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[Article]

Use of Passive Acoustics to Determine Red Drum Spawning in Georgia Waters

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Abstract.—Passive acoustic sampling to locate spawning sites of red drum *Sciaenops ocellatus* was conducted along the Georgia coast during July–October 1995–1997. Spawning red drum were observed in captivity to determine the level of sound associated with spawning. In 1997, a known red drum spawning site was sampled weekly with a mobile hydrophone and continuously with a remote hydrophone deployed from 23 September to 2 October 1997. Both field and tank observations indicated that red drum males make calls with four or fewer pulses per call without associated spawning. However, calls consisting of at least 8 pulses/call occurred only prior to spawning. In 1995 and 1996, a total of 372 hydrophone observations were made at regularly sampled stations in Doboy, Altamaha, St. Simon's, and St. Andrew sounds and at supplemental locations along the Georgia coast. Only one nearshore spawning site was located; it was found in St. Mary's channel at the mouth of Cumberland Sound. Duration of peak red drum sound production at this site varied from 1 to 4 h but generally occurred from 1600 to 1900 hours. The Cumberland Sound site was characterized by deep water (>13.7 m) and relatively high salinity (>30‰). Red drum spawning activity at this site was estimated to occur during August through mid-October based on calls.

The red drum *Sciaenops ocellatus* is one of the most important fishery resources of the southeastern U.S. coast and the Gulf of Mexico (Mercer 1984; ASMFC 1991). Postlarval and juvenile red drum inhabit estuarine and shallow nearshore waters (Holt et al. 1981; Peters and McMichael 1987; Daniel 1988), while adults are often found in large schools that move inshore and offshore seasonally (Vaughan 1993). The current distribution of red drum in the Atlantic Ocean, as indicated by commercial and recreational landings, extends from southern Florida to Chesapeake Bay (SAFMC 1990; Ross et al. 1995). Recent stock assessments (Vaughan 1993, 1996; Vaughan and Carmichael 2000) have divided this distribution into a northern region (Virginia and North Carolina) and a southern region (South Carolina, Georgia, and the eastern coast of Florida).

Although stock abundance has improved since the 1980s, there is continuing concern that the red drum stock in the southern region is overfished (Vaughan and Carmichael 2002). The target static spawning potential ratio (SPR) is 40%, but the current SPR estimate of 15% in the southern region is well below this target (Vaughan and Carmichael 2002). Red drum are particularly susceptible to recruitment overfishing because even with current regulations, the age at entry into the fishery (age 0–1) is well below the age at sexual maturity (age 3–6 for females: Murphy and Taylor 1990; Ross et al. 1995).

To properly manage red drum in the southern region, it is critical to have information on red drum spawning habitat and reproductive parameters. In eastern central

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Florida, nearshore red drum spawning habitat has been documented in Mosquito Lagoon (Johnson and Funicelli 1991), and reproductive parameters have been estimated (Murphy and Taylor 1990). However, along the rest of the Atlantic coast, there is little information on spawning requirements (e.g., location, water temperature, and salinity) because it is difficult to locate and capture adult red drum in spawning condition (Pafford et al. 1990).

Passive acoustic surveys can be used to cover large geographical areas to detect drumming aggregations of red drum (Johnson and Funicelli 1991; Luczkovich et al. 1999). Male sciaenids produce drumming sounds by using specially developed muscles to vibrate the gas bladder membrane (Gilmore 2002). These sounds or calls are species specific. A typical red drum call is made up of a burst of pulses (each pulse sounds like an individual "knock," and the call is often made up of multiple knocks or pulses), and the dominant sound energy is in the range of 240 to 1,000 Hz (Guest and Lasswell 1978). These drumming sounds are correlated with spawning season and location (Mok and Gilmore 1983; Saucier and Baltz 1993), thus making it possible to determine temporal and spatial aspects of red drum reproduction. This study was undertaken to (1) observe red drum in captivity to determine the level of sound production associated with spawning activity; (2) identify sites along the Georgia coast where nearshore red drum spawning occurs; (3) evaluate the habitat and environmental conditions associated with spawning; and (4) assess daily, seasonal, and interannual spawning activity at a known spawning site.

Methods

Study area.—Initial sampling (1995) was conducted in Doboy and Altamaha sounds (Figure 1). These locations were chosen based on past research indicating possible red drum spawning activity. Adult red drum were consistently located within Altamaha Sound just prior to the spawning season (Nicholson and Jordon 1994), and larvae were collected at the mouth of Doboy Sound (Setzler 1977). Regularly sampled stations corresponded to the lower, mid-, and upper regions of these two sounds. As of mid-September, the channels to Doboy and Altamaha sounds were also sampled.

The study area was increased in 1996. Sampling was conducted weekly in Doboy Sound and channel, Altamaha channel, St. Simon's Sound, and St. Andrew Sound (Figure 1). To increase the geographic coverage, supplemental sampling was conducted every other week in one of these locations: offshore to Cabretta Reef (25.7 km due east of Cabretta Inlet on Sapelo Island), throughout the length of the Brunswick channel going toward St. Simon's Sound (Figure 1), at the Savannah River entrance on Georgia's northern border, and at the mouths of Cumberland, Sapelo, and St. Catherine's sounds (Figure 2). In 1997, sampling focused on St. Mary's channel at the mouth of Cumberland Sound, where a spawning aggregation was located in 1996.

Sound production in captivity.—In April 1997, South Carolina Department of Natural Resources (SCDNR) broodstock were observed for three consecutive evenings, and sound production associated with spawning was recorded for comparison with that recorded in the field. Broodstock were held in two round fiberglass tanks, each of which had a viewing window on the side. Six fish were held in tank 1 (sex ratio = 2:1, females : males), and eight fish were held in tank 2 (sex ratio = 1:1). Brood fish were approximately 11.3–18.1 kg, and females were larger than males. Photoperiod was set for 13 h light : 11 h dark, and darkness commenced at 1900 hours. Salinity was 30‰ in tank 1 and 32‰ in tank 2. Water temperature during the first 2 d was approximately 27°C; on the third day, most of the water was drained off and new water was added, resulting in a lower temperature of 23.5°C.

Observations focused on whichever tank showed the most activity that evening. Fish were observed through the viewing window from 1500 hours until sound production ceased or until dark, whichever occurred first. It was possible to identify individual fish by the markings on their caudal peduncles (e.g., 1–5 spots). A hydrophone was lowered approximately 0.6 m below the surface. Sound production was monitored constantly, and a recording was made every 15 min (see equipment and acoustic protocols under *Data collection*). Recordings were then reviewed in the laboratory to determine the maximum and mean pulse repetition rate (number of pulses per call), as well as the number of calls per minute (Guest and Lasswell 1978). A maximum of 10 pulses/call was used, although some calls contained a greater number of pulses. This was done because the greatest sound energy occurred in the first 10 pulses and because it became difficult to distinguish individual pulses after this point.

