Long-term monitoring of captive red drum *Sciaenops ocellatus* reveals that calling incidence and structure correlate with egg deposition

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Running Page Head: SOUND PRODUCTION AND SPAWNING IN CAPTIVE *SCIAENOPS OCELLATUS*

1

In the present study, quantitative data were collected to clarify the relationship between calling, call structure and eggs produced in a captive population of red drum *Sciaenops ocellatus*. *Sciaenops ocellatus* were held in four tanks equipped with long-term acoustic loggers to record underwater sound throughout a simulated reproductive season. Maximal sound production of captive *S. ocellatus* occurred when the photoperiod shifted from 13.0 to 12.5 h of light, and the water temperature decreased to *c.* 25° C. These captive settings are similar to the amount of daylight and water temperatures observed during the autumn, which is the primary spawning period for *S. ocellatus*. *Sciaenops ocellatus* exhibited daily patterns of calling with peak sound production occurring in the evenings between 0.50 h before dark to 1.08 h after dark. Spawning occurred only on evenings in which *S. ocellatus* were calling, and spawning was more productive when *S. ocellatus* produced more calls with longer durations and more pulses. This study provides ample evidence that sound production equates to spawning in captive *S. ocellatus* when calls are longer than 0.8 s and contain more than seven pulses. The fact that more calling, longer calls and higher sound pressure levels are associated with spawns that are more productive indicates that acoustic metrics can provide quantitative information on spawning in the wild.

Key Words: passive acoustics; reproduction; Sciaenidae; soniferous fishes; sound production

INTRODUCTION

Fish sound production varies in form and function and is widespread throughout many fish families. Some of these families include catfishes (Ictaluridae, Pimelodidae, Doradidae and Mochokidae), grouper (Serranidae), haddock *Melanogrammus aeglefinus* (L. 1758) and cod *Gadus morhua* L.1758 (Gadidae), toadfishes (Batrachoididae), triglids (Triglidae), cichlids (Cichlidae), damselfishes (Pomacentridae), African freshwater fishes (Mormyyridae), and drums (Sciaenidae) (Tavolga, 1958; Fish & Mowbray, 1970; Holt *et al.*, 1985; Fine *et al.*, 1990; Mann & Lobel, 1995; Wilson *et al.* 2004; Locascio & Mann, 2005; Amorim, 2006; Gannon, 2007; Luczkovich *et al.*, 2008; Mann & Grothues, 2009; Parmentier *et al.*, 2009; Walters *et al.*, 2009; Mann *et al.*, 2010). Agonistic and courtship behaviours are the most common reasons for fish sound production. There is some debate, however, on

3

the relationship between sound production and spawning in soniferous fish species (Luczkovich *et al.*, 1999; Locascio *et al.*, 2012).

Fishes belonging to the Family Sciaenidae are known for their sound producing capabilities. These include such species as silver perch *Bairdiella chrysoura* (Lacépède 1802), spotted seatrout *Cynoscion nebulosus* (Cuvier 1830), black drum *Pogonias cromis* (L. 1766), weakfish *Cynoscion regalis* (Block & Schneider 1801), American star drum *Stellifer lanceolatus* (Holbrook 1855), Atlantic croaker *Micropogonias undulatus* (L. 1766) and red drum *Sciaenops ocellatus* (L. 1766) (Hill *et al.*, 1987; Nieland & Wilson, 1993; Sprague *et al.*, 2000; M.R. Collins, B.M.Callahan & W.C. Post, unpubl. data). Sciaenids are most common in turbid estuarine, coastal and bay systems. These fishes may have evolved mechanisms to produce sound to communicate more effectively in these murky environments (Holt *et al.*, 1981; Holt, 2008). Sound production anatomy in these species involves a sonic muscle that abuts a swimbladder. This muscle contracts and vibrates near the inflated swimbladder, which produces a drumming sound. Species in the family Sciaenidae have different swimbladder and sonic muscle shapes, as well as different sonic muscle and swimbladder configurations (Ramcharitar *et al.*, 2006; Fine & Parmetier, 2015), which create species-specific call types. In most sciaenids, only the males contain a sonic muscle and produce sound; however, both male and female *M. undulatus* and *P. cromis* contain sonic muscles and produce sound (Hill *et al.*, 1987; Tellechea *et al.*, 2010*b*).

4

Studies that have recorded underwater sound during reproductive seasons have revealed that patterns of fish sound production coincide with patterns of reproductive condition (Connaughton & Taylor, 1995). Studies have also demonstrated an association between sound production and spawning through the simultaneous collection of acoustic recordings and eggs in the wild (Mok & Gilmore, 1983; Saucier & Baltz, 1993; Luczkovich *et al.*, 1999; Aalbers & Drawbridge, 2008). Luczkovich *et al.* (1999) quantitatively compared the timing and levels of sound production in wild *C. regalis* with the timing and numbers of sciaenid-type eggs; these authors found a significant positive relationship. These types of comparisons are essential if scientists and managers plan to use passive acoustics as a tool to monitor fish reproduction in wild stocks. These data are challenging to obtain because it is difficult to ensure that the eggs that are collected are from the same population of fish that are producing sound (Locascio *et al.*, 2012). The number of eggs collected in the field is probably affected by predator activity, water currents, and the efficiency of plankton tows, making it an inefficient metric for estimating spawning activity.

