REPRODUCTIVE BEHAVIOR AND MATING SYSTEM OF SPOTTED SEATROUT *CYNOSCION NEBULOSUS*

by

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ABSTRACT

Spotted Seatrout *Cynoscion nebulosus* is an important estuarine-dependent finfish along the Texas Gulf coast. Sound production is an important component of Spotted Seatrout reproductive behavior and could potentially serve as a useful metric in monitoring the reproductive output of Spotted Seatrout spawning aggregations. My objective was to assess the relationship between sound production and egg production in captive breeding population of Spotted Seatrout. I used a hydrophone to monitor Spotted Seatrout production tank during the 2013 spawning season. Eggs were collected daily using a surface skimmer and counted. I was able to identify four types of calls characteristic of spawning described in previous literature. Multiple-pulse calls and long grunts were produced more frequently than paired dual-pulse calls during the spawning season, while staccato call was the least common among the four call types. The number of eggs produced was positively correlated to the sound production, and sound production varied between spawning nights and non-spawning nights. The quantity of paired dual-pulse calls were correlated to egg production, and that of long grunts also indicated the similar pattern, while multiple-pulse calls and staccato calls showed little effect on egg production. This may suggest that paired dual-pulse calls and long grunts are courtship-related calls and multiple-pulse calls and staccato calls are associated with agonistic behavior among males and/or attract females to lek. In terms of the quality of each call type, Spotted Seatrout produce lower, softer but higher pitched calls on nights where eggs were discovered compared to the nights where no eggs were discovered, indicating that males produced more intensive calls aiming for potential females from far

way when the ones nearby did not respond. My study provided more detailed analysis of Spotted Seatrout acoustic behavior and could potentially lead to non-invasive methods to evaluate reproductive output in the field.

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CHAPTER I

INTRODUCTION

The population-level implications of complex mating systems in pelagic broadcast-spawning (PBS) marine fishes have not traditionally played a significant role in management decisions. This is problematic because there is evidence that a lack of information regarding fish mating systems may impede fisheries management, conservation, and recovery (Rowe and Hutchings 2003; Quader 2005). Male intra-sexual competition, female selection and other components of the mating systems of commercially exploited marine fishes can render populations more vulnerable to exploitation, especially at declining and/or low levels of abundance (Rowe and Hutchings 2003). Reduced mating efficiency, declined fertilization rate and increased variance in fertilization rate (Møller and Legendre 2001; Rowe et al. 2004) potentially can result in lower reproductive output exacerbating the effects of overfishing. These impacts can be compounded if the spawning aggregations of these species are targeted by commercial or recreational fisheries (Sadovy and Domeier 2005; De Mitcheson et al. 2008) or otherwise disturbed by anthropogenic activities (Rowe and Hutchings 2003). For example, many species of serranid groupers form large, temporally and spatially predictable spawning aggregations that have been targeted by commercial and recreational fisheries (Morris et al. 2000). Furthermore, fishing tended to be size-selective and resulted in a reduced number of large fish in these aggregations (Law 2000; Fenberg and Roy 2008).

Unfortunately, most serranid groupers are sequential hermaphrodites and fisheries management failure to account for the change in sex ratio of these aggregations has contributed to their decline (Claydon 2004). Similar scenarios have been described for other PBS marine species with complex mating systems, such as Atlantic Cod *Gadus morhua* (Nordeide and Folstad 2000), Spotted Seatrout *Cynoscion nebulosus* (Blanchet et al. 2001), and Red Drum *Sciaenops ocellatus* (Wilson and Nieland 1994).

These examples only represent species for which relatively detailed data exist regarding reproductive behavior, ecology, and mating systems. For most PBS marine fishes, mating system details are limited. Members of this reproductive guild release buoyant eggs directly into the water column (Balon 1975), and no parental care is provided after spawning (DeWoody and Avise 2001). The long-held assumption is that the majority of these species employ a relatively simple, promiscuous mating system with little or no mate selection and limited male intra-sexual competition, that exists primarily in the form of sperm competition (Breder and Rosen 1966). This apparent lack of complexity pertaining to broadcast-spawning mating behavior suggests no potential connections between reproductive behavior and reproductive success, furthermore failing to match probable mating behavior explanations, such as theories of mating system, life history or parental care (Hutchings et al. 1999). As an alternative, a promiscuous mating system was suggested by some scientists to explain the mating behavior of PBS marine fishes (Breder and Rosen 1966; Balon 1975; Berglund 1997). However, based on more thorough examinations of the reproductive behavior of PBS marine fishes, surprising diversity and complexity have been revealed in their mating systems. For example, a lekking mating system, more frequently associated with galliform birds and other terrestrial animals, has been described in many species of pelagic broadcast-spawning fishes, such as Atlantic Cod (Nordeide and Folstad 2000), synodontid lizardfishes (Donaldson 1990), and labrid wrasses (Warner and Robertson 1978; Moyer and Yogo 1982). A lek is a polygamous mating system in which males spend the majority of the reproductive period aggregated for the purpose of displaying to females (Emlen and Oring 1977; Höglund and Alatalo 1995). Male display behaviors serve as a signal of male quality when females visit the aggregation to select mates (Höglund and Alatalo 1995).

Pelagic broadcast-spawning marine fishes that engage in lekking behavior are primarily agonistic between males, and they compete in displays that attract females. Agonistic behaviors are often an important component of lekking mating systems that allow males to establish and maintain a dominance hierarchy and defend territories thereafter (Hutchings et al. 1999). Courtship displays are species specific and can vary in complexity. In many species of gadoid and sciaenid fishes, courtship involves pre-copulatory nudges and circling combined with visual and auditory displays. In Atlantic Cod, there is a "song and dance" consisting of a male or group of males attracting females through a series of calls (Nordeide and Folstad 2000). The female arrives at the lek and remains near the substrate as the male circles her. Eventually if the female is receptive to this display, the two raise off the substrate into a ventral mount and release their gametes, sometimes accompanied by trailing satellite males (Brawn 1961; Hutchings et al. 1999; Nordeide and Folstad 2000; Rowe and Hutchings 2006). Other species do not seem to exhibit as complex a repertoire of reproductive behaviors. Red

Drum, may exhibit very complex series of calls to attract females, but the courtship behavior seems to be relatively simple. A male will attend a receptive female and begin nudging her urogenital opening as she starts swimming actively, which may also attract other males to join in (Guest and Lasswell 1978). Sound production is a relatively common ability within many taxa of marine PBS fishes used to attract mates and potentially to intimidate rivals in agonistic displays (Mok and Gilmore 1983; Nordeide and Kjellsby 1999; Ueng et al. 2007). This mating system’s acoustic component offers opportunities to locate spawning sites and identify spawning time and preferred spawning habitat (Lowerre-Barbieri et al. 2008; Walters et al. 2009; Lowerre-Barbieri et al. 2013). However while there would seem to be great potential for using passive acoustics to monitor reproductive output, there have been no attempt to relate sound production to reproductive output of a spawning aggregation.