Data collection.—Sampling methods varied with the year of data collection. In 1995, an acoustic survey using an underwater hydrophone (InterOcean; Model 902, frequency range = 20–10,000 Hz) to detect drumming aggregations of red drum was conducted during mid-July through October. Three-minute surface and bottom plankton tows (1-m-diameter net with 0.50-mm mesh) were made weekly in Doboy Sound and intermittently in Altamaha Sound to collect red drum eggs and larvae. The acoustic survey included 7 regularly sampled acoustic stations within Altamaha

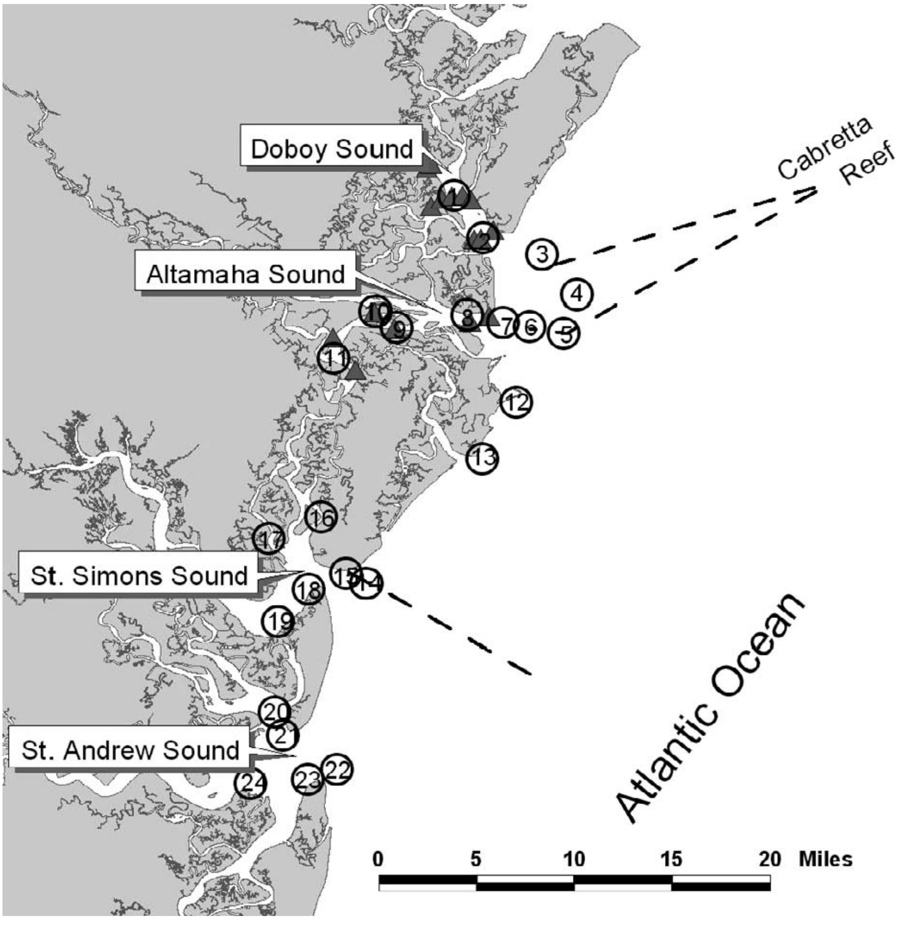

FIGURE 1.—Map of Georgia, showing regular sampling stations where red drum sound production was used to locate spawning aggregations in 1995 (triangles) and 1996 (numbered circles); supplemental offshore sampling transects in Cabretta Reef and Brunswick channel are also illustrated (dashed lines).

Sound and 10 stations in Doboy Sound. In association with acoustic sampling, surface and bottom salinity, surface and bottom temperature, and depth were recorded at each station, as was time of day (all reported times are local time), tide and lunar phase. The hydrophone was lowered 1 m below the surface for 5–10 min while the boat drifted (with the motor shut off). The hydrophone acoustic level was kept constant at 130 dB relative to (re) a reference effective pressure of 1 μP so that sound amplitudes from all stations could be compared (Mok and Gilmore 1983). When drumming was heard, a recording (recording level = 2) was made on a Sony TCD-D8 (DAT) recorder (frequency range = 20–22,000 Hz ± 1 dB). To confirm species identification, our recordings were compared to recordings of red drum spawning in captivity (SCDNR, unpublished data).

In 1996, sampling was conducted during July through October and included a total of 24 regularly sampled stations, as well as supplemental stations along the coast and offshore (Figure 1). By using this much greater geographic coverage, a nearshore spawning aggregation was located in Cumberland Sound. This site was then sampled weekly through the end of October (except the first week in October, when a tropical storm occurred). In 1997, sampling focused on the Cumberland Sound spawning site. Our objectives were to determine (1) diel periodicity of red drum sound production in the field; (2) spawning seasonality; (3) interannual site fidelity; (4) whether a spotter plane could be used to locate the aggregation; and (5) whether either long-lining or recreational hook-and-line fishing could be used to sample fish from the aggregation.

Diel periodicity of sound production was determined based on 24-h observations made with a remote

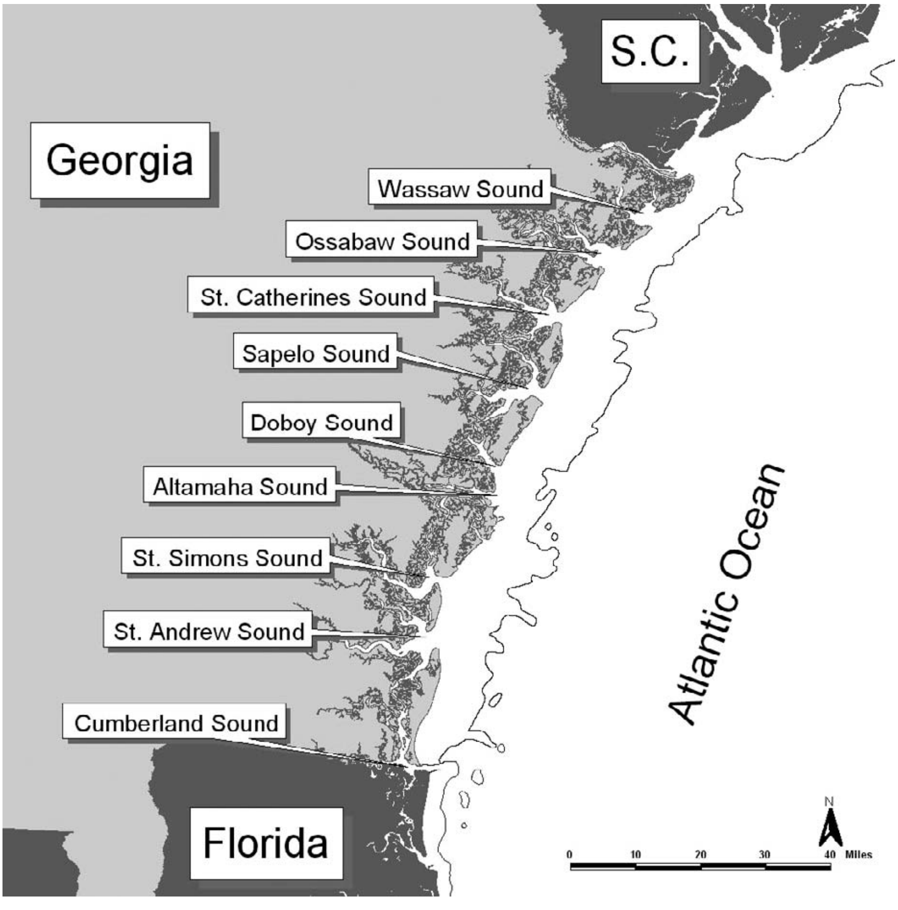

FIGURE 2.—Map of the Georgia coast, where red drum sound production was used to locate spawning aggregations. The 9.1-m (30-ft) isopleth is denoted by a solid line offshore.