Studies using fishes held in a captive environment can control for some unaccounted variables that are present in the wild. A few studies have used this captive approach to examine the behavioural associations of sound production and spawning (Guest & Lasswell, 1978; Connaughton & Taylor, 1996; Aalbers & Drawbridge, 2008). Guest & Lasswell (1978) observed that drumming and nudging in captive *S. ocellatus* intensified prior to spawning. Connaughton & Taylor (1996) illustrated the association between courtship behaviour, male drumming and spawning in *C. regalis* held in laboratory tanks. Aalbers & Drawbridge (2008) documented call types and the association of sound production

with courtship behaviour and spawning in white seabass *Atractoscion nobilis* (Ayres 1860) maintained in a net-pen. These studies were important in providing qualitative information on the association between sound production and courtship behaviour.

In the present study, the overall goal was to collect quantitative data to understand the relationship between the amount of calling and the call structure with the number of eggs collected. Wild caught *S. ocellatus* held in laboratory tanks were used as a model species and acoustic loggers were deployed that recorded the underwater tank environment throughout an entire, simulated reproductive season. *Sciaenops ocellatus* is an estuarine-dependent species ranging from Massachusetts to Key West, Florida, on the U.S. Atlantic coast and from south-west Florida to northern Mexico in the Gulf of Mexico (Lux & Mahoney, 1969). The primary spawning period occurs during mid-August through to October along the Atlantic coast and the Gulf of Mexico with sexually mature adults, larvae, and small *S. ocellatus* (<150 mm) occurring only in the fall (Murphy & Taylor, 1990; Ross *et al.*, 1995). Guest & Lasswell (1978) were the first to show that male *S. ocellatus* produce a drumming sound associated with courtship and spawning. Through laboratory experiments, Parmentier *et al.* (2014) have demonstrated that sound production occurs only in male *S. ocellatus*. The specific objectives in the present study were to: (1) describe and characterize the calls of wild *S. ocellatus* held in captivity; (2) determine if *S. ocellatus* exhibited daily patterns of sound production; (3) investigate the relationship between the timing and levels of sound production with the timing and number of eggs collected; (4) determine if changes in call structure affected spawning productivity.

MATERIALS AND METHODS

Sexually mature adult *S. ocellatus* were captured from the wild and placed into captivity by researchers at the South Carolina Department of Natural Resources (SCDNR) in Charleston, South Carolina (Table I). Two male and three female *S. ocellatus* were held in each of four 3.67 m diameter fibreglass tanks (tank 1, tank 2, tank 3 and tank 4) in individual recirculating aquaculture systems equipped with UV sterilizers, protein fractionators and bead filters. All tanks were circular, 1.7 m deep and were kept indoors. Tanks were filled with settled, sterilized Charleston Harbor sea water. *Sciaenops ocellatus* were fed equal parts of Boston mackerel *Scomber scombrus* L. 1758, squid and shrimp species three times a week. Water temperature and diel periodicity were maintained on a predetermined cycle that followed scheduled photoperiod and temperature adjustments that encouraged spawning and resembled a natural reproductive season. Tank temperatures were individually controlled. Acoustic monitoring occurred from 23 July to 19 December 2012, a period when spawning would most likely occur. Floating eggs were collected from a surface, skimming port in the side of the tank that drained into an egg collection tank equipped with a 250 micron mesh net. Collection nets were checked each morning for the presence of eggs. If eggs were present, they were collected and placed in a 15 l *Artemia* sp. hatching cone for separation into floating (*i.e.* fertile) and sinking (*i.e.* unfertilized) eggs. Once separated, eggs were drained into graduated cylinders where they were enumerated volumetrically. A subsample of 200 floating eggs and sinking eggs were evaluated using microscopy to determine if embryos were present. Floating eggs were then transferred to 500 l incubation cones until hatching occurred.

7

Long-term acoustic recorders (DSG-Oceans, Loggerhead Instruments; www.loggerhead.com) were deployed into each tank prior to the onset of spawning activity at a sampling rate of 50 kHz, using a 35 kHz 3-pole low-pass filter on the hydrophone input. DSG-Oceans were scheduled to record sound for 2 min every 20 min (*e.g.* 1200 to 1202; 1220 to 1222; 1240 to 1242, 1300 to 1302 hours, *etc.*) as DSG files on a 128 GB SD-card from 23 July to 19 December 2012. The DSG-Ocean is composed of a cylindrical PVC housing with a High Tech Inc. hydrophone (-185 dBV μPa^{-1}) attached to a microcomputer circuit board and powered by 24 D-cell alkaline batteries. The DSG board incorporates an additional 20 dB of gain and was calibrated with a 0.1 V (peak) frequency sweep from 2 to 100 kHz. Recorders were retrieved twice during the experiment, once on 11 and 12 October to change batteries and download the recorded files and again on 19 December to download final data. The DSG files were then transferred to a hard drive and batch converted into wav files using DSG2wav© software (Loggerhead Instruments).