Spotted Seatrout is one of the most intensively managed marine finfish in the Gulf of Mexico (Anderson and Karel 2009) and a good candidate to establish relationships between sound production and reproductive output. Unlike many other sciaenids, Spotted Seatrout spend their lives within a natal estuary (Tabb 1966; Music Jr. 1981). Estuaries are both productive and sensitive to habitat change and human activities (Vasconcelos et al. 2007) which could directly affect Spotted Seatrout' populations as their natal estuaries receive limited numbers of immigrants from other estuaries (Tabb 1966). Similar to Atlantic Cod (Robichaud and Rose 2001; Skjaeraasen et al. 2011), Spotted Seatrout tend to aggregate in dense schools during spawning season and have a high level of site fidelity (Saucier and Baltz 1993). Studies show that fishing activities targeting aggregated

Atlantic Cod population reduce the spawning stock of the population, and disrupt aggregation behavior which can contribute to decreased reproductive success (Brander 1994; Rowe and Hutchings 2003; Dean et al. 2012). Many researchers have indicated that Spotted Seatrout is vulnerable to habitat alteration and disturbance and overfishing (Tabb 1966; Blanchet et al. 2001). Even though the population currently is considered relatively stable in Texas, it has experienced dramatic declines both in mean size of fish caught by anglers and estimated spawning stock biomass in the past (McEachron et al. 1984; Blanchet et al. 2001; Vega et al. 2011). As such, in order to supplement natural recruitment and manage the population, an ongoing marine stock enhancement Spotted Seatrout program has been conducted by Texas Parks and Wildlife Department (TPWD) since 1993. Currently, approximately one million Spotted Seatrout fingerlings (about 40 mm total length) are released annually into Texas estuaries (Neahr et al. 2010). However, aside from this long-term stock enhancement program, detailed information on the mating system of Spotted Seatrout is needed to compliment fisheries management practices intended to prevent potential decline in abundance of this species. Generating the details of their mating system could also benefit the stock enhancement program by improving captive broodfish spawning techniques.

Research on the reproductive biology of Spotted Seatrout has primarily focused on life history, larval development and sound production (Mok and Gilmore 1983; Brown-Peterson et al. 1988; Gilmore Jr. 1994; Brown-Peterson and Bortone 2003), while relatively little is known about the mating system of the species and the role of sound production. One aspect of Spotted Seatrout reproductive behavior is that they only produce sound during the spawning season (Tabb 1966) and their sound production seems to be associated with lunar patterns (McMichael and Peters 1989; Walters et al. 2007). It is believed that peaks in sound production coincide with new and full lunar phases (Walters et al. 2007). Only male Spotted Seatrout aggregate and produce sound (Tabb 1966; Hein and Shepard 1979). It is used to attract females to visit the area of activity and conduct female choice. No conspicuous attributes are showed to females by these soniferous aggregations other than the males themselves. This aggregation behavior of males and sound production for the purpose of quality displaying are critical elements of the lekking mating system of Spotted Seatrout. Mok and Gilmore (1983) described their sound characters and recognized four major sound types along with those of two other sciaenid species. According to Mok and Gilmore (1983), the call produced most often in Spotted Seatrout species is the paired dual-pulse calls, also known as short grunt. And continuously produced dual-pulse calls and periodic long-grunts will be heard during lek call periods. Staccato call the rarest, which is not surprising since it uses the most metabolic energy among all types of calls (Gilmore Jr. 2010). However, no clear quantitative relationship between sound production and their reproductive activities have been discovered. If we have more knowledge of potential connection between sound production and reproduction, sound production could also potentially serve as a useful metric in monitoring the size and reproductive output of Spotted Seatrout spawning aggregations.

The objectives of my research were: 1) evaluate the relationship between total sound production and egg production over the course of a spawning season, as well as the relationship between each type of call and the egg production, 2) assess how total call number and each type of call number produced changed during one night between nights with eggs produced and nights with no eggs produced, and 3) evaluate whether the call quality was associated with the probability of spawning during the same time period.

CHAPTER II

METHODS

Spotted Seatrout maintenance and spawning

Adult Spotted Seatrout were maintained by Texas Parks and Wildlife Department (TPWD) at the Coastal Conservation Association Marine Development Center (MDC) in Corpus Christi, Texas. This facility produces juvenile Spotted Seatrout using broodstock captured from the bay systems of the middle and lower Texas coast for marine stock enhancement programs in these systems. Spotted Seatrout were maintained and spawned following the protocols developed by TPWD. Briefly, adult Spotted Seatrout are maintained in groups of 15-20 individuals with approximate sex ratio of 1:1. Each group is housed in a 4-m diameter circular tank with recirculating, natural seawater and fed frozen shrimp, mackerel, and squid three times per week. Tanks are topped with a conical lid to maintain control over temperature and photoperiod. Spawning occurs over a single reproductive cycle per year during May through September, following the natural annual cycles of temperature and photoperiod. Fertilized eggs were collected using a surface skimmer and counted using a volumetric method established by TPWD. All these data were acquired from TPWD.

Collection of audio data

A VH180 hydrophone (Vemco, Bedford, Nova Scotia, Canada) was used to record audio across a range of 10Hz-20KHz. An M-Audio Fast-Track audio interface device (Avid, Burlington, MA) was used to connect the hydrophone with the desktop computer running Surveillance System v. 8.4 (Geovision Inc., Irvine, CA) software recording and archiving the audio files. The audio files were saved as waveform (.wav) audio files with a bit rate of 32 kbps and they were limited to five minutes in length for the purpose of easier storage and later analysis. Consultation with hatchery personnel and preliminary trials conducted during August-September 2011 established that the Spotted Seatrout held at the MDC typically initiated spawning activity around 21:00-22:00 and completed activity by 02:00-03:00. Thus, recordings were restricted to a 7.5-h period between 19:45 – 03:15 to conserve hard drive space and allow for recordings to be made during every night of the protracted spawning season. Sound data were collected from 14 May 2013 to 7 September 2013.