hydrophone (built by Harbor Branch Oceanographic Institute for SCDNR using an omnidirectional hydrophone, frequency range = 20–10,000 Hz, and a Sony TCD-D8 recorder) deployed in Cumberland Sound from 23 September to 2 October 1997. The hydrophone was attached to a solid rod, approximately 1 m off the bottom anchor. Fifteen-second recordings were made every 0.5 h. Recordings of red drum sounds were categorized by group size: (a) an individual fish (i.e., each call was continuous with no overlapping calls); (b) several fish (i.e., calls overlapped but individual calls were still discernible); and (c) a drumming aggregation (i.e., calls completely overlapped and those of individuals were indistinguishable). Each call was also categorized by the number of pulses it contained: 1–3, 4–7, and 8 or more.

To determine spawning seasonality and site fidelity in 1997, field sampling was conducted weekly in Cumberland Sound during July through October. On each sampling date, hook-and-line fishing was conducted at the mouth of the channel for roughly 3–4 h. Acoustic sampling (see above for protocol) was then conducted in the late afternoon and evening from approximately 1500 to 1900 hours. Acoustic sampling was conducted along St. Mary's channel from midway within Cumberland Sound to an area past the jetties at the channel entrance (Figure 3). Seven stations, corresponding to the channel markers, were sampled. Group size and calls were categorized as for the remote hydrophone. Drumming aggregations or drum roll calls were considered indicative of spawning activity.

Results

Sound Production in Captivity

Fish in both tanks demonstrated some level of drumming and courtship activity each night, although spawning occurred only on 14 April 1997. A typical call consisted of multiple pulses per call, and the

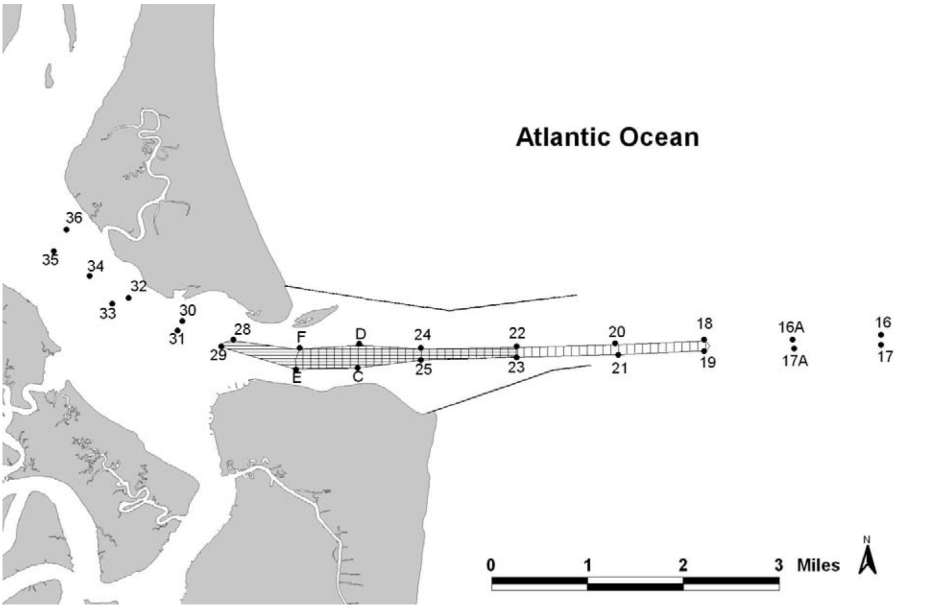

FIGURE 3.—Map of St. Mary's channel at the mouth of Cumberland Sound, Georgia, where red drum sound production was used to locate spawning aggregations. Boundaries of spawning-level sound production are indicated (vertical lines = 1996; horizontal lines = 1997). The hatched area indicates where an aggregation was located in both years. Individual channel markers used as sampling stations are indicated by numbers or letters.

majority of the sound energy occurred from 100 to 1,200 Hz (Figure 4). However, frequency ranges varied somewhat among individual fish.

Although spawning did not occur, drumming and courtship activity were observed in tank 1 on 12 April 1997. Drumming began at 1515 hours and was made up of intermittent calls with only 1 pulse/call. By 1630 hours, calls had become more frequent and each call contained 1–3 pulses. There was also a noticeable increase in swimming activity relative to that of fish in tank 2, which were not drumming. By 1745 hours, the two males in tank 2 could be identified by their individual calls (one individual was much larger and had a deeper call; see Figure 5), drumming had increased to 7.9 calls/min with up to 4 pulses/call, and courtship activity (males chasing and nudging females) was observed. Both males took on courtship coloration by 1815 hours, becoming silvery white ventrally and blue-black dorsally, and could be clearly differentiated from the females. However, by 1845 hours, this coloration had faded and drumming had decreased to 3.7 calls/min and 1–2 pulses/call. Intermittent calls continued through 2300 hours; these calls occasionally contained 3 pulses/call but usually had only 1–2 pulses/call.

On 13 April 1997, intermittent calls were heard in both tanks and fish became agitated. However, by 1800 hours, the pulse repetition rate had not exceeded 2 pulses/call and activity had decreased in both tanks. Males did not take on courtship coloration.

On 14 April 1997, two of the four males in tank 2 had courtship coloration by 1500 hours, although no calls were observed until 1515 hours. By 1615 hours, calls were intermittent but contained 3–4 pulses/call. By 1630 hours, at least three of the four males were drumming and sound production had dramatically increased to 30 calls/min and a maximum of 7 pulses/call. Activity had also increased by this time; males swam much faster, nudged females from below, and occasionally splashed the surface. However, this activity centered on only two of the four females, while the other two were left unattended. Between 1700 and 1715 hours, sound production peaked at 39.5 calls/min and at least 8 pulses/call; the nature of the calls had changed. Calls consisted of several strong initial pulses and then many weaker pulses that were so close together that they could not be individually detected by ear. We termed this sound pattern the drum roll (Figure 5). At this point, all four males had courtship coloration, were extremely agitated, and displayed increased swimming speeds. They tended to form small schools in which all attended to one female at a time, surrounding her and nudging her near her urogenital opening. Although females were active, they were much less so than the

