

Sexual Differences in the Spawning Sounds of the Japanese Croaker, *Argyrosomus japonicus* (Sciaenidae)

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Jinn-Pyng Ueng, Bao-Quey Huang, and Hin-Kiu Mok (2007) Sexual differences in the spawning sounds of the Japanese croaker, *Argyrosomus japonicus* (Sciaenidae). *Zoological Studies* 46(1): 103-110. Sexual differences in the calls voluntarily emitted during the spawning season of the Japanese croaker (*Argyrosomus japonicus*) raised in tanks and ponds in the Penghu Archipelago, Taiwan, are described. Calls are composed of a train of pulses of drumming sounds and were heard primarily after dusk. The spawning-season advertisement calls of the male and female differ; females generated significantly more pulses per call, and their calls had a longer call duration, a shorter pulse period, and a lower dominant frequency than those of males. Both sexes vocalized during the actual spawning, and their activities are described herein. Possible roles of these sounds are discussed. <http://zoolstud.sinica.edu.tw/Journals/46.1/103.pdf>

Key words: Fish sounds, Penghu Islands, Sound production, Spawning sounds, Sexual dimorphism.

Members of the Sciaenidae, comprising about 270 species within 70 genera (Chao 1986), have long been known as soniferous fishes. Their sounds, composed of bursts of knocking, drumming, or croaking sounds (Tavolga 1971), are emitted by vibrating a pair of striated swim bladder muscles closely associated with the lateral body wall musculature (Tower 1908, Takemura et al. 1978). Sciaenid sound production is primarily limited to the spawning season (Mok and Gilmore 1983, Saucier and Baltz 1993, Connaughton and Taylor 1995), suggesting that it might play a role in reproduction. Sound production during the reproductive season has been reported in a number of sciaenid species, such as the drumfish, *Argyrosomus argentatus* (Takemura et al. 1978); red drum, *Sciaenops ocellatus* (Guest and Lasswell 1978); black drum, *Pogonias cromis*; silver perch, *Bairdiella chrysoura*; spotted seatrout, *Cynoscion nebulosus* (Mok and Gilmore 1983,

Saucier and Baltz 1993); and weakfish, *Cynoscion regalis* (Connaughton and Taylor 1996).

The Japanese croaker, *Argyrosomus japonicus* is a commercial marine food-fish species in Taiwan. Fishermen in the Penghu Archipelago culture this species in saltwater net cages. In local aquaculture farms, both sexes of Japanese croaker mature at 5-6 yr of age and body lengths of 70-80 cm (Lin et al. 1998). There is no sexual dimorphism in any of the secondary sex characters including the presence of sonic muscles (Griffiths and Hecht 1995). Japanese croakers begin to call when they reach an age of 6 mo (Ueng et al. 1999). In culture ponds, these young individuals aggregate in groups during the day when less locomotion and fewer sounds are noted. At dusk, they became more active leading to increasing inter-individual encounters which could be the cause for an obvious increase in sound production. Adults more than 5-yr-old emit calls during

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the spawning season (Mar. to June in Penghu), and the most vigorous period of their soniferous activity is at dusk (Ueng and Huang 1998). The croaking sounds can clearly be heard without the aid of hydrophones when standing about 3 m away from the pond. Some aquaculturists in Penghu believe that these sounds may induce early spawning if mature fish are stimulated with conspecific sounds. Therefore, they play back calls of males and females into breeding ponds during the early part of the spawning season.

Sciaenids form spawning aggregations in the wild (Saucier and Baltz 1993). The increase in spawning activity is associated with an increase in the repetition rate of male red drum calls (Guest and Lasswell 1978). It has been suggested that sciaenid sounds, like those of other soniferous fishes (Lobel 1992), may play important roles in reproductive behavior, including formation of aggregations of spawning individuals and successful courtship. In most sciaenid species, such as *C. regalis*, *Leiostomus xanthurus* (Connaughton et al. 2002, Hill et al. 1987), *Johnius macrorhynchus*, *J. belangerii*, *Pennahia pawak*, *Otolithes ruber*, *Chrysochir aureus*, and *Atrobucca nibe* (pers. obs.), only males have sonic muscles and call in the spawning season. Conversely, both sexes of *Micropogonias undulates*, *Argyrosomus japonicus*, *Nibea albiflora* (Fish and Mowbray 1970, Hill et al. 1987, Takemura 1978, Griffiths et al. 1995), *Pogonias cromis* (Chao, 1986), *Argyrosomus argentatus* (= *Pennahia argentata*), *Pennahia macrocephalus*, *Protonibea diacanthus*, *J. tingi*, *J. amblycephalus*, and *J. sina* (pers. obs.) possess sonic muscles. In *A. argentatus* and *N. albiflora*, male and female sounds have different fundamental frequencies (Takemura et al. 1978), with the male sound being higher than that of the female in both species.