I used Audacity v 2.0.1 (Audacity Team, 2008) for file format conversion as well as noise removal. Noise removal was performed using the feature included with Audacity (Mazzoni 2007). A 5-min file containing only background noise was used as a noise profile and the program was run with the following settings: noise reduction: -24 dB; sensitivity: 0.00 dB; frequency smoothing: 150 Hz; and attach/decay time: 0.15 s. I then used Raven Pro 1.5 Beta (Bioacoustics Research Program 2013) to select Spotted Seatrout calls from the cleaned files. I applied the band limited energy detector in Raven Pro 1.5 to each sound file using the following parameter settings: minimum frequency:

520Hz, maximum frequency: 1300Hz, minimum duration: 0.208s, maximum duration 0.592s, minimum separation 0.092. Each putative Spotted Seatrout call identified by the software was verified by visual and audio inspection its spectrograph and oscillograph and false positives were deleted from the dataset. Each file was also checked for calls missed by the detector.

Measurements of selected calls were performed for each individual call for classification (Table 1). I used SAS 9.3 (SAS Institute, Inc., Cary, North Carolina) for data analysis. I used discriminant function analysis (DFA) to classify the calls into the four types. First, I haphazardly chose approximately 25% of total calls and manually classified them to serve as a training dataset for the DFA based on findings reported for classifying four distinct call types of Spotted Seatrout (Gilmore Jr 2010). The distinguishable character used in my analysis among paired dual-pulse calls, multiple-pulse call and long-grunt was the pulse number, and staccato call was also easy to differentiate because of its pulse number and long call duration (Figure 1). Tests for multivariate normality and multicollinearity were performed and variables were transformed as necessary to meet the normality assumption. Also, since high correlation of variables used in DFA could generate difficulties for interpretation (Morrison 1969), only variables with $r < 0.7$ were included in the analysis. For every two variables with $r > 0.7$ indicating high correlation, one of them will be dropped from the analysis. I kept the ones which were either normal distributed or were able to be transformed to meet the normality assumption. I performed a stepwise discriminant analysis procedure (PROC STEPDISC; SAS Institute Inc. 2011) to identify the most informative variables to classify the known calls from those listed in Table 1. I then performed a DFA using the training dataset to generate the discriminant functions needed to classify unknowns into multiple-pulse call, staccato call and a combined paired dual-pulse call and long grunt category. Due to the fact that combined paired dual-pulse call and long grunt category. Due to the fact that paired dual-pulse call and long grunt had similar discriminant functions which resulted in higher overall error rate, a secondary DFA was performed by generating new discriminant functions specifically for separating paired dual-pulse calls and long grunts in the unknown data. Then all the classified calls were gathered as one dataset.

Table 1. Descriptions of the variables used to characterize the calls of spawning Spotted Seatrout maintained in captivity at the Coastal Conservation Association Marine Development Center, Corpus Christi, Texas.

Variables	Brief description
Duration*	Duration in seconds of each call.
Average entropy*	Higher entropy values correspond to greater disorder in the sound whereas a pure tone with energy in only one frequency bin would have zero entropy. The average entropy measurement describes the amount of disorder for a typical spectrum within the selection.
Bandwidth 90%*	The difference between the 5% and 95% frequencies, in which the 5% frequency is the frequency that divides the selection into two frequency intervals containing 5% and 95% of the energy in the selection, similar for 95% frequency.
Maximum power*	The maximum power in the selection, in which power is measured as sound energy per time unit.
Maximum frequency*	The frequency at which max power occurs within the selection.
Peak frequency contour minimum frequency*	The contour is formed by plotting the value of the peak frequency measurement, and the minimum frequency of the contour is the lowest value of the peak frequency measurement in the selection box
RMS amplitude*	The root-mean-square amplitude of the selected part of the signal.
Leq*	Defined as the steady sound pressure level, which over a given period of time has the same total energy as the actual fluctuating noise.
Maximum amplitude*	The maximum of all the sample values in the selection.
Filtered RMS amplitude*	Measured by calculating RMS amplitude after applying a band-pass filter to the selection.
SEL*	Measured as constant sound level which has the same amount of energy in one second as the original noise event.
Energy	Total energy in dB within the selection bounds.

Data analysis and data processing

I performed logistic regression analysis to examine whether the probability of nightly eggs recovery was associated with total call produced per night and date and each of the individual call types. In addition, I assessed whether the number of nightly egg produced was correlated with the number of total call produced and the production of each individual call type using Pearson's correlation coefficient test. I used a square-root transformation for the nightly totals of long grunt and staccato calls to fit the parametric assumptions of normality and randomness of residuals.

Analysis of covariance (ANCOVA) was performed to evaluate whether the total call number per hour was different among hours every night and whether the total call number per hour differed between nights where eggs were recovered and nights where no eggs were recovered. Parametric assumptions of normality and randomness of residuals were validated, as well as the independence of the covariate and treatment effect and homogeneity of regression slopes. Also, multivariate analysis of covariance (MANCOVA) was performed to assess whether the call number per hour of each call type was different among hours every night and whether the call number per hour of each call type differed between nights where eggs were recovered and nights where no eggs were recovered. Parametric assumptions of normality, homogeneity of variances and homogeneity of variance were also validated by checking the residuals. Multicollinearity was also checked before analysis. If multicollinearity was found, I would estimate models that have separate slopes across groups.