The number of calls within each 2 min, wav file, was enumerated manually in Adobe Audition (Adobe Systems incorporated; www.adobe.com). For each tank, the number of calls per day was determined by summing all calls that occurred between 1540 and 0000 hours, which was the time in which the majority of calling occurred. The received sound pressure level (SPL; dB re 1 μPa; between 50 and 2000 Hz) of the entire, 2 min wav file (*i.e.* the signal) was determined using automated MATLAB scripts (The MathWorks, Inc.; www.mathworks.com). Received SPL calculations were

completed by first applying a band pass filter to the signal, then calculating the root mean square (RMS) voltage, and then converting the RMS voltage to a received SPL by incorporating the hydrophone sensitivity (-185 dBV µPa^{-1}) and the DSG gain (*i.e.* 20). Files that contained noise artifacts created from tank filters, tank maintenance and fish hitting the tank walls or recorders were not included in SPL analysis. The average background noise levels for tanks 1 to 4 were 117, 113, 115 and 113 dB re 1 µPa, respectively. The highest received SPLs for tanks 1 to 4 were 148 (*i.e.* 56 calls detected), 145 (*i.e.* 66 calls detected), 140 (*i.e.* 45 calls detected) and 143 (*i.e.* 53 calls detected) dB re 1 µPa, respectively. For each tank, the mean SPL per day was calculated by taking the mean of the SPLs between 1540 and 0000 hours. For each day during the recording period, the wav file that contained the most numerous calls was used to estimate the mean duration and mean number of pulses in a call for that day. Call duration was calculated by manually subtracting the time of call termination from the time of call initiation. The pulse number was determined by manually counting each individual pulse in a call.

Microsoft Excel (Microsoft; www.microsoft.com/en-us), MATLAB and SYSTAT 13 (Systat Software, Inc.; www.systat.com) were used for data and statistical analysis. The time and frequency domains were illustrated for three *S. ocellatus* calls that varied in duration and pulse number. *Sciaenops ocellatus* spawning productivity, the number of calls and SPLs and call characteristics were summarized for each tank. The relationship between calls and received SPL for each tank was determined using a Pearson correlation analysis test. The number of calls, water temperature and

photoperiod adjustments were plotted with date. To examine the daily patterns of sound production in each tank, the mean number of calls was determined for each time interval and for each photoperiod (*i.e.* 14.0, 13.5, 13.0, 12.5 and 11.0 h light). In addition, the mean hours before or after dark in which sound production began, peaked and ended for all tanks were calculated.

The relationship between sound production and spawning was examined. To determine if spawning was associated with *S. ocellatus* calling, the number of calls per day and the number of eggs collected (*i.e.* the next morning) and the date for each tank were plotted. To examine whether or not more calling (*i.e.* the number of calls between 1540 and 0000 hours) and higher SPLs (*i.e.* the mean SPL between 1540 and 0000 hours) occurred on evenings with spawning, paired *t*-tests were performed. Linear regressions were completed with the number of calls or mean SPL per evening as the independent variable and the number of eggs collected as the dependent variable. To examine whether or not calls of longer duration with more pulses occurred on evenings with spawning, paired *t*-tests were performed. Linear regression analysis was performed with the number of pulses or the call duration as the independent variable and the number of eggs collected as the dependent variable.

RESULTS

ACOUSTIC CHARACTERIZATION OF *S. OCELLATUS* CALLS

Sciaenops ocellatus held in captivity produced one distinct call type, which consisted of a repetitive drumming sound. These calls varied in the number of pulses and overall duration (Fig. 1). The number of pulses in a call varied from two to 29 with a range in call duration of 0.19 to 3.53 s (Table II). The call frequency ranged from 50 to 2000 Hz; however, most acoustic energy occurred between 50 and 300 Hz (Fig. 1). Increased calling led to higher average SPLs, and the number of calls produced correlated positively with SPL in all tanks (Pearson correlation test; $P < 0.001$; $r = 0.919$ for tank 1; $r = 0.941$ for tank 2; $r = 0.608$ for tank 3; $r = 0.829$ for tank 4; Fig. 2).