The purpose of this study is to report on sexual differences in sound characteristics of the Japanese croaker as a contribution to our knowledge about the role of acoustic cues in spawning.

MATERIALS AND METHODS

On 9 Feb. 1998, 84 *A. japonicus* were supplied by a private aquaculture farm in Hu-Shien Township, Penghu, Taiwan. They were kept in a concrete holding tank until Feb. 13 when they were sorted by sex. Sexes were determined by examining the fish for the presence of sperm or eggs after gentle pressure was applied to the abdomen.

Males and females were kept in 2 separate concrete tanks (10 x 6 x 1.2 m). The tanks were under a natural photoperiod, with water temperature held between 18.5 and 21.8°C, and a salinity of 34-35 ppt, with flow-through seawater. Fish were fed once a day with smashed fish flesh. The 46 eight-year-old males (with a mean total body length of 92.2 cm and weight of 7.18 kg) and 40 females of the same age (with a mean body length of 91.9 cm and weight of 7.07 kg) did not significantly differ in terms of these 2 parameters ($t = 0.72$, $p > 0.05$; Student's t -test).

Calls were recorded from these unisex tanks using a hydrophone (B&K, model 8104; frequency range 0.1 Hz to 120 kHz, manufactured in Denmark), amplifier (B&K, model 2635), and a tape recorder (TC-D5, Sony, Tokyo, Japan). The hydrophone was suspended vertically at 1 m in depth in the center of the tank. Sounds were analyzed using Kay sound processing hardware and software package (Computerized Speech Lab 4300B, U.S.A.). The number of pulses per call and the call duration were quantified from the sonograms. The pulse period (in milliseconds) was obtained by dividing the duration (measured from the beginning of the 1st pulse to the beginning of the last pulse) by the number of pulses minus 1 (Mann et al. 1997). To calculate the dominant frequency of a call, each pulse was isolated from a multiple-pulsed call, its power spectrum was derived by Fast Fourier Transformation (FFT; Computerized Speech Lab 4300B), and the dominant frequency was taken as the highest peak from the power spectrum. As the sounds were from the unisex groups, they were considered to be advertisement calls.

On 20 Feb., all 84 fishes were transferred from the unisex tanks to a concrete breeding pond (10 x 6 x 1.2 m). Sound recordings were made from 17:00 to 24:00 between 23 Feb. and 3 Mar. Twenty-four-hour monitoring for sound production was in place between 4 and 12 Mar. Temperature and illumination levels were recorded hourly. To induce group spawning in all 86 fish, individuals were temporarily removed from the breeding pond for an injection of 400 IU/kg of human chorionic gonadotrophin (HCG), starting at 10:00 on 7 Mar. All males and females were transferred back to the breeding pond immediately after the injection. Sound recordings were made from 17:00 to 24:00 between 13 and 17 Mar.

All pre-spawning calls from males and females kept in the single-sex groups and those from the breeding pond were emitted voluntarily in

that they were not elicited as a result of human disturbance. Male and female sound characteristics were compared and tested by Student's *t*-test with statistical significance set at $p < 0.05$. The relationships between the call duration and number of pulses per call for males and females were separately estimated by regression analysis. The slopes of the 2 equations and sexual differences in call duration were tested using an *F* test for the interaction between gender and the number of pulses per call in determining the call duration, with statistical significance set at $p < 0.05$. To examine if there were any vocal interactions between males and females in the breeding pond during actual spawning, sequences of male and female calls in a long train of calls were analyzed using the nonparametric runs test (Brown and Downhower 1988).