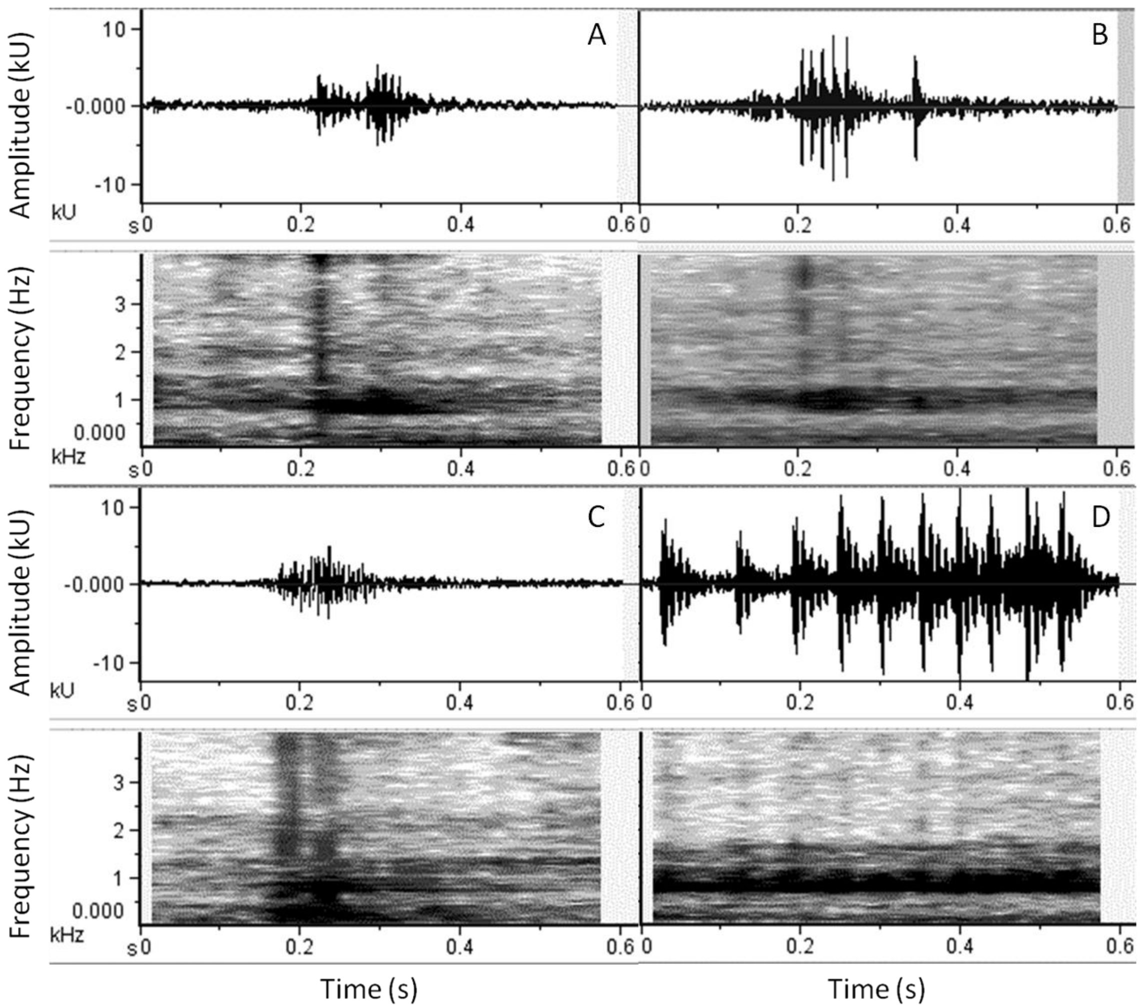

Figure 1. The spectrograms and oscillographs of four call types of captive Spotted Seatrout: paired dual-pulse call (A), multiple-pulse call (B), long-grunt (C), staccato call (D). Sounds were recorded from May to September 2013 at the Coastal Conservation Association Marine Development Center, Corpus Christi, Texas.

I performed MANCOVA to test for differences in call quality between groups means with a covariate of date, in which groups were the combination of four call types and a categorical variable describing whether or not eggs were recovered on the given evening. Assumptions of MANCOVA were also checked as mentioned above. Multicollinearity assumption was checked and duration and maximum amplitude were square-root transformed to meet the normality assumption. Basic measurements of calls were chosen to represent sound quality in the analysis (Table 1). All tests were considered significant at $P < 0.05$.

CHAPTER III

RESULTS

I analyzed Spotted Seatrout sound production from 16 nights, nine nights with eggs produced and seven with no eggs produced, scattered throughout the spawning season. A total of 2,964 Spotted Seatrout calls were identified and classified. Staccato calls was the rarest type during nights analyzed (mean $\pm$ SD = 4 $\pm$ 4 h^{-1}), while long grunts were the most common call type (mean $\pm$ SD = 12 $\pm$11 h^{-1}), accounting for about 47% of the total calls recorded. Multiple-pulse calls comprised 22% of the identified calls (mean $\pm$ SD = 5 $\pm$ 5 h^{-1}), and paired dual-pulse calls (mean $\pm$ SD = 4 $\pm$ 3 h^{-1}) accounted for 16%. It was relatively easy to distinguish between the calls using discriminant function analysis. The estimated total error rate was 24.1% ($F_{10,726}$ = 8.13, $P < 0.01$; Table 2) when distinguishing between multiple pulse calls, staccato calls, and combined paired dual pulse calls and long grunts. There was a similar overall error rate when discriminating between the paired dual pulse calls and long grunts (26.6%, $F_{11,516}$ = 11.96, $P < 0.0001$; Table 3).

Table 2. First-step discriminant function analysis (DFA) results for classifying calls of a captive breeding population Spotted Seatrout in the training dataset used in manual classification into multiple-pulse, staccato and a combined paired dual-pulse and long grunt category.

	Number of calls	Predicted group membership		
		Paired dual-pulse call and long grunt	Multiple-pulse call	Staccato call
Paired dual-pulse call & long grunt	528	80.11%	18.94%	0.95%
Multiple-pulse call	121	17.36	73.55%	9.09%
Staccato call	89	1.12%	24.72%	74.16%

Table 3. Secondary discriminant function analysis (DFA) results for separating the combined category of paired dual-pulse call and long grunt of a captive breeding population Spotted Seatrout in the training dataset used in manual classification.

	Number of calls	Predicted group membership	
		Paired dual-pulse call	Long grunt
Paired dual-pulse call	119	75.63%	24.37%
Long grunt	409	28.85%	71.15%

The probability of spawning occurred was associated with the overall call number per night (χ^2 = 3.85, P = 0.05; Figure 2). With more calls produced per night, the chances of fish spawning gradually increased. The number of paired dual-pulse calls was also associated with the probability of spawning (χ^2 = 4.32, P = 0.04; Figure 3). When the number of paired dual-pulse calls was over 15 calls per night, the chance of fish spawning increased sharply. For long grunts, there was a trend that the similar relationship existed, but ultimately, there was no relationship (χ^2 = 3.14, P = 0.08; Figure 3). Furthermore, there was no such relationship between the probability of spawning and the number of multiple-pulse calls or staccato calls ($\chi^2 \leq 1.82$, $P \geq 0.18$; Figure 3).

As for the number of eggs produced, it was correlated with the number of overall calls per night (r = 0.63, $P < 0.01$; Figure 2). The number of paired dual-pulse calls was also correlated to the number of egg produced the same night (r = 0.74, $P < 0.01$; Figure 3). The number of long grunts was not correlated to the egg production, but there was a trend that such correlation may exist (r = 0.48, P = 0.06; Figure 3). Also, there was no correlation between the number of multiple-pulse calls or staccato calls with egg production (r = 0.11, $P \geq 0.19$; Figure 3).

