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[Article]

Distribution of Red Drum Spawning Sites Identified by a Towed Hydrophone Array

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Abstract.—Knowledge about fish spawning habits and habitats is an essential component of fisheries management. This paper reports on a survey of potential spawning sites for red drum *Sciaenops ocellatus* in the nearshore western Gulf of Mexico conducted using a towed hydrophone array. Two classes of red drum sounds could be distinguished. One was a low-frequency rumble with a prominent energy peak at approximately 150 Hz. The other was a clearly distinguishable call made by individual or small groups of red drum. Calls of individual red drum were detected along most sections of all transects. There were extensive areas along each transect where no close drumming was heard and where drumming rates were primarily low (<16 calls/min). Calls were detected in both extensive clusters and isolated occurrences along the transects. The distribution of drumming fish suggests that some, if not most, spawning takes place among widely dispersed individuals as opposed to highly aggregated groups. Only 7% of the 1-min summaries recorded high drumming rates (≥16 calls/min), and even these typically were produced by only a few individuals. Most low drumming rates were produced by a single fish. Based on the distribution of sound production, red drum apparently spawn all along the nearshore region of the central Texas coast. This survey was not spatially comprehensive enough to fully delineate the spawning area, but it made clear that spawning activity is widespread and not concentrated at inlets, as has been suggested by earlier authors. The use of towed hydrophone arrays offers promise of an efficient means to determine the full extent of red drum spawning areas and their reproductive strategies.

Knowledge about spawning habits and habitats of fishes is an essential component of fisheries management. The location of spawning aggregations is often known and exploited by fishermen, and it has become clear that fishing activity on spawning aggregations can have catastrophic effects on fish populations (Coleman et al. 1996). The location of spawning areas has typically been inferred through capture of fish with mature gonads or the distribution of eggs and larvae, but these methods give only a general sense of where spawning takes place and provide little information about the details of mating strategies. It is crucial that fisheries scientists develop and employ new methods for locating and describing spawning sites.

The red drum *Sciaenops ocellatus* is an important recreational species throughout its range and is also important commercially in some locations. Adults range widely over the nearshore continental shelf waters throughout the year but apparently move to coastal waters to spawn (Overstreet 1983). The spawning season has been described as starting as early as mid-July along the west coast of Florida (Peters and McMichael 1982) and possibly lasting until February in Texas (Matlock 1984), but histological examination of ovarian development suggests that the primary spawning period occurs during mid-August through October in both the Gulf of Mexico and along the Atlantic coast (Murphy and Taylor 1990; Ross et al. 1995). Spawning has generally been thought to take place in coastal waters near inlets (Jannke 1971; Holt et al. 1985), although Lyczkowski-Shultz et al. (1988) found eggs and larvae out to 34 km from shore in the eastern Gulf of Mexico. There is also evidence of limited spawning activity within estuaries in Florida (Murphy and Taylor 1990; Johnson and Funicelli 1991) and in North Carolina (Luczkovich et al. 1999).

Male red drum make loud, characteristic sounds associated with courtship and spawning (Guest and Lasswell 1978); these sounds offer another potential means of locating spawning sites. Listening for the characteristic sounds has recently been used to locate red drum spawning sites in Indian River Lagoon, Florida (Johnson and Funicelli 1991), and in Pamlico Sound, North Carolina (Luczkovich et al. 1999). These surveys have been done with both hand-held hydrophones and remotely placed sonobuoys.

Red drum produce low-frequency sounds that are described as knocks (Fish and Mowbray 1970) or drumming (Guest and Lasswell 1978). Although Guest and Lasswell (1978) found that the "dominant energy" of their red drum recordings from a tank was around 240–1,000 Hz, I have found the fundamental frequency

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of red drum calls obtained from unconstrained fish in the field to consistently be around 140–160 Hz, as did Luczkovich et al. (1999). Each call consists of a variable number of pulses or knocks that are repeated at a range of pulse repetition rates (Guest and Lasswell 1978 from laboratory observations; my unpublished data from field observations). Whether specific behaviors are associated with specific call types is unknown, but the existence of numerous call pattern variants suggests at least some component of individual variability. Despite variation in call duration and pulse repetition rate, the consistency in fundamental frequency and general character of the call pattern makes recognition by ear relatively easy.

This paper reports on a survey of potential spawning sites in the nearshore western Gulf of Mexico using a towed hydrophone array. The objective of this study was to determine the spatial extent of spawning activity along the central coast of Texas. Limited ship time restricted the spatial coverage of the survey, but the study provides valuable information on the extensive distribution of spawning sites in red drum and provides the first assessment of using a mobile hydrophone to survey spawning activity in fishes.

Methods

Hydrophone surveys were conducted in 1999 and 2000 in the northwestern Gulf of Mexico along the central coast of Texas. In 1999, two exploratory transects were run from the Aransas Pass tidal inlet into the Gulf of Mexico. On 11 October, a cruise track was run from inside the Aransas Pass inlet straight offshore. At a point approximately 11 km from shore (32-m depth), the ship returned to the beach to continue the survey south of the inlet along the 10-m depth contour, about 2.5 km from the beach. On 12 October, a second survey was run from the Aransas Pass inlet north along the coastline, roughly following the 10-m depth contour.