PATTERNS OF SOUND PRODUCTION

Concerning general patterns of sound production, three major findings were observed. First, *S. ocellatus* calling occurred in all tanks. Second, the amount of calling differed among the tanks despite having the same number of males and females (tank 1 > tank 2 > tank 4 > tank 3; Table II and Fig. 3). Third, photoperiod and temperature adjustments affected sound production. Generally, maximal sound production of captive *S. ocellatus* occurred when the photoperiod was set to 12.5L:11.5D, and the water temperature decreased to *c.* 25° C (Fig. 3). In tanks 1, 2 and 4, calling began to decrease once the temperature fell below 25° C in November. In tank 3, sound production of *S. ocellatus* was different in that calling was most prevalent during the 12.5 h light cycle and during a period when the temperature

dropped from 26 to 23°C (*i.e.* from 14 to 19 November 2012) [Fig. 3(c)]. In tanks 1 and 2, abrupt

drops in temperature decreased calling, while abrupt rises in temperature increased sound production

(Fig. 3).

Sciaenops ocellatus exhibited daily patterns of calling (Table III and Fig. 4). Generally, sound

production began between 0.08 to 2.08 h before dark and continued for a period of 1.67 to 4.67 h,

depending upon the tank and light cycle. On average, peak sound production occurred sometime

between 0.50 h before dark to 1.08 h after dark (Table III). Generally, calling ended between 1.33 to

3.75 h after dark. In tank 1, peak sound production shifted to earlier times as the light cycle (*i.e.* sunset)

changed from 1915 to 1900 to 1845 hours [Fig. (4a)].

RELATIONSHIP BETWEEN SOUND PRODUCTION AND SPAWNING

Sound production played an important role in spawning of wild caught *S. ocellatus* held in

captivity. This overall theme was supported by four major findings. First, successful spawns (*i.e.* eggs

were present) occurred only on evenings in which *S. ocellatus* were calling (Fig. 5). *Sciaenops*

ocellatus did produce sound without a corresponding spawn, but spawning never occurred without a

substantial increase in calling the evening before eggs were collected. Second, significantly more

calling and higher mean SPLs occurred on evenings in which spawning occurred as compared to

12

evenings in which spawning did not occur [Table IV and Fig. 6(a)-(b)]. Third, spawning was more productive with more calling. For all tanks, more calling and higher SPLs were associated with more eggs released by females (Table V). Fourth, on evenings when *S. ocellatus* did spawn, the call structure was different as compared to the structure that was observed on evenings when spawning did not occur. On evenings when spawning did occur, the mean number of pulses in a call was higher and the mean call duration was longer as compared to the pulses and duration of a call on evenings when spawning did not occur [Table IV and Fig. 6(c)-(d)]. In addition, spawns that were more productive were associated with calls that were longer in duration and contained more pulses (Table V).

DISCUSSION

ACOUSTIC CHARACTERIZATION OF *S. OCELLATUS* CALLS

Sciaenops ocellatus calls were similar to the calls observed in other research studies (Guest & Lasswell, 1978; Lowerre-Barbieri *et al*., 2008; Parmentier *et al.*, 2014). Lowerre-Barbieri *et al*. (2008) found that *S. ocellatus* calling occurred within a frequency range of 100 to 1200 Hz, while Guest & Lasswell (1978) reported that *S. ocellatus* pulses contained sound energy up to 2500 Hz with dominant energy in the 240 to 1000 Hz range. Parmentier *et al.* (2014) found that captive *S. ocellatus* produced calls that contained three or four pulses, and the dominant frequency ranged from 78 to 157 Hz. In the

13

present study, variation in *S. ocellatus* call structure (*i.e.* number of pulses and call duration) was observed within a tank. Studies have demonstrated that differences in fish size can influence pulse duration and dominant frequencies. For example, in *C. regalis*, as fish increase in size, the frequency range of calling decreases and the sound pressure level and pulse duration increase (Connaughton *et al.*, 2000). In whitemouth croaker *Micropogonias furnieri* (Desmarest 1823), dominant frequency and interpulse interval decrease, while pulse duration increases with fish size (Tellechea *et al.* 2010*a*). In the present study, male *S. ocellatus* were of similar size, and variation in call structure was most likely attributed to whether or not spawning occurred. This observation is discussed further in the section below that focuses on how sound production influences spawning success.

For each 2 min wav file obtained, the broadband received SPL of that entire recording was calculated. The number of calls counted in the 2 min wav files correlated positively with the mean received SPL (see Fig. 2). Mean SPL is a function of the number of calls, the number of pulses in a call, the sound intensity of each call and the distance of the sound source from the recorder. The relationship between calling and received SPL is important because SPL is often the more useful metric in quantifying sound production in the wild, where it can be challenging to count overlapping calls of a spawning aggregation. In addition, long-term monitoring of spawning sites using autonomous acoustic recorders can generate thousands of acoustic files. Having a MATLAB code determine the mean received SPL of each acoustic file as a means to quantify sound production is much less time intensive than having an observer manually count calls. The one drawback in calculating received SPL is that the

14

level depends on the distance from the spawning aggregation, which is typically unknown in sciaenid recordings.