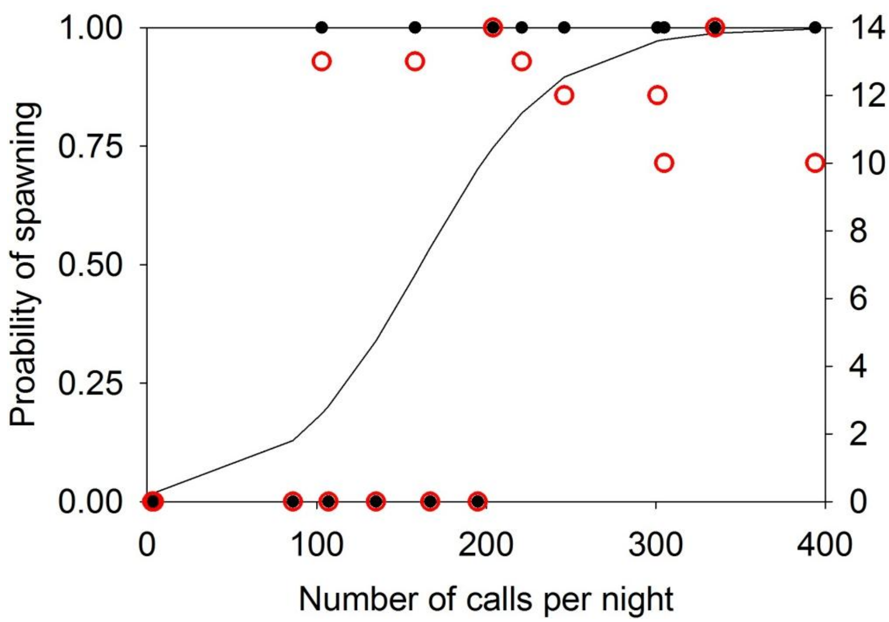

Figure 2. The relationships between the overall number of calls per night and the probability of egg production in a captive breeding population Spotted Seatrout from May–September 2013. Hollow dots represent the natural logarithm of the egg number at a particular night. Solid dots represent observation of probability of spawning and solid line represents the logistic regression curve fitted for this relationship.

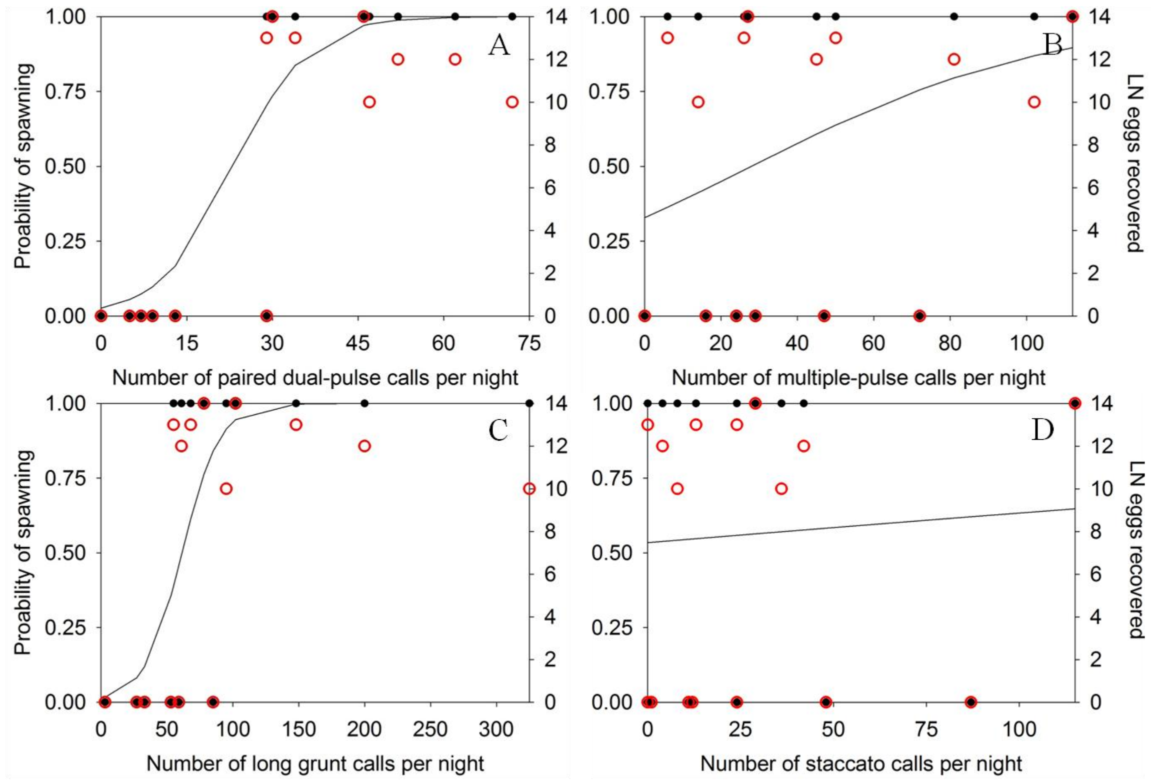

Figure 3. The relationships between the production and the number of paired dual-pulse calls (A), multiple-pulse calls (B), long grunts (C) and staccato calls (D) per night of a captive breeding population Spotted Seatrout observed May–September 2013. Hollow dots represent the natural logarithm of the egg number at a particular night. Solid dots represent observation of probability of spawning and solid line represents the logistic regression curve fitted for this relationship.

The number of total calls produced per hour by Spotted Seatrout varied between spawning nights and non-spawning nights ($F_{1,82} = 9.72$, $P < 0.01$). On nights with egg production (Figure 4), total calls per hour started around 25 calls and peaked around 120 calls at 20:00. Overall, the calls stayed fairly active from 19:45 to 21:00, then declined to about 10 calls hr^{-1} with small fluctuation for the rest of the recording. However, on nights with zero egg production (Figure 4), the number of total calls per hour ranges between 25 to 40 from 19:45 to 21:00, and call activity nearly stopped after 22:00.

The mean number of calls per hour for the individual call types exhibited two patterns depending on call type and whether eggs were recovered from the tank. The mean number of paired double-pulse calls ($F_{1,82} = 13.09$, $P < 0.01$) and long grunts ($F_{1,82} = 14.36$, $P < 0.01$) per hour were different between spawning nights and non-spawning nights (Figure 5). Furthermore, they shared similar patterns of sound production with total call production over the course of an evening. Paired dual-pulse call remained consistent at one to four calls per hour then declined to nearly zero after about two hours on non-spawning nights, but on spawning nights, call number reached 25 calls per hour on peak time and stayed active with 1 call per hour. Also for long grunts, the call number on spawning nights peaked at 48 calls per hour compared to 13 calls per hour on non-spawning nights, and rather than stopping after two hours, the Spotted Seatrout continued producing this call at about 10 per hour for the rest of the recording period. However in contrast to paired double-pulse call and long grunts, multiple-pulse calls ($F_{1,82} = 2.84$, $P = 0.10$) and staccato calls ($F_{1,82} = 0.14$, $P = 0.71$) did not show clear difference between spawning and non-spawning nights (Figure 5). On both types of nights, these call types were only produced for the first two hours after the tank lights were turned off. During that period, number of multiple-pulse calls ranged from 7-21 calls per hour, and number of staccato calls ranged from 5-19 calls per hour.

