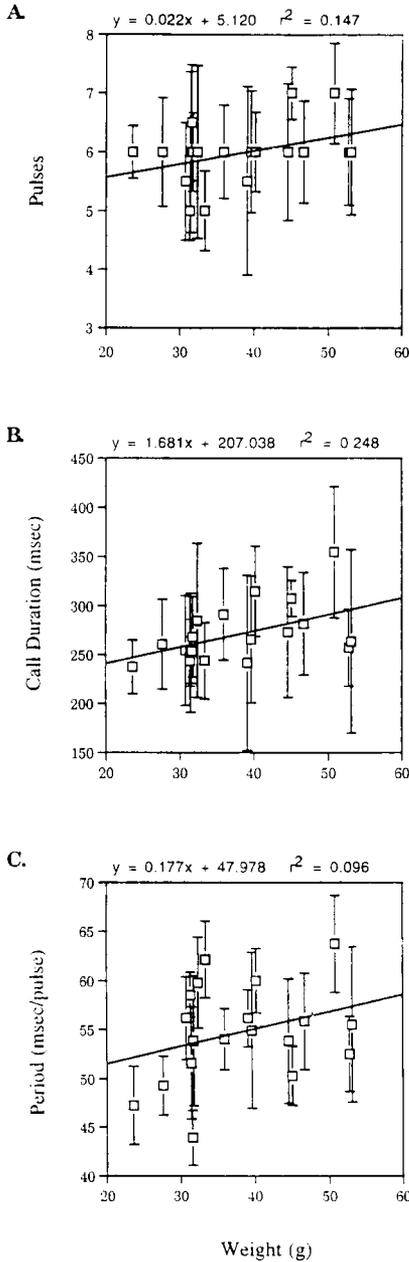


Figure 3. Relationships between male weight and three characteristics of the courtship sound. A. Number of pulses in a courtship call. B. Duration of a courtship call. C. Pulse period of the courtship calls. Squares represent the median value for an individual male with error bars showing the standard deviation. Median values are fitted with a linear regression and the equation for the regression is given above each graph.