LIGHT CYCLE AND TEMPERATURE AFFECTS SOUND PRODUCTION

Maximal sound production of captive *S. ocellatus* occurred when the photoperiod shifted from 13.0 to 12.5 h of light, and the water temperature decreased to *c.* 25°C. These captive settings are similar to the amount of daylight and water temperatures observed during the autumn, which is the primary spawning period for *S. ocellatus* (Murphy & Taylor, 1990; Ross *et al.*, 1995; Luczkovich *et al.*, 2008). In the south-eastern U. S., sound production of *S. ocellatus* has been detected from August to mid-October (Lowerre-Barbieri *et al.*, 2008; M.R. Collins, B.M.Callahan & W.C. Post, unpubl. data). This seasonal shift in calling frequency is due to changes in testosterone levels, which affects the output of the central nervous system and sonic muscle mass. For example, in *C. regalis*, the sonic muscle triples in mass as the spawning season approaches (Connaughton & Taylor, 1994). This hypertrophy is driven by elevated androgen levels, which are triggered by photoperiod and temperature cues that initiate sexual recrudescence (Connaughton & Taylor, 1994). Sonic muscle hypertrophy also coincides with seasonal patterns of sound production, with drumming increasing abruptly to near peak levels in mid-May and declining in late July (Connaughton & Taylor, 1995). Wild and captive *S. ocellatus* may follow similar endocrine, neurological, anatomical and physiological changes.

15

Wild caught *S. ocellatus* held in captivity exhibited daily patterns of calling with peak sound production occurring in the evenings between 0.50 h before dark to 1.08 h after dark. Other sciaenid species held in captivity have been shown to exhibit a similar daily pattern of spawning including *M. undulatus*, sand seatrout *Cynoscion arenarius* Ginsburg 1930 and *C. nebulosus*, all spawning during or soon after laboratory-simulated dusk (Holt *et al.,* 1985). *Sciaenops ocellatus* sound production has been documented to occur in the wild from 1500 to 2200 hours with peaks occurring in the late evening at several locations in the south-eastern U. S. including Charleston Harbor, South Carolina (W.A. Roumillat, G.H.M. Riekerk & S.J. Tyree, unpubl. data), Cumberland Sound, Georgia (Lowerre-Barbieri *et al.*, 2008) and Pamlico Sound, North Carolina (Luczkovich *et al.*, 2008). Additionally, Locascio & Mann (2011) showed that *P. cromis* sound production occurred during a similar timeframe, between 18:00 and 02:00, in Charlotte Harbor, Florida.

It is a consensus that spawning at dusk is a reproductive strategy for sciaenids living in a temperate environment (Holt *et al.*, 1985), which may provide a fitness advantage for their offspring. Holt *et al.* (1985) speculates that sound production and spawning for sciaenids occurs in the evening to limit predation on eggs. Many fishes including those of the families Crangidae, Lutjanidae and Sciaenidae prey on recently released sciaenid eggs. Holt *et al.* (1985) suggest predation by these fishes occurs mostly during the day due to an inability of the fishes to detect prey during the night. Thus, evening spawning allows for maximum dispersal of eggs prior to dawn when predators become more

active. Holt *et al.* (1985) performed plankton tows and found that *C. nebulosus* egg densities were reduced from 100 m^{-3} during spawning to < 1 m^{-3} the next afternoon, after 24 h of wind and tide dispersal.

Data from the present study indicate that *S. ocellatus* adjust the time of their peak sound production according to the light cycle. In tank 1, peak sound production shifted to earlier times as the tank environment became darker earlier (*i.e.* from 1915 to 1900 to 1845 hours). In a captive environment, Holt *et al.* (1985) kept *S. ocellatus* on a 12 h day and night cycle and then shifted the night cycle to occur 3 h earlier; *S. ocellatus* shifted their spawning accordingly. Schneider (1967) gradually decreased the artificial light intensity in tanks of tiger bass *Terapon jarbua* (Forsskål 1775) and recorded sound production. Maximal sound production occurred at the lowest light intensity level (*i.e.* a simulated twilight level), which indicated that light levels directly influenced calling.

As previously noted, maximal sound production of captive *S. ocellatus* occurred when the photoperiod shifted from 13.0 to 12.5 h of light, and the water temperature decreased to *c.* 25° C, which simulated daylight and water temperatures observed during the autumn (Fig. 3). These photoperiod and temperature cues initiate the spawning season of *S. ocellatus*. In tanks 1 and 2, however, rapid temperature changes also affected calling within this simulated season. Generally, abrupt drops in temperature decreased calling, while abrupt rises in temperature increased sound production. Because most fishes are ectotherms, the capability and speed of metabolic and physiological processes are

17

influenced by surrounding water temperature; ectotherms are more active when the environmental temperature is warmer. Schneider (1967) demonstrated that the number of calls and the number of pulses in a call produced by *T. jarbua* increased at higher temperatures. Fine (1978) found that elevated water temperatures increased the fundamental frequency and occurrence of mating calls produced by wild oyster toadfish *Opsanus tau* (L. 1766). Connaughton *et al.* (2000) found that an increase in water temperature affected captive *C. regalis* sound production by increasing the mean sound pressure level, the mean number of pulses in a call and the mean frequency in Hz. Maruska & Mensinger (2009) reported that higher water temperatures were correlated with a greater number of grunt emissions, higher fundamental frequencies and shorter call durations in *O. tau*.