Based on the 1999 survey results, the 2000 study was designed to concentrate on the 10-m depth contour between the Aransas Pass tidal inlet and Pass Cavallo, the next major tidal inlet 93 km to the north. Three transects were established: one near each inlet and one at the midpoint between them. Transects were surveyed (1 night/transect) between 28 September and 5 October.

The towed array was composed of eight hydrophones in an 80-m cable connected to a 200-m towing cable and towed at approximately 7.4 km/h (4 knots) from the 32-m (105-ft) stern-trawler *Longhorn*. The array is spectrally flat (i.e., no peaks in sensitivity) from 6 Hz to 18 kHz and has a sensitivity of approximately −191 dB relative to a reference of 1 V/μPa at 7.2 kHz. The signals from each of the eight separate hydrophones were saved to an eight-track digital recorder (Tascam DA-88) sampling at 44 kHz. Sampling commenced about 30 min before sunset, which occurred at 1911 hours (Central Daylight Time) on 4 October. The daily time frame used in this acoustic survey was determined from a study of red drum daily sound production in the Aransas Pass tidal inlet (Holt 2002). A hydrophone mounted on a pier in the Aransas Pass tidal inlet recorded sounds of red drum spawning activity every evening during the September–October spawning period. Red drum produced characteristic spawning sounds from about 1 h before sunset to about 3 h after sunset (the most intense activity occurred during the 2 h after sunset) and did so essentially every day during the spawning season. These times closely match the spawning times for red drum determined from egg and larval collections from the same site (Holt et al. 1985). The combination of a temporal window for detecting spawning vocalizations (about 4 h) and an optimum towing speed for the array of about 7.4 km/h limited each nightly transect to about 25 km.

Recorded signals from the array were analyzed by listening to two of the eight channels (the first and last hydrophones in the array) while observing the real-time power spectra and real-time sonogram on a computer screen (Sound Technology, Inc.; SpectraPro 3.32). Two classes of red drum sounds could be distinguished. One was a low-frequency rumble with a prominent energy peak at approximately 150 Hz. This was presumed to be from large numbers of red drum producing sounds simultaneously but at some distance from the hydrophone. The other class of sounds included clearly distinguishable calls made by an individual or small group of red drum. Note that the sound produced by the ship and the hydrophone itself had dominant energy in the range of 250–300 Hz. Gain levels on the recording system, once adjusted for ambient sound levels, were not changed over the entire survey period. Thus, the relative sound pressure levels are consistent even though absolute sound pressure levels are not known. The oscillogram for an 18-s segment of a daytime tow, when biological sounds are at their minimum, represents the relative sound level attributable to the ship and flow noise over the hydrophones (Figure 1a). The oscillogram from a 22-s segment of an evening tow in a red drum spawning area (Figure 1b) shows the higher-amplitude sound of red drum calls against a backdrop of ambient biological sounds. The ambient biological sounds are clearly louder than the background sound produced by the ship and hydrophone (Figure 1a). Calls of individual red drum were clearly evident by ear and could be