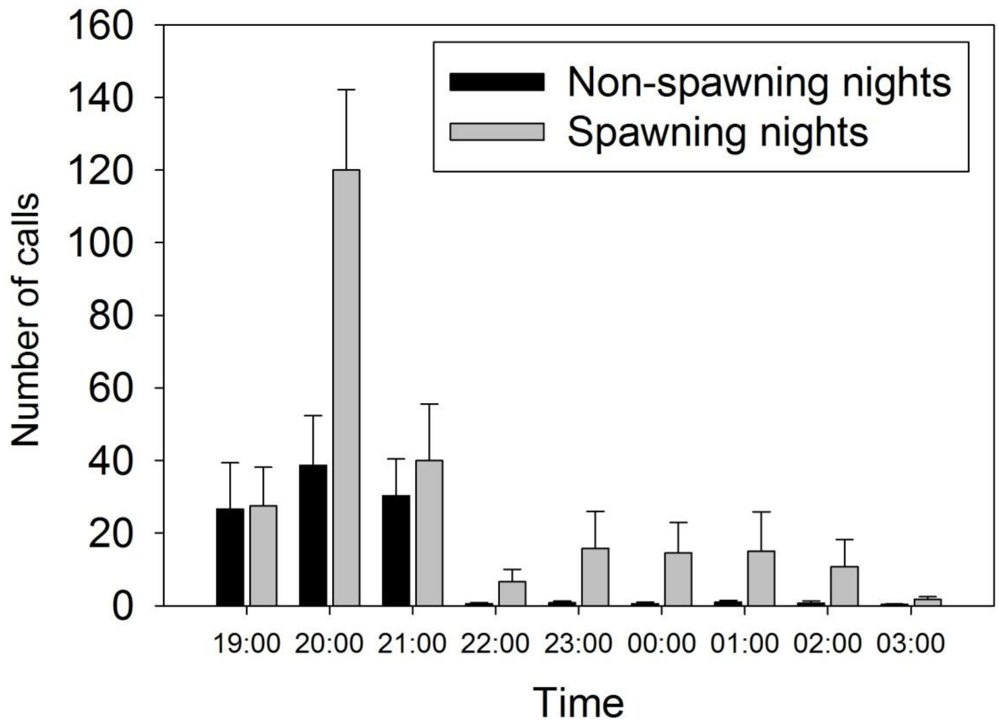

Figure 4. The mean and standard error of number of total calls made by a captive population of Spotted Seatrout during their spawning season for each hour on nights where no eggs was produced and nights where eggs were produced. Bars represent the mean of number of calls per hour for each hour. Line segment above the bar represent the standard error of number of calls per hour for each hour.

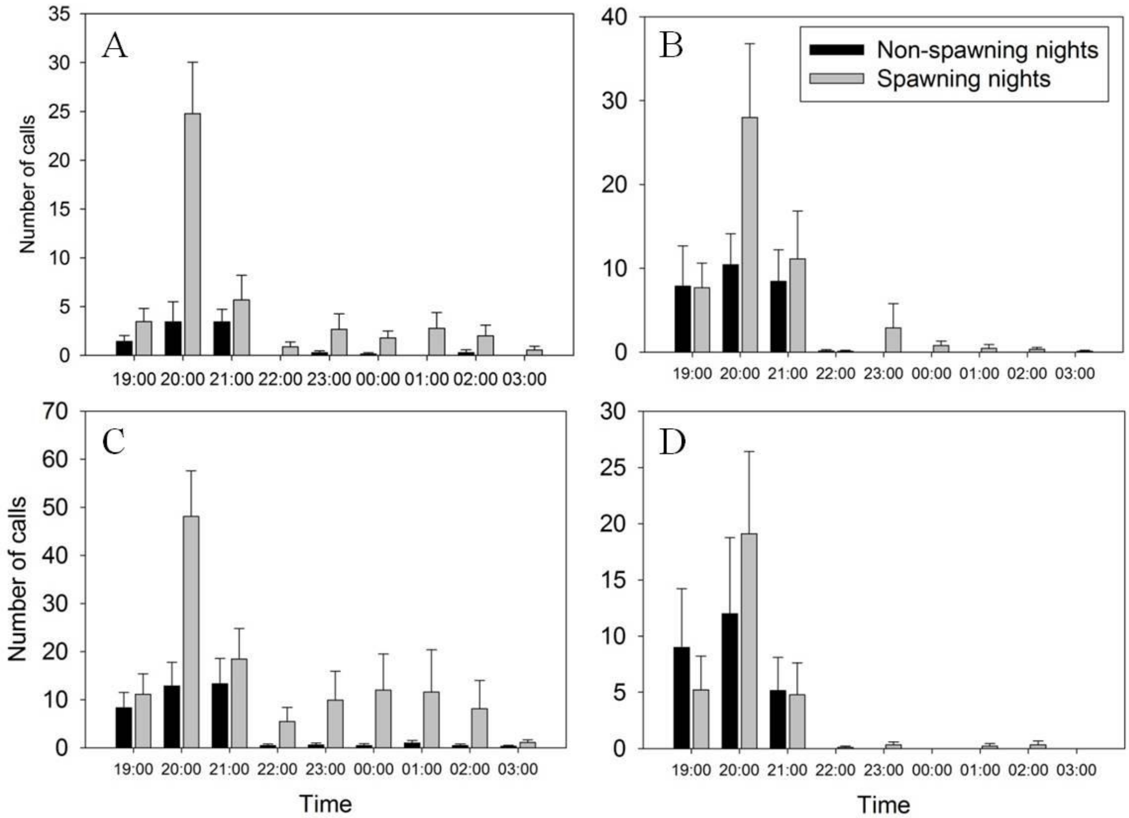

Figure 5. The mean and standard error of number of paired dual-pulse calls (A), multiple-pulse calls (B), long grunts (C) and staccato calls (D) made by a captive population of Spotted Seatrout during their spawning season for each hour on nights where no eggs was produced and nights where eggs were produced. Error bars represent the standard error of number of calls per hour for each hour.