Morphometric data (length was the maximum distance from the anterior to the posterior end of the muscle, width was the maximum distance from side to side of the muscle, and thickness was the maximum depth of the dorsoventral axis of the muscle) and weight (i.e., total muscle mass) of the sonic muscles for 8 mature males and 10 mature females were recorded (Table 1). These data were normalized by converting to percentages of total body length and total body weight, respectively as the body lengths and weights of these specimens differed (Table 1). Data of these parameters for the sonic muscles of each specimen were arcsine-transformed before being subjected to the statistical tests.

RESULTS

Oscillograms and sonograms of spawning-season sounds produced by male and female Japanese croakers kept in separate tanks as single-sex groups are shown in figure 1. A comparative summary of the sound characteristics of both sexes is shown in table 2. The sounds are composed of a series of pulses produced at regular intervals. Gender-related differences in call characteristics were examined for 213 male and 164 female sounds (Table 2). Female sounds showed a longer call duration ($t = -13.188$, $p < 0.001$), a higher pulse number ($t = -14.286$, $p < 0.001$; Fig. 2), a longer inter-pulse interval ($t = 12.125$, $p < 0.001$), and a lower pulse duration ($t = -9.184$, $p < 0.001$) and pulse period ($t = 14.95$, $p < 0.01$) than male sounds (Table 2). The slopes of the 2 call durations vs. the number of pulses per call equations for the 2 genders (Fig. 3) significantly differed ($F = 35.35$, $p < 0.0001$), suggesting that an interaction existed between the number of pulses per call and gender in determining the call duration.

The calls contained sound energy up to 3.5 kHz, with the dominant frequency between 334 and 991 Hz. The frequency of male sounds was higher than that of females (685.9 ± 202.9 vs. 586.6 ± 189.8 Hz; Table 2).

Figure 4 shows the diel changes in the number of calls per hour by both sexes from 4 to 12 Mar. (the hormone was injected on 7 Mar., and actual spawning began on 8 Mar.; also see below), with associated illumination and water temperature data from the breeding pond. The number of

Table 1. Morphometric parameters and weight of the sonic muscles of eight 3-yr-old males and 10 females of *Argyrosomus japonicus*. Length was the maximum distance from the anterior to the posterior end of the muscle, width was the maximum distance from side to side of the muscle, and thickness was the maximum depth of the dorsoventral axis of the muscle

Parameter	Male	Female	Range		Significance
	Mean \pm SD	Mean \pm SD	Male	Female	
Length (cm)	14.9 \pm 0.61	12.53 \pm 0.82	14.4 - 15.5	11 - 13.5	
Length (%)	27.5	23.6	26.9 - 28.5	21.2 - 25.4	*
Width (cm)	2.34 \pm 0.1	1.86 \pm 0.12	2.2 - 2.5	1.6 - 2.1	
Width (%)	4.3	3.5	4.1 - 4.7	3.2 - 3.7	*
Thickness (mm)	2.76 \pm 0.12	1.95 \pm 0.15	2.5 - 3.1	1.8 - 2.1	
Thickness (%)	5.1	3.6	4.7 - 5.5	3.4 - 3.7	*
Weight (g)	6.02 \pm 0.53	2.63 \pm 0.4	5.3 - 7.5	1.53 - 3.3	
Weight (%)	2.08	0.97	1.8 - 2.35	0.7 - 1.0	*

* $p < 0.01$.

sounds emitted was consistently highest at dusk about 1 h after sunset. A sample of sound taken from the breeding pond prior to injection of the hormone showed that males were vocally more active than females; 84% of the 119 calls were emitted by males and the other 16% were by females. After injection of the hormone, acoustical activity and chasing behavior within the breeding pond increased with time, the number of sounds emitted obviously increased in 8 h, and spawning peaked at about 34 h after the hormone injection (Fig. 4).