SOUND PRODUCTION INFLUENCES SPAWNING SUCCESS

This study provides quantitative data on the relationship between sound production and spawning. Findings indicate that the amount of calling and the call structure play an important role in spawning success. Previous studies performed in captive environments have demonstrated a qualitative association between sound production and spawning (Guest & Laswell, 1978; Connaughton & Taylor, 1996; Lowerre-Barbieri *et al.*, 2008; Aalbers & Drawbridge, 2008). In a laboratory setting, Guest & Lasswell (1978) demonstrated that drumming and nudging intensified prior to spawning in captive *S. ocellatus*. Based on observing the behaviour of captive *S. ocellatus* in laboratory tanks over three consecutive evenings, Lowerre-Barbieri *et al.* (2008) found that the number of calls and the number of

pulses per call were much higher on evenings in which spawning occurred. Connaughton & Taylor (1996) reported that drumming in captive *C. regalis* was associated with spawning behaviour in the laboratory; however, calling ceased during gamete release. Aalbers & Drawbridge (2008) documented that *A. nobilis* maintained in net-pen enclosures increased their calling rates and produced specific vocalizations during gamete release.

In a wild setting, floating eggs and juveniles of many sciaenids have been collected with plankton tows on the same night and at the same location in which species specific calls have been recorded, demonstrating an association between sound production and spawning (Mok & Gilmore, 1983; Saucier & Baltz, 1993; Connaughton & Taylor, 1995; Luczkovich *et al.*, 1999). Mok & Gilmore (1983) showed that maximum daily sound production of *P. cromis*, *B. chrysoura* and *C. nebulosus* occurred between 1700 and 2200 hours in the Indian River Lagoon, Florida; these maximums coincided with the appearance of eggs and larvae in the water column at these locations. Connaughton & Taylor (1995) discovered that wild *C. regalis* reproductive data (*i.e.* gonad condition of males and females, male plasma androgen levels and sperm motility and the percentage of males producing milt when handled) peaked during the seasonal period of maximal drumming activity. Luczkovich *et al.* (1999) found that the maximum sound pressure levels of *C. regalis* and *B. chrysoura* calls at stations in Pamlico Sound, North Carolina, positively correlated with sciaenid-type egg densities collected at the same locations. In the only study that provided specific quantitative data (*i.e.* the comparison of sound and species-specific egg production), however, Locascio *et al.* (2012) reported that the timing and levels of sound production were negatively associated with those of egg production in *P. chromis*

inhabiting an estuarine canal basin of Cape Coral, Florida. These findings were unexpected and may be explained by the possible differences in the spawning potential of the female population in the study area over the period in which sampling occurred.

What function does male drumming play in the reproduction of *S. ocellatus*? One possibility is that male drumming may aid in the attraction of a gravid female, similar to what Connaughton & Taylor (1996) proposed for *C. regalis*. This type of behaviour occurs in female *O. tau* in response to 'boat whistle' calls of males (Winn, 1972). Male drumming may also provide females with information about the male, as suggested by Connaughton & Taylor (1996) in their evaluation of *C. regalis* sound production. In fact, the present study found that spawns were more productive on evenings when calls were longer in duration and contained more pulses. The variability in call structure may indicate that males compete with each other to be chosen by females (*i.e.* intersexual selection). Calling may also function in forming and maintaining spawning aggregations as suggested by Connaughton & Taylor (1996). Templeman & Hodder (1958) speculated that sound production of male *M. aegletinus* during the spawning season attracts both males and females to a specific location, leading to the formation of a spawning aggregation. More research is needed to better understand the function of male drumming and the dynamics of *S. ocellatus* spawning aggregations.

FISHERY MANAGEMENT IMPLICATIONS

This study is the first to record underwater sound and monitor spawning success of a captive, soniferous fish population over an entire simulated reproductive season. It is the first captive study that reports quantitative data on the positive relationship between sound production and egg production. Findings indicate that the amount of calling and the call structure play a very important role in spawning success. This study provides ample evidence that sound production equates to spawning in captive *S. ocellatus* when calls are longer than 0.8 s and contain more than seven pulses. The fact that more calling, longer calls and higher sound pressure levels are associated with spawns that are more productive in captivity indicate that acoustic metrics can provide quantitative information on spawning in the wild. These data are important because it is not clear how accurately field sampling of eggs can be used to draw inferences about spawning activity because egg capture is likely to be affected by predator activity, water currents and the efficiency of plankton tows. Thus, these findings are critical and provide instrumental information to scientists and managers who plan to use or are using passive acoustics as a tool to monitor *S. ocellatus* reproduction.