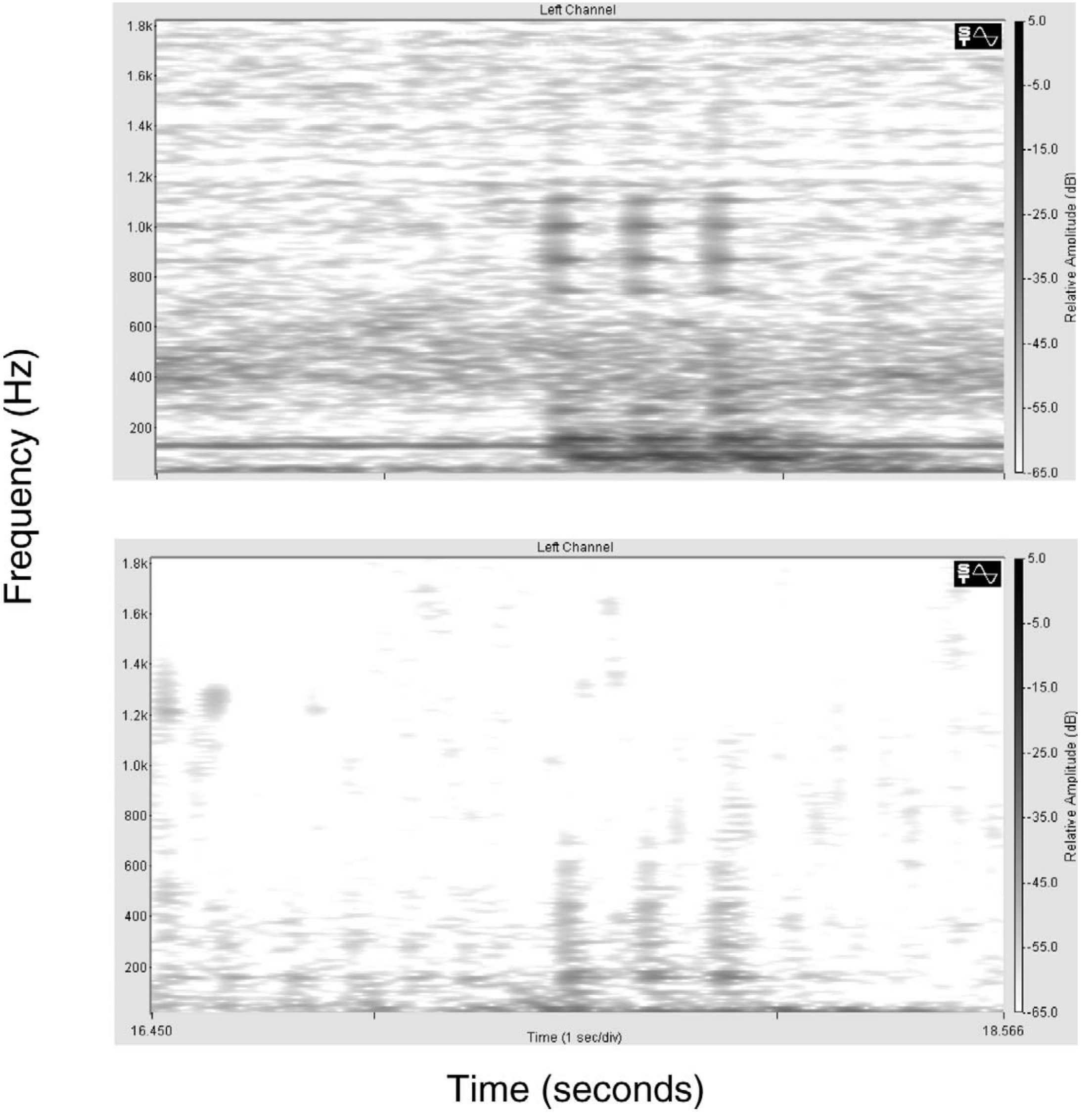

FIGURE 4.—Spectrograms of red drum calls (3 pulses) recorded in captivity (top) and in the field (bottom). Recordings of captive fish contained background noise due to the recirculating water (indicated by the band at 300–500 Hz).

males; females appeared to try to swim away from the males, which often pushed them up against the side of the tank. Although no clear act of spawning was observed, fertilized eggs were collected by 1725 hours. By 1730 hours, only one male still exhibited courtship coloration and drumming had decreased to 3–5 pulses/call. At 1745 hours, all four males again exhibited courtship coloration, calling frequency and pulse repetition rate increased, and some calls contained eight or more pulses. After this point, sound production steadily decreased and drum rolls stopped.

Although red drum sound production occurred even when there was no spawning, sound production clearly differed between spawning and nonspawning periods. On 12 April 1997, sound production was never greater than 10 calls/min and the mean pulse repetition rate was less than 3 pulses/call (Figure 6). In comparison, on 14 April 1997, the calling frequency just prior to spawning was over 30 calls/min and the mean pulse repetition rate was greater than 5 pulses/call. In addition, many calls had at least 8 pulses/call, thus producing the drum roll. This level of sound production occurred from 1645 to

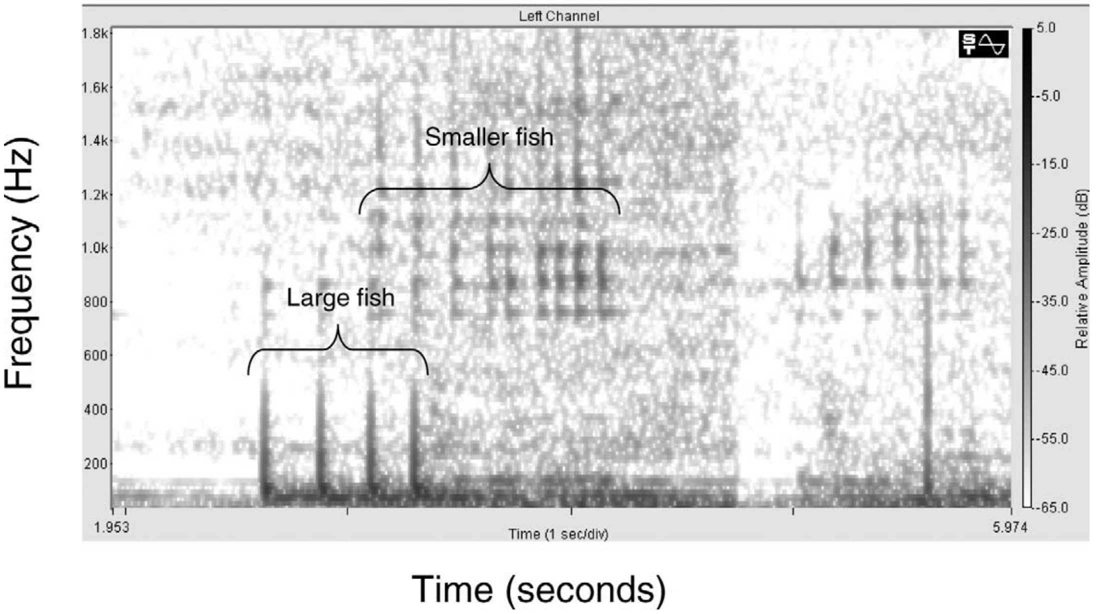

FIGURE 5.—Spectrogram of red drum calls recorded in captivity. Note the lower frequencies of the four-pulse call, which was made by the larger of two calling males. The other call is made up of nine pulses (i.e., a drum roll). Calls containing eight or more pulses were associated with spawning.