Actual spawning episodes took place in the

evenings of 8-14 Mar. Egg masses respectively recorded on each of these evenings were 155, 2550, 335, 60, 795, 300, and 100 g. Fish remained scattered along the bottom of the breeding pond from dawn to mid-morning and emitted very few sounds. Around 11:00, the fish gathered in a group and swam in a large circle close to the bottom. Some foam was found on the water surface which was possibly from excretions by the fish. The size of the swimming path enlarged around 15:00. Fish occasionally rubbed their bodies against the floor of the pond. Sound events

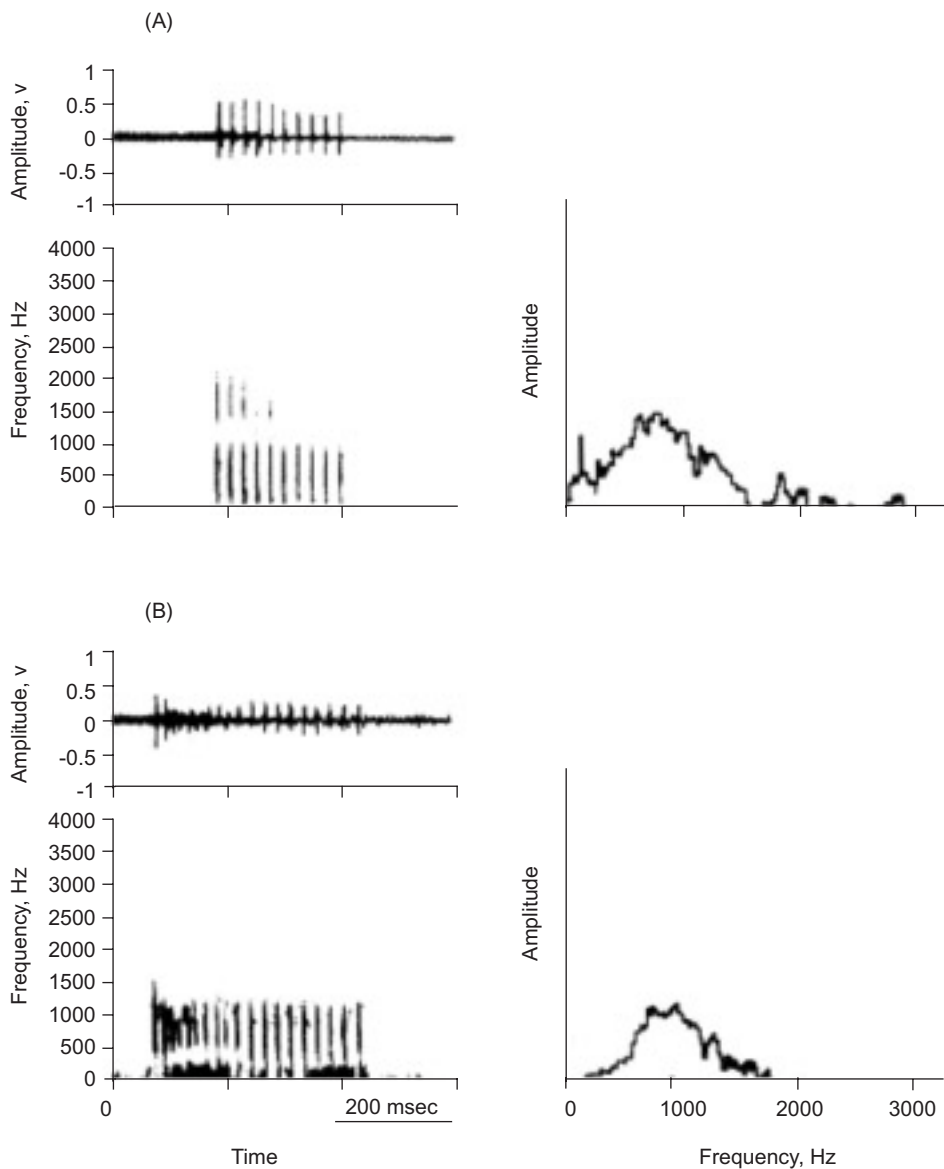


Fig. 1. Oscillograms, sonograms, and spectrograms of advertisement calls produced by *Argyrosomus japonicus* in single-sex groups during the spawning season. (A) A male call and (B) a female call. The spectrum is for the last pulse of the call. Note that the male call included 10 pulses in 220 ms and the female call included 19 pulses in 380 ms.