The quality of Spotted Seatrout calls, as measured by energy, maximum amplitude, maximum power, and bandwidth, was different on spawning nights compared to nights where spawning did not occur (Wilks' λ, $F_{15,8147} = 5.64$, $P < 0.01$, Table 4). Among those variables of sound used in the analysis, only duration was not different between spawning nights and non-spawning nights (Wilks' λ, $F_{3,2960} = 0.98$, $P = 0.40$, Table 4). On non-spawning nights, energy, maximum amplitude and maximum power were mostly higher than on spawning nights (Table 4), while bandwidth 90% was lower than that on spawning nights. That is, Spotted Seatrout produced louder, stronger but low pitched calls on non-spawning nights. Even when comparing variables among call types despite of the spawning status of nights, multiple-pulse call and staccato call were stronger, louder than paired double-pulse call and long grunt, especially on spawning nights (Wilks' λ, $F_{15,8147} = 244.35$, $P < 0.01$, Table 4).

CHAPTER IV

DISCUSSION

Four types of calls

I identified four types of calls characteristic of spawning described in previous literature (Mok and Gilmore 1983;Gilmore Jr 2010). The staccato call, is the most energetic call produced by Spotted Seatrout (Gilmore Jr 2010), but was the least common among the four call types during nights examined in the 2013 spawning season. In previous studies of the acoustic behavior of Spotted Seatrout, the staccato call was also noted as being rare relative to the other types (Gilmore Jr. 2010). Multiple-pulse calls and long grunts were produced more frequently than paired dual-pulse calls during the nights examined. However, other studied have suggested the paired dual-pulse call is the most often produced call since it requires least energy to produce and likely carries the lowest risk of detection by predators (Barros and Odell 1995; Gilmore Jr. 2010).

Table 4. The mean ± standard error of variables used to represent the sound quality of Spotted Seatrout at different combinations of call type and whether they spawned. Spotted Seatrout were kept in the captivity of Coastal Conservation Association Marine Development Center, Corpus Christi, Texas.

	Spawning Status	N	Energy (dB)	Duration (sec)	Bandwidth 90% (Hz)	Maximum Amplitude (Hz)	Maximum Power (dB)
Paired dual-pulse call	Not Spawned	63	91.00 ± 0.39 *	0.31 ± 0.01	682.04 ± 51.22*	4473.75 ± 205.24*	83.46 ± 0.49*
	Spawned	401	89.33 ± 0.16*	0.33 ± 0.00	755.07 ± 24.75*	3442.71 ± 70.42*	81.79 ± 0.21*
Multiple-pulse call	Not Spawned	188	95.48 ± 0.15*	0.35 ± 0.01	614.36 ± 31.37*	5756.70 ± 140.08*	87.04 ± 0.23*
	Spawned	463	94.99 ± 0.09*	0.35 ± 0.00	768.90 ± 33.55*	5888.85 ± 81.53*	86.58 ± 0.13*
Long grunt	Not Spawned	263	90.08 ± 0.25*	0.31 ± 0.00	733.01 ± 27.31*	3306.35 ± 108.09*	82.06 ± 0.29*
	Spawned	1132	88.03 ± 0.11*	0.30 ± 0.00	621.44 ± 15.51*	2480.09 ± 35.61*	80.32 ± 0.12*
Staccato call	Not Spawned	183	100.59 ±0.21*	0.43 ± 0.01	933.57 ± 57.30*	9380.38 ± 264.33*	90.40 ± 0.25*
	Spawned	271	100.42 ±0.18*	0.43 ± 0.01	1131.58 ± 64.20*	9768.10 ± 216.33*	90.42 ± 0.21*

* There was significant effect of the variable on the possibility of spawning.

These observed differences between my study and previous studies may be due to the fact that the majority of previous studies concerning Spotted Seatrout reproduction have been conducted in the field. There are mainly two different factors that could have certain effects on these two populations. First, the females are always within close proximity of the males, rather than having to locate the spawning aggregation site.

Second, without the predators in captivity, the males observed in this study may not have exhibited as much caution in their acoustic signaling as their counterparts in the wild. Therefore, this disparity of results obtained from studies with different populations of Spotted Seatrout may suggest the potential function of different call types. One aspect that was worth noticing is that the paired dual-pulse calls and long grunts were hard to distinguish by Raven, which resulted in the higher error rates of the classification. Even during manual classification process, I also encountered difficulties differentiating these two types. When considering this, larger sample size would likely to more convincing in terms of the proportions of each call type in captivity.

Relationships between egg production and sound production per night

Sound production in Spotted Seatrout is used exclusively by males to attract females to spawning aggregations and to establish their dominancy hierarchy using agonistic sound displays at the spawning site (Hein and Shepard 1979; Mok and Gilmore 1983). My results suggested that there was a direct relationship between Spotted Seatrout sound production and the probability of fish spawning in a given night. While sound production has been hypothesized to be correlated to spawning activity (Tabb 1966; Mok and Gilmore 1983), the relationship has not been quantitatively validated before. This study represents the first attempt to quantify a relationship between the possibility of egg production and sound production in a Spotted Seatrout spawning aggregation, albeit a captive one.

The captive population I used for analysis may be artificial as compared to field studies mentioned above, but there are also advantages for assessing egg production of

Spotted Seatrout. Instead of detecting only the appearance of eggs and larva, I have accurate counts of the egg produced after every spawning night. With that, I found that there was a correlation between the number of eggs produced and overall sound production. More vocalizations by the males may not necessarily resulted in more eggs produced by individual females, but it may indicate there are more females around to be courted in a spawning aggregation. Previous studies stated that Spotted Seatrout eggs and larvae collected during early spawning season and calls heard during the same period suggested that these sounds were actually related with spawning activity (Gilmore Jr. 1994; Gilmore Jr. 2010). Although they did not demonstrate this correlation between total call number and the egg number produced. Similarly, the number of paired dual-pulse calls has an effect on the number of eggs produced, which may due to the number of females involved in a given spawning night, while the multiple-pulse call and staccato call show little effect. For long grunts, larger sample would likely lead to the determination that while it was less important than paired dual-pulse calls, it is likely to still have some relationship to egg production. The direct relationships between the number of paired dual-pulse calls and long grunts and egg production and the lack of relationships between multiple-pulse call and staccato call and egg production supported the potential function of different call types proposed above, which is also correspond to previous study of important acoustic cues of fish species that the call function could be reproductive-related or for other purposes (McCauley and Cato 2000).