1745 hours; eggs were observed at 1725 hours; and simulated sunset occurred at 1900 hours.

Spawning Location

In 1995 and 1996, 372 hydrophone observations were made along the Georgia coast. Sampling occurred during July through October within the diel window of peak sound production (1600–1900 hours; see below). In 1995, sampling focused on Doboy and Altamaha sounds (Figure 1) and red drum calls were only detected on 15 September 1995 at the mouth of Altamaha Sound. The calls were made by two individuals and had low pulse repetition rates (4 pulses/call). Because their pulse repetition rates were less than that associated with spawning activity, these fish were not considered part of a spawning aggregation. Two females with regressing ovaries were caught on hook and line in the surf off Altamaha Sound on the same date, suggesting that the males heard at the mouth of Altamaha Sound had completed their spawning season and were moving into the shoals to feed. No sciaenid eggs were collected in our plankton samples.

In 1996, only one drumming aggregation was located. It occurred in St. Mary's channel at the entrance to Cumberland Sound. No red drum calls were observed in Doboy, Altamaha, St. Simon's, or St. Andrew sounds. Red drum calls were not observed in our supplemental sampling at the Savannah River entrance, the mouth of St. Catherine's Sound, the mouth of Sapelo Sound, Brunswick channel, or offshore at Cabretta Reef.

Although a drumming aggregation occurred in St. Mary's channel in both 1996 and 1997, drumming did not occur equally at all stations. In 1997, group size (no fish, one individual, several fish, or an aggregation) and pulse repetition category (1–3, 4–7, or $\geq$8 pulses/call) differed significantly by station over the dates sampled (analysis of variance [ANOVA], group size: $N = 97$, $P = 0.01$; pulse repetition category: $N = 97$, $P = 0.01$). Mean group size and pulse repetition category were greatest at markers 22 and 23, just within the tips of the jetties (Table 1). The easternmost detection of a drumming aggregation in either year was at markers 18 and 19. No red drum calls were observed at markers 16 and 17, the sample sites located furthest offshore. The westernmost observation of a drumming aggregation was at markers E–F (1996) and 28–29 (1997), although some red drum calls of 4–5 pulses/call were detected as far west as channel marker 35 (Figure 3).

Drumming aggregations could not always be detected with the surface hydrophone. In 1996, category-3 calls (drum rolls; associated with spawning in captivity) were detected only at sites where there was also a drumming aggregation. However, in 1997,

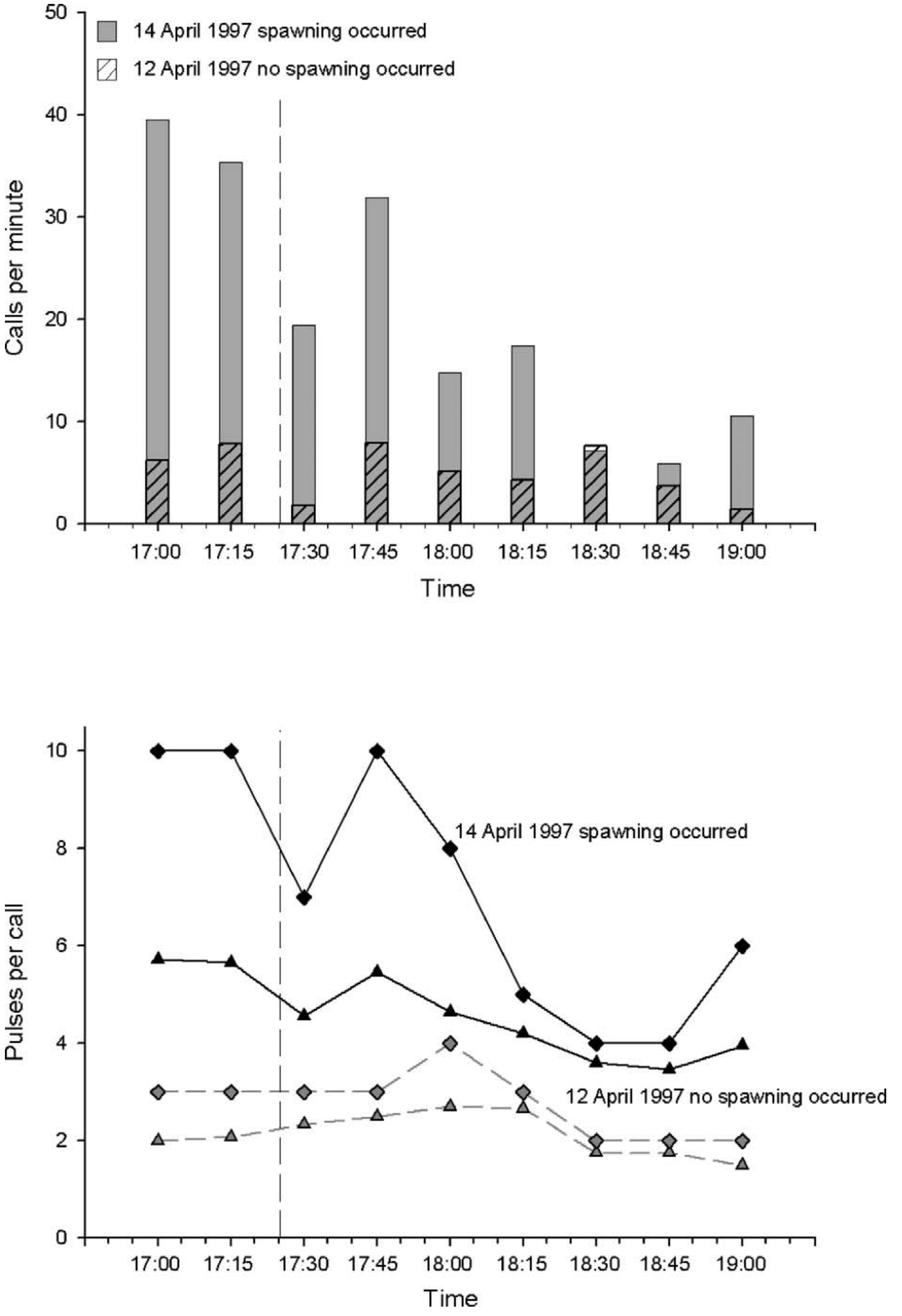

FIGURE 6.—Comparison of sound production between spawning and nonspawning captive red drum. Sound production is expressed as calling frequency (calls/min; top) and pulse repetition rate (pulses/call; bottom). Vertical dashed line indicates the time of spawning on 14 April 1997. Maximum (diamonds) and mean (triangles) pulse repetition rates were calculated for the spawning date (solid line) and a date of no spawning activity (dashed line).

TABLE 1.—Description of red drum sound production in Cumberland Sound, Georgia, during 1997, by station marker and date. The first number is group size category (0 = no fish; 1 = 1 fish; 2 = several fish; 3 = spawning aggregation); the second number is maximum pulse repetition rate category (pulses/call; 0 = none [no call], 1 = 1–3; 2 = 4–7; 3 = 8 or more). Blank indicates that station was not sampled due to bad weather.