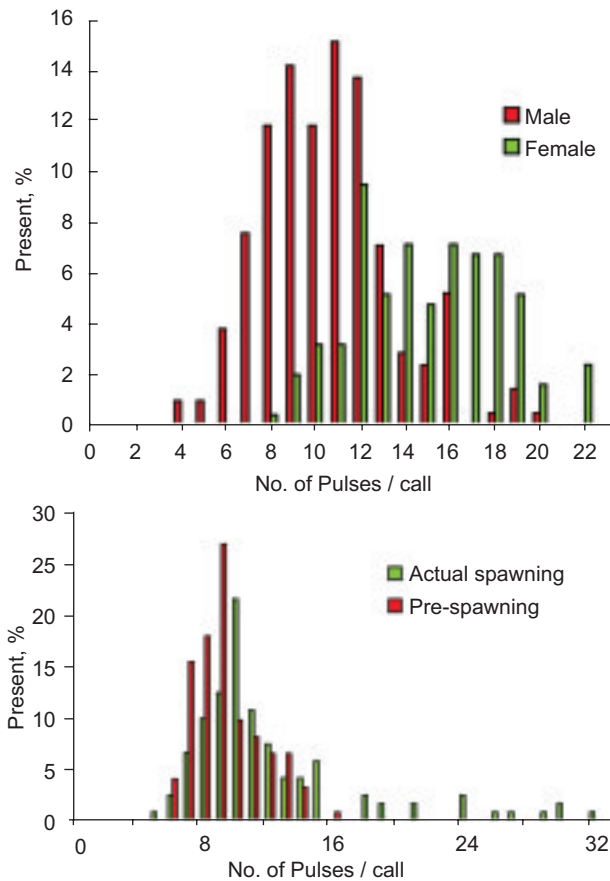


Fig. 2. Comparisons of variations in sex and spawning conditions on the percentage of advertisement calls which varied in the composition of the number of pulses. Top histogram: advertisement calls recorded from the 2 unisex tanks; 213 male calls and 164 female calls were analyzed. Bottom histogram: spawning calls from the breeding pond during actual spawning on the evening of 8 Mar. We analyzed 235 male and 211 female calls.

associated with courtship and spawning occurred from 15:00 to 21:00. From 15:00 to 16:00, the fish school moved along the sides of the pond, accompanied by sound emissions. Head-tail chasing intensified; chasing occurred in groups and between individuals. We could not tell if males chased after females or vice versa. These activities further intensified from 15:00 to 17:00 such that sounds could be heard all over the pond. Soon after 18:00, the amount of foam on the surface increased, and some eggs appeared on the water surface. Meanwhile, chasing further intensified, with fish rubbing their bodies against each other and emitting even more sounds including some with more pulses (Fig. 5). Although sexual dimorphism exists in the acoustic characteristics of the Japanese croaker call, it is clear that both males and females emitted sounds during the courtship and spawning phases (Fig. 5). At the moment of spawning, sounds with longer duration and more pulses per call were heard (Fig. 5) along with the regular croaking calls from both sexes. No obvious difference in sound frequency between the longer and regular calls was observed. Males seemed to be vocally more active than females; male calls made up 61.7% of a sample of 162 calls recorded during spawning. In a sequence of calls composed of 32 male calls and 29 female calls, the arrangement of these 2 types of calls was random (run test, number of runs = 31, $t = 0.03$, $p = 0.46$). After this peak of spawning, the fish swam in a group along the sides of the pond, but sporadic spawning and vocalization still continued for about 3 h. Then vocal activity steadily subsided toward dawn and finally ceased at sun-

Table 2. Duration, pulse number, pulse duration, pulse interval, pulse period, and dominant frequency of advertisement calls produced by *Argyrosomus japonicus* in a single-sex group during the spawning season. The sounds were recorded from a tank of male and female fish; fish of different sexes did not significantly vary in body length. We analyzed 210 male and 164 female calls in the unisex tanks

Sound characteristic	Male	Female	Range		Significance
	Mean \pm SD	Mean \pm SD	Male	Female	
Duration (ms)	231 \pm 65	316 \pm 62	110 - 386	210 - 374	*
Number of pulses/call	10.5 \pm 3.0	15 \pm 3.2	5 - 19	8 - 23	*
Pulse period (ms)	24 \pm 3	23 \pm 3	12 - 30	18 - 30	*
Pulse interval (ms)	11 \pm 1	14 \pm 1	9 - 15	11 - 17	*
Pulse width (ms)	13 \pm 2	10 \pm 1	10 - 16	8 - 13	*
Dominant frequency (Hz)	686 \pm 203	587 \pm 190	334 - 991	246 - 944	*

* $p < 0.01$.

rise. Afterward, fish were scattered on the bottom, and sounds were heard only occasionally.