This approach and these data illustrate and provide a means to acoustically identify spawning aggregations of *S. ocellatus* in the wild using long-term acoustic recorders. This technology allows scientists and managers to examine the reproductive activity and distribution of animals non-optically, which is extremely useful in environments where the water visibility is limited, as is the case in the tidal creeks, rivers and estuaries of South Carolina. It sets forth a framework to monitor the underwater

soundscape continuously and long-term in order to understand the spatial and temporal patterns of spawning and the possible impacts of anthropogenic stressors (*e.g.* climate change, noise pollution and environmental pollutants) on these reproductive patterns.

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TABLE III. Hours before or after dark in which sound production occurred in captive *Sciaenops ocellatus*. Values represent means of all four tanks. Light cycle 1: 16/07/2012 to 05/08/2012: 14.0 h light; 1930 hours lights off. Light cycle 2: 06/08/2012 to 26/08/2012: 13.5 h light; 1915 hours lights off. Light cycle 3: 27/08/2012 to 09/09/2012: 13.0 h light; 1900 hours lights off. Light cycle 4: 10/09/2012 to 17/12/2012: 12.5 h light; 1845 lights hours off. Light cycle 5: 18/12/2012 to 25/12/2012: 11.0 h light; 1800 hours lights off

Sound Production	Light cycle 1	Light cycle 2	Light cycle 3	Light cycle 4	Light cycle 5
Start time	ndp	-0.25	-1.33	-1.30	ndp
Peak time	ndp	+1.08	-0.50	+0.47	ndp
End time	ndp	+3.75	+1.33	+2.70	ndp
Total time calling (h)	ndp	4	2.67	4	ndp

-, hours before dark; +, hours after dark;

ndp, no daily pattern observed.

TABLE II. *Sciaenops ocellatus* call data and characteristics. Means ± S.D. reported for individual tanks and means ± S.E. of all four tanks

Tank Information	Tank 1	Tank 2	Tank 3	Tank 4	Means ± S.E .
Number of spawns	61	32	4	33	33 ± 12
Eggs collected	94,604,000	55,418,000	10,040,000	72,710,000	58,193,000 ± 17,941,842
Viable eggs collected	89,970,000	50,270,000	8,740,000	61,650,000	52,657,500 ± 16,851,149
Number of calls	53,329	20,681	8,238	8,795	22,761 ± 10,586
Number of calls between 1540 to 0000 hours	41,801	20,244	3,349	7,479	18,218 ± 8,644
Number of calls between 1540 to 0000 hours (no spawning)	17,403	8,664	2,366	820	7,313 ± 3,767
Number of calls between 1540 to 0000 hours (spawning)	24,398	11,580	983	6,659	10,905 ± 4,992
Mean calls between 1540 to 0000 hours (no spawning)	200 ± 203	75 ± 132	17 ± 28	7 ± 11	75 ± 44
Mean calls between 1540 to 0000 hours (spawning)	393 ± 81	341 ± 155	246 ± 151	202 ± 97	296 ± 44
Mean SPL from 1540 to 0000 hours (no spawning)	120 ± 3	116 ± 3	117± 1	114 ± 1	117 ± 1
Mean SPL from 1540 to 0000 hours (spawning)	122 ± 1	121 ± 3	123 ± 2	119 ± 2	121 ± 1
Mean call duration (s)	0.70 ± 0.14	0.73 ± 0.17	0.41 ± 0.11	0.56 ± 0.24	0.60 ± 0.07
Duration range of calls (s)	0.20 to 2.24	0.19 to 2.10	0.23 to 2.23	0.21 to 3.53	0.21 ± 0.01 to 2.52 ± 0.34
Mean call duration (no spawning) (s)	0.63 ± 0.16	0.66 ± 0.17	0.40 ± 0.10	0.43 ± 0.10	0.53 ± 0.07
Mean call duration (spawning) (s)	0.78 ± 0.05	0.82 ± 0.12	0.75 ± 0.05	0.92 ± 0.12	0.82 ± 0.04
Mean number of pulses in a call	6.62 ± 2.39	5.89 ± 2.41	2.26 ± 0.65	3.59 ± 2.59	4.59 ± 1.01
Pulse range of calls	2 to 25	2 to 25	2 to 17	2 to 29	2 ± 0 to 24 ± 2
Mean number pulses (no spawning)	5.43 ± 2.62	4.67 ± 2.01	2.19 ± 0.50	2.20 ± 0.38	3.62 ± 0.84
Mean number pulses (spawning)	8.02 ± 0.88	7.48 ± 1.93	4.61 ± 0.79	7.49 ± 2.06	6.90 ± 0.77

SPL, received sound pressure level in dB re 1μPa.