	Marker						
Date	16–17	18–19	22–23	C–D	28–29	32–33	35
31 Jul			0, 0	2, 3	0, 0	0, 0	0, 0
11 Aug			0, 0	0, 0	0, 0	0, 0	0, 0
18 Aug	0, 0	0, 0	2, 3	0, 0	0, 0	0, 0	0, 0
28 Aug	0, 0	0, 0	2, 3	2, 2	2, 2	2, 2	2, 2
2 Sep			2, 3	0, 0	0, 0	0, 0	0, 0
9 Sep	0, 0	0, 0	2, 2	2, 3	2, 3	2, 2	2, 2
19 Sep	0, 0	0, 0	3, 3	0, 0	0, 0	0, 0	0, 0
23 Sep		1, 1	2, 3	2, 2	1, 1	1, 2	0, 0
1 Oct	0, 0	0, 0	3, 3	0, 0	0, 0	0, 0	0, 0
9 Oct			2, 2	2, 3	1, 2	0, 0	1, 2
16 Oct			0, 0	0, 0	0, 0	0, 0	0, 0
23 Oct	0, 0	0, 0	0, 0	0, 0	0, 0	0, 0	0, 0
Total		1, 1	18, 22	10, 13	6, 8	5, 6	5, 6

drum rolls were observed on seven occasions with no corresponding aggregation sound (Table 1). On 23 September 1997, the remote hydrophone (deployed 1 m from the channel bottom) and our field hydrophone (deployed approximately 1 m below the surface) made concurrent recordings at markers 22 and 23. The remote hydrophone recorded a drumming aggregation, whereas the field hydrophone recorded drum rolls of several fish but no aggregation sound. This difference occurred because most of the drumming fish were near the bottom of the channel and the sound was absorbed before it reached the surface. Based on this, it was assumed that sites with drum rolls in 1997 also had undetected drumming aggregations.

Although the drumming aggregation in Cumberland Sound was centered at markers 22 and 23, the location of aggregation sound shifted somewhat from date to date. On 13 September 1996, aggregation sound was heard at markers 18–19, 22–23, and 24–25. On 24 September 1996, the aggregation had shifted westward and aggregation sound was recorded at markers 22–23, 24–25, and E–F but not at markers 18 and 19. In 1997, the center of maximum sound production was more restricted. Drum rolls were predominantly located at markers 22 and 23 (Table 1). However, on 9 September 1997, drum rolls were also heard at markers C–D and 28–29.

Diel Periodicity of Courtship Sound

Red drum calls consisting of one to three pulses occurred over a greater time period than that observed in captivity. The initiation of sound production (often by just one individual) was variable, ranging from 900 to 1330 hours (mean = 1126 hours). Termination of red drum calls also varied from 1930 to 0200 hours (mean = 2112 hours). Other than the detection of an individual's call at 0200 hours (3.5 h after the previous call detection that night), no red drum calls were recorded from 2230 to 0830 hours.

Peak sound production was detected from about 1600 to 1900 hours. Group size category, pulse repetition category, and maximum pulse repetition rate all showed similar periodicities (Figure 7). Mean initiation time of aggregation sound occurred at 1612 hours (range = 1500–1730 hours). Termination of aggregation sound was often prior to sunset (sunset ≈ 1915 hours) and varied from 1800 to 2000 hours (mean = 1851 hours). Duration of aggregation sound varied from 1 to 4 h (Figure 8). Maximum duration of aggregation sound occurred when slack high tide fell within the window of aggregation sound (Figure 8). However, aggregation sound was detected nightly, both on flood tides and ebb tides.

Spawning Habitat

A depth greater than 13.7 m and salinity greater than 20‰ characterized the sites sampled in Cumberland Sound. Mean salinity at the Cumberland Sound stations was 31.2‰ in 1996 and 32.5‰ in 1997. The lowest salinity at which red drum calls were detected in Cumberland Sound was 23.8‰. However, aggregation sound or drum rolls were never heard at salinities below 30‰.

Although the Cumberland Sound stations were all deep sites with relatively high salinity, red drum sound was not equally distributed across them. Depth was the only recorded environmental variable that differed significantly by station (ANOVA: $N = 92$, $P < 0.001$) in 1997. Mean depth ranged from 13.9 m at marker 35 to 16.9 m at markers C–D and 28–29. Mean surface

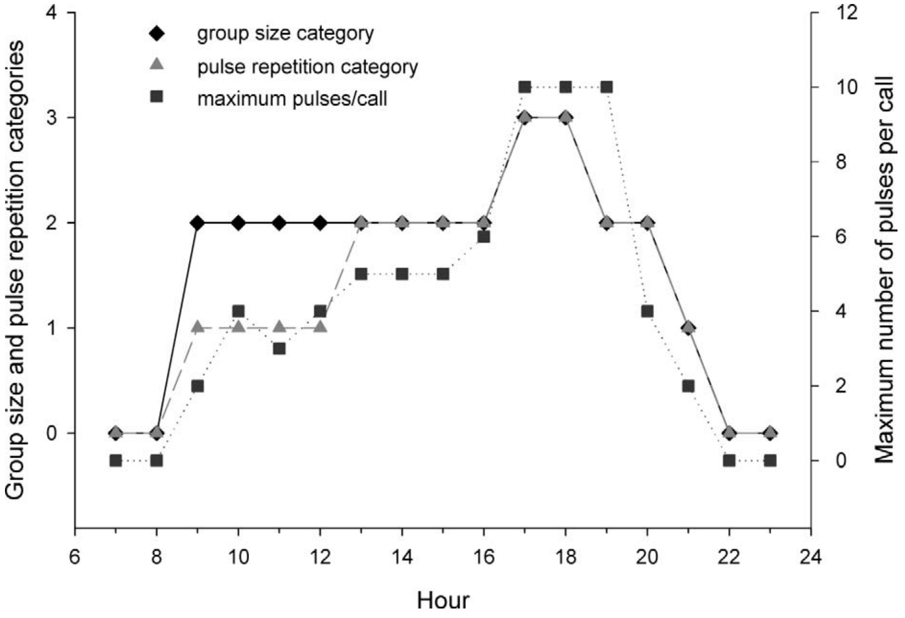

FIGURE 7.—Diel periodicity of red drum calls in Cumberland Sound, Georgia, on 25 September 1997. Sound was evaluated in terms of group size (0 = no fish; 1 = 1 fish; 2 = several fish; 3 = spawning aggregation), pulse repetition category (pulses/call; 0 = none [no call]; 1 = 1–3; 2 = 4–7; 3 = 8 or more), and maximum pulse repetition rate.

salinity by station ranged from 31.0‰ at marker 35 to 33.3‰ at markers 18 and 19. However, salinity and depth did not appear to be the only factors driving spawning site selection; mean salinity was 33.2‰ and mean depth was 14.9 m at markers 16 and 17, but red drum were never heard this far offshore.