A comparison of the sonic muscles of 8 mature males and 10 mature females of Japanese croaker showed that females' sonic muscles were thinner ($t = -5.325, p < 0.002$), lighter ($t = -8.141, p < 0.001$), and shorter ($t = -6.432, p < 0.001$) than those of males (Table 2).

DISCUSSION

Among the approximately 270 sciaenid species, there are relatively few species (e.g., *J. amblycephalus*, *J. sina*, *J. tingi*, and *Protonibea*

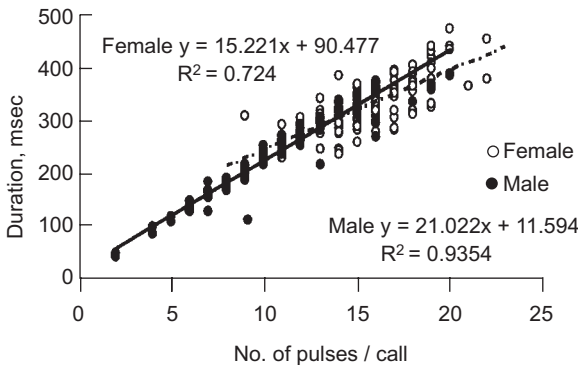


Fig. 3. Regression equations for male (solid line) and female (dashed line) *Argyrosomus japonicus* calls for estimating the relationships between call duration and pulse numbers.

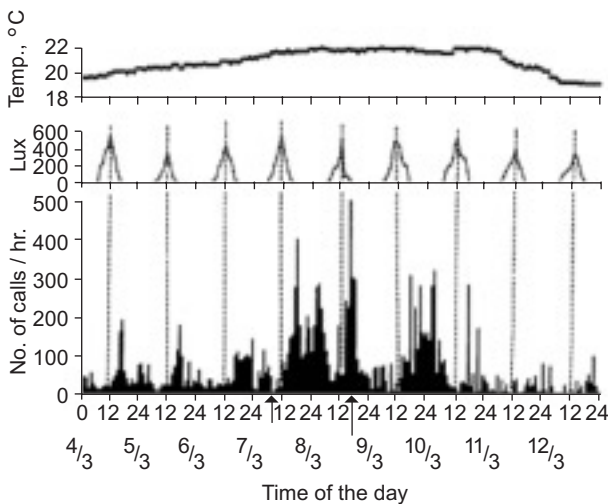


Fig. 4. Temperature (upper) and illumination (middle) changes and the diurnal occurrence (lower) of sounds emitted by *Argyrosomus japonicus* in the breeding pond from 4 to 12 Mar. 1998. Fish were introduced into the pond on 20 Feb. Short and long arrows along the abscissa respectively indicate the HCG injection date and the date when the 1st spawning occurred after the hormonal injection.

diacanthus) in which both sexes possess sonic muscles. Little information is available about the female sounds of these species, and consequently, questions concerning the selective factors that lead to the occurrence of sonic muscles in females remain speculative. The present dataset demonstrates for the 1st time that female Japanese croakers emit sounds during the spawning season including at the time of actually spawning, and that their sounds differ from those of males. Under a pre-spawning condition in the spawning season, mature females were less vocally active than mature males. Spawning was accompanied by increased vocal activity in both sexes. However, females elevated their vocal activity more eminently compared to when they were in the pre-spawning stage. This observation suggests that both genders vocally take part in spawning. The presence of sounds with a longer duration and a greater number of pulses during spawning deserves further study. It is not clear whether these sounds were emitted by 1 or both sexes. Future experiments, in which sounds are recorded from tanks holding (1) females and males separately injected, (2) injected mature males and untreated females, or (3) injected mature females and untreated males, should provide answers to this question.