Timing of calls between nights where eggs were recovered and nights where no eggs were recovered

For lekking species, male display activity is positively related to individual mating success (Fiske et al. 1998). Although I could not identify calls to individual males, when comparing call production between nights where eggs were recovered and nights where no eggs were recovered, the number of calls produced was still larger, indicating that more calls were used to communicate by males on nights where the females were willing to respond, especially with those courtship-related calls. Studies of other species suggest that females behavior influence the behavior of the males, especially when females were signaling their receptivity to copulation (Langmore et al. 1996; Semple and McComb 2000; Balsby and Dabelsteen 2002). At this stage, I could only suspect that Spotted Seatrout, females in this study were giving visual signals or other forms of signals since they do not produce sound when males were displaying. Actually, video was recorded simultaneously with audio data for the intention of analyzing the behavior of females. However, the data collecting process was greatly hindered due to the design of the tank covers in the production tanks that made it impossible to mount a camera high enough above the tank to collect video of the whole tank viewing area. With fish moving in and out of frame, it was impossible to get a full sense of what was going on. There was also no way to automate the process.

My results discriminate four call types between nights where eggs were recovered and nights where no eggs were recovered supports my proposition that different types of calls are associated with different functions during reproductive process. I found that on nights where there were eggs produced, the number of calls of paired double-pulse calls and long grunts were larger than those nights with no egg production, and call activity also lasted longer. However for multiple-pulse and staccato, their activity patterns seems more constant every night during spawning season, which may suggest the function of these two calls are to establish the dominant status among the males or to attract females to lek. Furthermore, the number of calls of multiple-pulse and staccato are larger at the beginning of the night than that of paired double-pulse calls and long grunts, which may suggest that males would attempt to obtain mating priority with the females every night during the spawning season using aggressive calls like multiple-pulse and staccato. But at the same time, they may also interact with the females with paired double-pulse and long grunts. And the patterns of spawning nights suggest that if the females are ready to spawn, the calls of paired double-pulse and long grunt of males would continue and function along with their body movement, which is consistent with Tabb (1966) that the spawning activity includes side-to-side body contact with soft croaking of the males, suggests that these calls might be courtship-related calls. Previous studies also found that for Spotted Seatrout, sound production was used to defend relatively small territories and display to aquire mating oppotunities from the females (Hein and Shepard 1979).

Because of various difficulties in studying acoustic communication in an aquatic environment, limited information is available in describing precise functions of calls in Sciaenidae (Gannon and Taylor 2007; Zelick et al. 1999). Potential functions of acoustic communication have been proposed to be associated with intersexual communication, intrasexual competitive interaction, courtship or spawning (Connaughton et al. 2000; Gannon and Taylor 2007; Guest and Lasswell 1978; Taylor and Villoso 1994). However, a few species of frogs and toads, which also make extensive use of sound production in their mating systems, have been studied systematically (Martin 1972; Paulsen 1967; Zelick et al. 1999). And like the male Spotted Seatrout, female frogs are usually assessing male frogs choruses, which may also be considered as leks (Bourne 1992), and they use the vocal communication system to convey information and for mating advertisement (Zelick et al. 1999). For example, according to Bee and Perrill (1996), call types with different duration, dominant frequency or intensity were used between males of green frog *Rana clamitans* for different interaction purposes. Similar lekking behaviors were also described in the neotropical frog *Ololygon rubra* with a lekking mating system and lekking birds (Bourne 1992; DuVal and Kempenaers 2008). The status rank of the male birds affected their reproductive success. And within status, intrasexual competition of males largely reflected female choice (DuVal and Kempenaers 2008).

Referring back to the differences of the number of calls produced by Spotted Seatrout between captive and wild populations, the disparity might suggest similar conlusions that different types of calls are associated with different functions. In terms of the threat of predators, the proportion of different call types produced may have been adjusted by Spotted Seatrout based on their surroundings. In detail, when in the field, to balance the trade-off between displaying for females and the risk of being heard by predators, paired dual-pulse were produced continuously during displaying along with periodic long grunts (Gilmore Jr. 2010). However, since predators are no longer an issue in the tank, long grunts were used more often by competent males during their displaying towards females. Staccato calls, on the other hand, remained the least common calls both in captivity and in the field, with the multiple-pulse calls being the second most common call type produced. Therefore, these two types are most likely to be associated with agonistic behavior between males or to attract females (Mok and Gilmore 1983).

Call quality between nights where eggs were recovered and nights where no eggs were recovered

The variables used to characterize call quality also suggested that different call types have different functions as part of their reproductive behavior. The variables yielded different results among combinations of the occurrence of egg production and four call types. In terms of the differences of call quality between spawning and non-spawning nights, within the same call types, louder, stronger but low pitched calls were produced on non-spawning nights, in which the low pitched call suffer less energy loss during attenuation (Thomson 1995). Therefore, the differences suggested that call production was more intense on non-spawning nights. One of the possible explanations might be that due to the fact that females are always within distance when in captivity, the males would initiate courtship calls in the beginning. However, on non-spawning nights, females would not respond to them. In this case, males might produce calls more intensively to attract the females from further distance, which do not exist in captivity.

Management implications and future research

My research investigating the relationship of sound production and reproductive output conducted in tanks has its limitation. Even so, I provide detailed analysis of the Spotted Seatrout mating system, and there seems to be a relationship between sound production and reproductive output. Using sound production to directly predict reproductive output could be a very efficient application for fisheries managers. Considering its limitation, field studies are needed to verify the conclusions of my research, which could potentially lead to more detailed analysis of Spotted Seatrout mating systems, acoustic behavior and non-invasive methods to evaluate reproductive output in the field.

Also, this method could also be applied to other fish species exhibiting lek-like mating systems, but problems encountered during this research associated with tanks, such as extensive, reflected sound energy caused by the near surface that became a large portion of the total sound energy which create unpredictability of acoustic behavior should be considered. Apparently the hearing specialist Spotted Seatrout' hearing sensitivity allow them to detect both particle motion and pressure transductions of sound. But other fishes, even species within Sciaenidae, have a diversity of swim bladder configurations resulting in different hearing sensitivities (Ramcharitar et al. 2006). Fortunately, methods suggestions for solving this problem were discussed by Popper and Fay (1993). For studies conducting in the field, even with efficient underwater technology for sound recording, it is recommended to have supplemental devices including transducers, hydrophones and recorders (Fish and Mowbray 1970; Gilmore Jr

2010). As mentioned above, verification of my research conclusions is needed, and we could further assess the differences between studies using different spawning populations, which could potentially evaluate the utility of captive broodstock behavior studies in general. Also, studies are still needed to examine the behavior of Spotted Seatrout females.

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