Although numerous sites were sampled along the Georgia coast (Figures 1–3), few had the depth and high

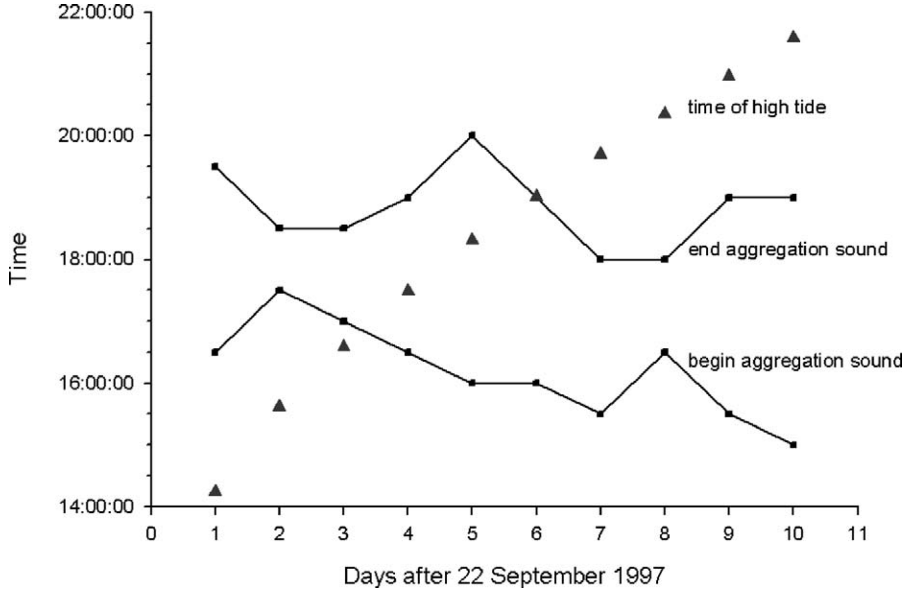

FIGURE 8.—Duration of calls produced by a red drum aggregation in Cumberland Sound, Georgia, as recorded over a 10-d period in 1997. Times of evening slack high tide at the mouth of Cumberland Sound are indicated (triangles). Two lunar phases occurred during this time period, third quarter on day one and new moon on day nine.

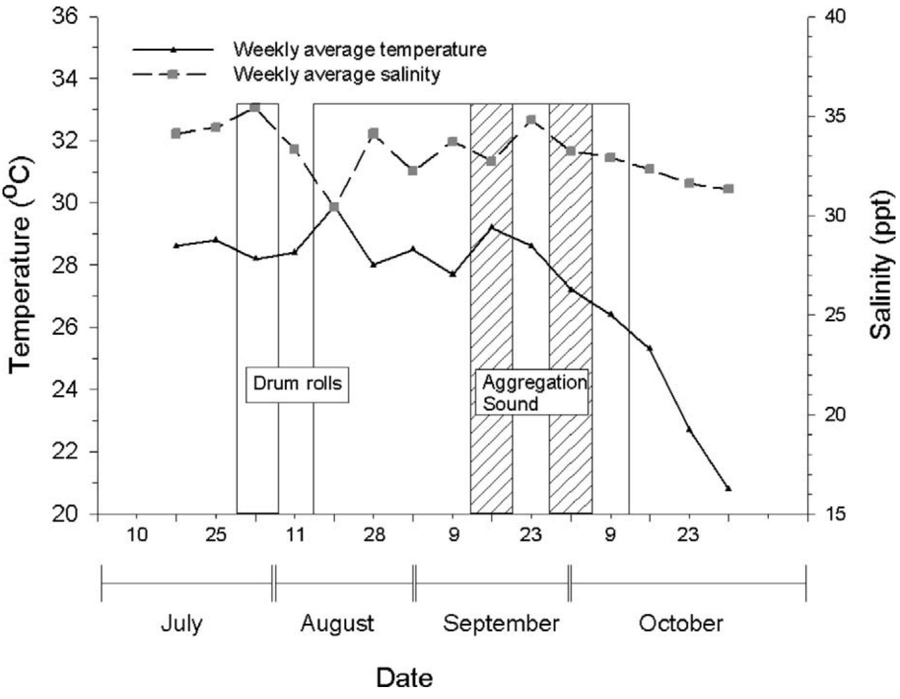

FIGURE 9.—Mean temperature (°C; solid line), salinity (‰; dashed line), and dates of red drum sound production (open bars = drum roll; hatched bars = aggregation sound) at markers 22 and 23 in Cumberland Sound, Georgia, during July–October 1997.

salinity of those in Cumberland Sound. Only five sites had a depth of 11.8 m or greater; one of these was Cabretta Reef, located offshore (Figure 2). The other four were all isolated holes: (1) mouth of Doboy Sound (Figure 1, site 2); (2) south end of Jekyll Island (Figure 1, site 20); (3) southern tip of St. Simon's Island (Figure 1, near the fishing pier, site 15); and (4) just off the entrance of St. Andrew Sound (Figure 1, "shark hole," site 22). Mean salinity at these sites ranged from 28.7‰ to 29.2‰. The sampled areas that were the most similar to St. Mary's channel were Brunswick channel (entering St. Simon's Sound) and the Savannah River entrance (Figure 3). However, both channels had depths that ranged from roughly 9.1 to 12.2 m and surface salinities less than 30‰ at all stations. Cumberland Sound is also different from the rest of the Georgia coast in that the 9.1-m (30-ft) isopleth comes much closer to shore (Figure 3).

Spawning Season

In 1996 and 1997, red drum sound production in Cumberland Sound was most intense during the month of September. In 1996, aggregation sound was observed on our first sampling date of 13 September and was last heard on 24 September; the greatest sound production (from presumably the largest number of fish) occurred on 13 September. From 25 September to mid-October 1996, red drum sound production was limited to several individuals making calls of 4–5 pulses/call. By the third week in October, sound production was reduced to one individual at one station. No red drum calls were detected after this time.

In 1997, spawning activity was estimated to occur during August through mid-October based on red drum calls. Cumberland Sound was sampled from 3 July to 23 October, and aggregation sound or drum rolls were first observed on 31 July (Figure 9). No red drum calls were detected on 11 August. Drum rolls were observed again on 18 August and heard through 9 October. Aggregation sound was detected with our surface sampling only on 19 September and 1 October. No red drum calls were heard after 9 October 1997.

Temperature seems to have affected termination of spawning. Water temperatures at which aggregation or drum roll sounds were observed ranged from 26.2°C to 30.0°C. In 1996, water temperature on 24 September (the last date on which aggregation sound was heard) was 27.0°C. By 11 October 1996, water temperature had dropped to 23.1°C and remained below 25°C throughout the rest of the month. In 1997, water temperature fluctuated during the spawning season (Figure 9). Temperature was 26.2°C on 9 October, the last date on which spawning-level sound production was observed. After this, water temperature steadily decreased from 25.2°C on 16 October to 20.7°C on 30 October.