TABLE I. Life history information of *Sciaenops ocellatus* held in captivity

PIT numbers		Sex	L_F (mm)	L_T (mm)	Date captured	Number of acclimation days
Tank 1						
6C00124233	AB176	M	888	939	08/11/2010	623
48211B7904	AB162	M	811	867	28/10/2009	999
48207B3E62	AB127	F	839	897	25/06/2008	1489
4821270352	AB170	F	931	991	03/11/2009	923
4569230F18	AB133	F	na	na	03/10/2008	1389
Tank 2						
6C00124200	AB179	M	965	1038	08/11/2010	623
48205E207B	AB138	M	1010	1077	03/12/2008	1328
48207C6917	AB143	F	822	871	03/12/2008	1328
4820551E4A	AB129	F	815	866	25/06/2008	1489
48212A3F3C	AB152	F	871	938	27/10/2009	998
Tank 3						
4821105A34	AB164	M	873	930	03/11/2009	923
6C00125044	AB181	M	na	na	27/10/2011	270
4820761D39	AB144	F	920	985	03/12/2008	1328
48206A6362	AB151	F	971	1036	27/10/2009	998
48241E0B14	AB145	F	880	932	04/12/2008	1329
Tank 4						
48237D5E60	AB139	M	857	912	03/12/2008	1328
6C00125004	AB182	M	na	na	27/10/2011	270
48242D592F	AB167	F	853	916	03/11/2009	923
482129507E	AB172	F	855	920	03/11/2009	923
4820513C71	AB171	F	893	959	03/11/2009	923

L_F, fork length; L_T, total length; na = not available; M, male; F, female.

TABLE IV. Results of paired *t*-tests that tested if sound production and call structure differed significantly between non-spawning and spawning nights for *Sciaenops ocellatus* held in captivity. Number of calls and mean received sound pressure level in dB re 1 μPa (SPL) are measurements per evening from 1540 to 0000 hours

Tank	Variable	*t*	d.f.	*P*
Tank 1	Number of calls	-7.114	147	<0.001
Tank 1	Mean SPL	-7.072	147	<0.001
Tank 1	Number of pulses per call	-7.432	133	<0.001
Tank 1	Call duration (s)	-7.490	133	<0.001
Tank 2	Number of calls	-9.901	147	<0.001
Tank 2	Mean SPL	-8.963	145	<0.001
Tank 2	Number of pulses per call	-6.216	76	<0.001
Tank 2	Call duration (s)	-4.729	76	<0.001
Tank 3	Number of calls	-13.855	147	<0.001
Tank 3	Mean SPL	-7.571	147	<0.001
Tank 3	Number of pulses per call	-9.313	137	<0.001
Tank 3	Call duration (s)	-7.417	137	<0.001
Tank 4	Number of calls	-21.251	147	<0.001
Tank 4	Mean SPL	-15.706	147	<0.001
Tank 4	Number of pulses per call	-23.768	123	<0.001
Tank 4	Call duration (s)	-22.488	123	<0.001

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TABLE V. Results of linear regression analysis that tested the significance of the amount of calling, received sound pressure level in dB re 1 µPa (SPL) and call structure in relation to spawning success of *Sciaenops ocellatus* held in captivity. In all cases, the dependent variable is the number of eggs collected. Number of calls and mean SPL are measurements per evening from 1540 to 0000 hours

Tank	Independent variable	Fitted equation	r^2	P	d.f.
Tank 1	Number of calls	y = 2,048x + 59,953	0.111	<0.001	147
Tank 1	Mean SPL	y = 160,897x -18,856,673	0.130	<0.001	147
Tank 1	Number of pulses per call	y = 161,524x - 368,184	0.103	<0.001	133
Tank 1	Call duration (s)	y = 3,469,953x -1,724,330	0.172	<0.001	133
Tank 2	Number of calls	y = 2,536x + 30,901	0.272	<0.001	147
Tank 2	Mean SPL	y = 104,904x - 11,932,342	0.215	<0.001	145
Tank 2	Number of pulses per call	y = 229,454x - 635,090	0.262	<0.001	76
Tank 2	Call duration (s)	y = 2,591,122x -1,180,564	0.158	<0.001	76
Tank 3	Number of calls	y = 8,400x -123,794	0.582	<0.001	147
Tank 3	Mean SPL	y = 141,911x - 16,578,129	0.189	<0.001	147
Tank 3	Number of pulses per call	y = 502,307x - 1,063,484	0.339	<0.001	137
Tank 3	Call duration (s)	y = 2,175,336x - 811,314	0.190	<0.001	137
Tank 4	Number of calls	y = 10,182x -23,074	0.708	<0.001	147
Tank 4	Mean SPL	y = 379,448 - 43,281,784	0.572	<0.001	147
Tank 4	Number of pulses per call	y = 413,695x - 904,994	0.779	<0.001	123
Tank 4	Call duration (s)	y = 4,125,540x - 1,732,276	0.660	<0.001	123

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