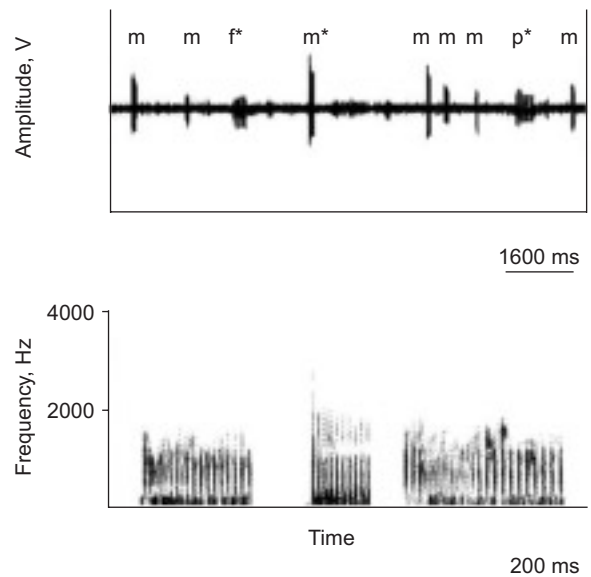


Fig. 5. Time series (top oscillogram) showing the occurrence of male calls (m), female spawning calls (f), and prolonged calls (p) recorded during actual spawning. Sonograms for a particular female call, male call, and prolonged call as indicated by asterisks in the oscillogram are shown in the bottom figures (left, middle, and right sonogram, respectively).

Although it is an aquaculture species in Taiwan and live females are available for bioacoustic studies, the lack of sexual dimorphism in external characters makes it difficult to clarify details of the courtship and spawning behaviors. Only close observations of numerous spawning episodes with tagged, sexually mature individuals (i.e., tagging the fish by sex) will help reveal these facts.

This study describes sexual dimorphism in the call parameters of the Japanese croaker (i.e., the frequency, pulse duration, and inter-pulse interval). It is well known that larger individuals with larger sonic muscles produce sounds with a lower fundamental frequency than those emitted by smaller individuals (Fish 1954, Lobel and Mann 1995, Connaughton et al. 2000). Connaughton et al. (2000 2002) suggested that the lower dominant frequency of larger fish is caused by a longer pulse (i.e., a longer muscle twitch). Hill (1950) and Wainwright and Barton (1995) also agreed that a larger fish takes more time to contract a longer muscle resulting in a lower dominant frequency. As the sizes of the spawning male and female Japanese croakers used in the acoustic recordings were approximately equal, sexual differences in the fundamental frequencies of the male and female sounds were not due to differences in body-size per se; other factors (e.g., sexual dimorphism in the size of the sonic muscles or swimbladder; also see below) may have accounted for such acoustic differences in frequency.

Connaughton et al. (2002) demonstrated that the dominant frequency of a fish sound is not determined by the natural frequency of the swimbladder, indicating that the sonic muscle is likely the source for determining this acoustic parameter. For Japanese croakers, females' sonic muscles are thinner, lighter, and shorter than those of males. A similar sexual dimorphism was also noted in Japanese croaker (Griffiths et al. 1995) and *Micropogonias undulates* (Hill et al. 1987). Accordingly, the shorter fibers of the Japanese croaker female's sonic muscles should take less time to complete a single twitch, and therefore the sounds emitted should have a higher fundamental frequency. This predicted result for the spectral characteristics of the female's sound contradicts what we found for the female Japanese croaker.

As the fundamental frequency (f) of the croaking sound is positively related to muscle tension (force), but inversely related to the length of the muscle fiber (L) and the mass per unit length of fiber (u), $(f) = (1/2L) * (T/u)^{0.5}$ (Sprague 2000), the

thinner female sonic muscles should generate a weaker tension which may be related to the lower frequency of their sounds. According to Sprague's model (2000), a significantly higher muscle tension in the male relative to differences in the mass and length of the sonic muscle may account for the high fundamental frequency in male sounds. Connaughton et al. (1997) demonstrated that the dominant frequency did not vary with atrophy of the weakfish male's sonic muscles - a result contrary to our earlier view of the possible reason for the lower frequency of sounds of the Japanese croaker female. However, an increase in the sound pulse duration with atrophying sonic muscles in male weakfish in the non-spawning season was demonstrated by those authors, which might parallel the longer pulse duration in the thinner muscle-bearing females of Japanese croaker.

The Japanese croaker's calls were observed to have sound energies up to 3000 Hz (Fig. 1). These higher frequencies are more likely to be a result of tank effects or other reasons not related to the sonic muscles, as sonic muscles rarely produce sounds above 1000 Hz.

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