Other Sampling Methods

Although hook-and-line sampling was conducted weekly at the Cumberland Sound spawning site, it was productive only on two dates. On 9 September 1997, one male (total length [TL] = 925 mm) and one female (TL = 904 mm) were captured. The female possessed developed ovaries with yolked oocytes and was capable of spawning. After this date, hook-and-line sampling was unproductive until our last day of sampling on 30 October, when five red drum were caught. Four were males and produced drumming as a startle response while being taken from the water. They did not, however, have flowing milt. Similarly, our attempt to capture fish by long-lining on 23 September 1997 was unproductive.

We were equally unsuccessful with aerial detection and plankton collection. A spotter plane was deployed on 19 September 1997, a date at which aggregation sound was observed. However, the water was more turbid than usual and the pilot could not visually detect the aggregation. On 23 September 1997, a surface plankton tow was taken in the channel at Cumberland Sound but no sciaenid eggs were collected.

Discussion

Sound Production in Captivity

For passive acoustics to successfully delineate spawning habitat, it is necessary to fully understand the relationship between sound production and spawning activity. Our description of red drum calls and their diel periodicity in captivity agreed well with that of Guest and Lasswell (1978). Red drum make a distinctive deep, knocking sound, and there was an increase in both calling frequency and pulse repetition rate in the hours prior to spawning; calls containing at least eight pulses were associated with spawning activity. However, calls characterized by four or fewer pulses occurred without any spawning activity. Based on this, we were able to evaluate red drum calls in the field and categorize them as spawning-related or nonspawning sounds, regardless of the number of fish calling. This became especially important at the Cumberland Sound sites, where aggregation sounds were present but only a few individuals could be heard from the surface.

Diel Periodicity of Courtship Sound

Diel spawning and peak sound production in Atlantic red drum were earlier than those reported for Texas red drum. The SCDNR's red drum broodstock spawned at roughly 1725 hours, approximately 1.5 h prior to simulated sunset (1900 hours). Similarly, peak sound production of the Cumberland Sound aggregation occurred from 1600 to 1900 hours, a 3-h period prior to sunset. This was similar to the diel period of peak sound production (1500–1900 hours) reported for South Carolina red drum (Roumillat et al. 1995). In contrast, red drum in Texas waters were estimated to spawn between dusk and 3 h after dark (Holt et al. 1985) and Texas broodstock reportedly spawned at dusk (Thomas et al. 1995).

Further research is necessary to better understand the diel periodicity and variability of sciaenid sound production. In general, temperate sciaenids have been reported to spawn at times close to dusk (Holt et al. 1985), but our results suggest that diel periodicity of spawning differs by location. There also appears to be temporal variability associated with time of peak sound production. In Cumberland Sound, the duration of peak sound production varied from 1 to 4 h. There are several possible explanations for this variability, including (1) a fixed listening location and a shifting spawning aggregation center; (2) a fluctuating number of fish spawning on any given day; or (3) the effect of current strength on male energy reserves. An understanding of this variability and its causes is necessary to compare a species' sound production over a large geographic range.

Spawning Location and Habitat

This is the first study to document a red drum spawning site in Georgia waters. Preliminary biotelemetry work in coastal Georgia indicated that adult red drum move into Altamaha Sound in August and September, and a few fish collected from these areas had developed gonads (Nicholson and Jordon 1994). Doboy Sound was also indicated as a possible spawning location. Setzler (1977) reported the collection of red drum larvae at the mouth of the Doboy Sound on incoming tides during August through October. However, we did not detect red drum calls, eggs, or larvae in either of these locations.

Red drum spawn both offshore and in nearshore waters throughout their range (Johnson and Funicelli 1991). Red drum with developed gonads were collected from offshore schools and estuarine and nearshore locations in North Carolina (Ross et al. 1995). In South Carolina, drumming aggregations were detected at the mouth of Charleston Harbor and in St. Helena Sound (Roumillat et al. 1995). In Florida, red drum spawning was detected in Mosquito Lagoon on the east coast (Johnson and Funicelli 1991). On Florida's west coast, spawning was documented offshore in the Gulf of Mexico, in the vicinity of passes, and within estuaries (Murphy and Taylor 1990). In the northern Gulf of Mexico, Wilson and Nieland (1994) collected reproductively active fish in shallow coastal waters from Alabama to Texas.

The environmental conditions necessary to induce red drum spawning in captivity are well known. Red drum broodstock, exposed to a seasonal cycle of temperature and photoperiod beginning with late-autumn conditions (23°C; 9 h light : 15 h dark), spawned 1.5 months after their second exposure to autumn conditions (Thomas et al. 1995). Optimal salinity for spawning in captivity is 30‰ (Thomas et al. 1995). In addition, Holt et al. (1981) reported that the highest rate of red drum hatching and survival occurred at 30‰ and 25°C and that the eggs did not float at salinities less than 25‰.

Salinity appears to play an important role in red drum spawning site selection. Although the majority of our 1996 stations had salinities exceeding 25‰ (as did the Brunswick channel and Cabretta Reef), we did not find any spawning activity in areas where salinity was less than 30‰. However, other Atlantic inshore spawning sites have been reported at slightly lower salinities. South Carolina inshore spawning sites had salinities ranging from 26‰ to 34‰ (Roumillat et al. 1995), and spawning sites in Mosquito Lagoon had salinities ranging from 29‰ to 33‰ (Johnson and Funicelli 1991).

The Cumberland Sound spawning site differed from our other sampling sites in that it was an area of consistently deep water bordered by jetties and relatively close to the 9.1-m isopleth. Depth alone does not seem to be critical, given that red drum consistently spawn in captivity in tanks less than 3 m deep. However, steep banks may play a more important role. Male red drum were observed to "herd" reproductively ready females in captivity, pushing them up against the side of the tanks. Steep banks would facilitate this type of behavior and occurred at all three of the known red drum spawning sites in South Carolina and Georgia.

Spawning Seasonality

Based on sound production, we estimated that the red drum spawning season occurred during August through mid-October. Similarly, Ross et al. (1995) reported peak spawning in August and September in North Carolina. The spawning season appears to be somewhat more extended in Florida, as both Johnson and Funicelli (1991) and Murphy and Taylor (1990) reported spawning through November. However, our estimated spawning seasonality agreed well with the mid-August to early October spawning season observed in the northern Gulf of Mexico (Wilson and Nieland 1994).

The temperature at which we no longer detected either aggregation or drum roll sounds was less than that reported for cessation of spawning in captivity. Holt et al. (1981) reported optimal hatching at 25°C, yet we did not observe spawning-level sound at temperatures below 26°C. Thomas et al. (1995) also reported that temperature profoundly affected spawning, which decreased at temperatures less than 23°C and ceased at temperatures less than 20°C. A possible explanation for these differences is that relative changes in temperature may have a greater effect on spawning than actual temperature.

Conclusions

Given the status of the Atlantic red drum stock and increased coastal development, it is important to delineate and protect red drum essential spawning habitat. We found that passive acoustics was the best method for covering large areas and for sampling habitats where traditional capture methods cannot be deployed. The greatest disadvantage of this method was sound interference by boats or water conditions (rushing current, waves, high winds), which made it somewhat more difficult to use offshore. Further work is necessary to fine tune this methodology and to better define offshore and inshore red drum spawning sites along the southeastern U.S. coast.

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