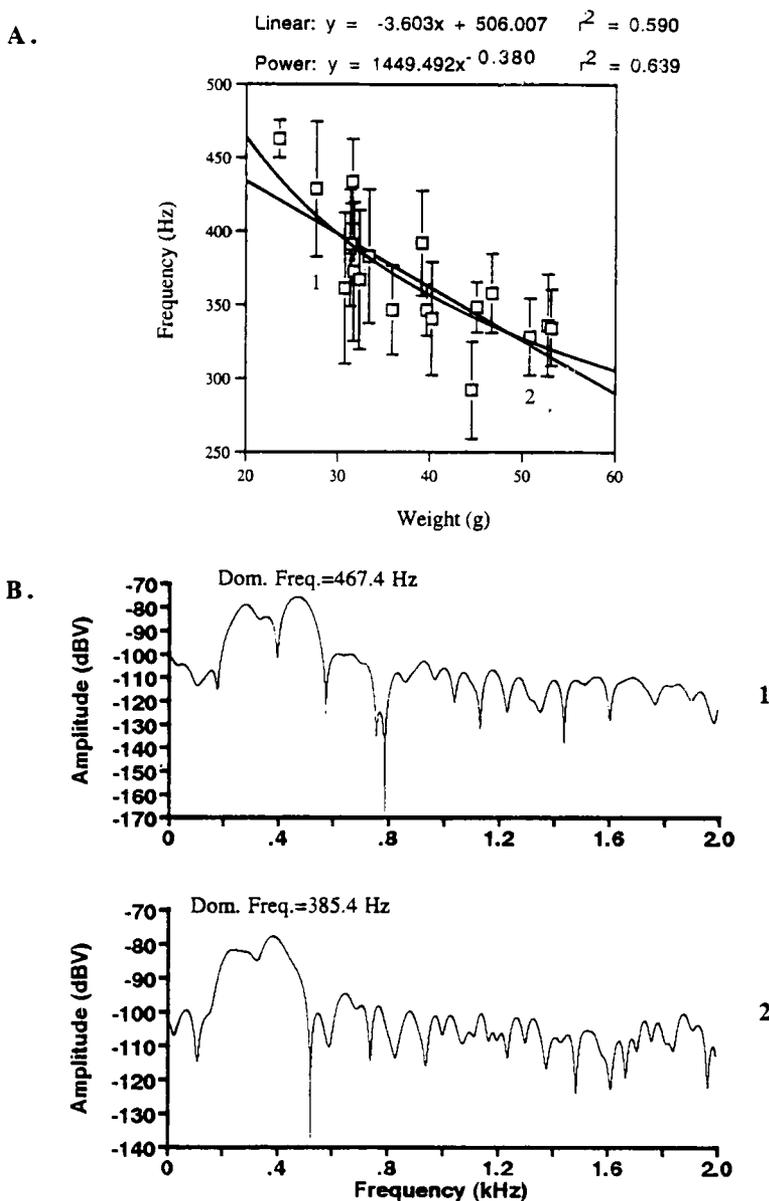


Figure 4. A. Relationship between male weight and the dominant frequency of the courtship call. Squares represent the median value for an individual male with error bars showing the standard deviation. Median values are fitted with a linear regression and a power regression and the equations for the regressions are given above each graph. B. Power spectra of one pulse from one courtship call for each of two males. The dominant frequency of the pulse is indicated above the spectra. The corresponding males that produced these sounds are labelled as 1 and 2 in Figure 4a.

The mating sound is produced both before and during female egg-laying. It may function as a final stage of courtship as well as in the mating process. It may be functionally similar to the 'grunt' of *S. partitus*, which occurs as the female enters the male's nest during the final stages of courtship (Kenyon 1993).

Myrberg et al. (1993) also showed a negative relationship between the dominant frequency of the courtship call and male size in *S. partitus*. However, regression of the data for *D. albisella* explained less of the variation ($r^2 = 0.64$) than a similar regression for *S. partitus* ($r^2 = 0.85$, Myrberg et al. 1993). One difference in our methods was that Myrberg et al. (1993) measured the dominant frequency of a call by calculating the peak frequency of the entire call, while we calculated the dominant frequency as the average of the dominant frequencies of the pulses using the 3dB-down technique. We re-analyzed the calls of nine fish calculating the frequency with the peak energy, and found that the power regression of dominant frequency against weight explained even less of the variation than the 3dB-down pulse averaging method ($r^2 = 0.34$ frequency with peak energy vs. $r^2 = 0.62$ by 3dB-down pulse averaging method). We also recalculated the data using the 3dB-down technique on entire calls as opposed to pulses within calls ($r^2 = 0.40$). The difference in the r^2 values was largely due to whether the dominant frequency was calculated from the whole call or from the average of individual pulses. These differences between species may be due to differences in the mechanisms of sound production or swimbladder shape. *D. albisella* are much larger than *S. partitus*, produce more pulses per call, and are likely to swim farther during signal jumping.

Can differences in call frequency be used by a female fish to evaluate male size or provide individual recognition of males? Non-ostariophysine fishes, including *Gobius niger* (Gobiidae), *Corvina nigra* (Sciaenidae) and *Sargus annularis* (Sparidae) can discriminate tones differing in frequency of about 10%; the frequency discrimination ability at 400 Hz is about 40 Hz for non-ostariophysine fishes (Fay 1988). If the discrimination ability of *D. albisella* is similar, then it could detect differences between males weighing 35g and 47g, which produce sounds of 375 Hz and 335 Hz, respectively (a 40 Hz difference). The ability of *D. albisella* to discriminate frequency differences of courtship calls may be different from that derived from this example, because the discrimination tests were performed with tonal sounds, not broad-band pulsed sounds.

The association of specific sound patterns with courtship and mating behavior suggest that bioacoustic signals may be an important component of mate choice in *D. albisella*. Our results showing a size-dependent frequency of the courtship sound, and those of Myrberg (1993) for *S. partitus*, support the hypothesis that dominant frequency is morphologically determined by swimbladder and body size.

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