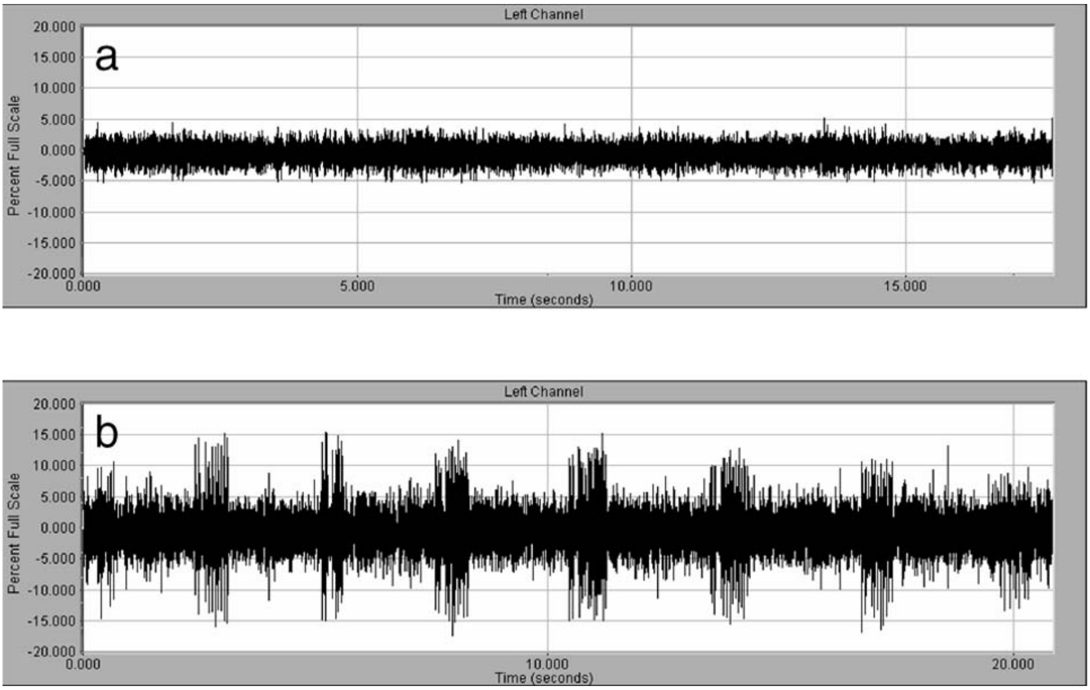

FIGURE 1.—Comparison of oscillograms from recordings made by a towed array of eight hydrophones along the Texas coast during **(a)** a daytime tow (1100 hours) with minimal biological sounds (i.e., background) and **(b)** an evening tow (2145 hours), showing close red drum calls (high-amplitude peaks) with lower-amplitude intervals composed of more-distant red drum, other biological sounds, and background sound.

confirmed through reference to a spectrogram (Figure 2) of any tape segment in question.

The occurrence of background rumble indicates spawning activity in the vicinity of the hydrophone, but more work is needed before a meaningful interpretation can be applied to those sounds, as the spatial scale over which they travel is not known. For this paper, I will describe only the distribution of clearly distinguishable individual or small-group calls. The distance over which the call of individual red rum can be heard can only be estimated, since the sound pressure level produced by red drum is unknown. Luczkovich et al. (1999) estimated that the call of an individual weakfish *Cynoscion regalis*, a sciaenid of substantially smaller maximum size (8 kg) than red drum (40 kg), could be heard from a distance of about 50 m based on a cylindrical spreading model. Numerous observations with this array showed that an individual red drum could first be heard on the leading hydrophone but not the trailing one (which were 80 m apart). As the array passed the fishes location, it could be heard on both hydrophones and finally only on the trailing hydro-

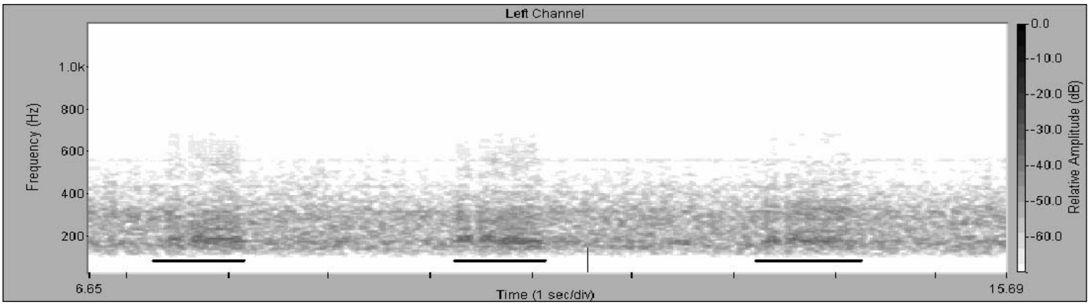

FIGURE 2.—Spectrogram from an expanded segment of the oscillogram in Figure 1b, beginning at about the 10-s mark. Horizontal lines indicate position of red drum calls in the time series.

phone. It can be concluded from these observations that an individual can be heard over a distance of at least 40 m and—based on the size difference between red drum and weakfish—probably somewhat farther. Thus, we can roughly define the spatial distribution of individual red drum detected by the hydrophones as a 100–200-m swath along the transect.

The physical location of each observation was determined by comparing the underway data recorded from the ship's system for automated integrated logistics (which included time, latitude, longitude, and several water quality parameters) and the clock time on the digital recorder, which was synchronized with the ship's clock before each recording. The data set was initially constructed by recording the hour, minute, and second of each identifiable call. The data were then summarized by counting the number of calls heard in each 1-min segment (the ship's location was recorded once per minute, representing the finest scale of spatial resolution available). Guest and Lasswell (1978) reported that the maximum call rate of red drum was around 16 calls/min. Dividing the number of calls per minute into two groups (low drumming rate: <16 calls/min; high drumming rate: ≥ 16 calls/min) allowed for a rough separation of calls originating from single versus multiple fish. Finally, the drumming rate (i.e., none, low, or high) was plotted on the cruise track.

The distribution of calling males along all transects was examined by a goodness-of-fit test for a random (i.e., Poisson) distribution (Zar 1996). As described above, the ship's location was determined at 1-min increments. At an average speed of 7.4 km/h, the ship would travel approximately 124 m/min, but the actual distance traveled during each minute (herein called a segment) varied somewhat due to various factors (currents, wind, swells, etc.). Although the number of calls per segment could be determined, the actual number of fish calling could only be roughly estimated. For this analysis, the unit of measure is the presence or absence of calling fish per segment. All survey transects were divided into sections of eight segments each, each section averaging 1,000 m along the transect. The null hypothesis is that the number of segments with calling fish is randomly distributed among sections and is tested with χ^2 (Zar 1996).

With one exception, the data presented here represent a single snapshot of drumming activity at each location and do not allow for temporal comparisons of individual sites. That exception is in the Aransas Pass tidal inlet, where we surveyed the same section on two consecutive days. The common survey area extended 2.7 km but due to differences in ship speed, towing time was 25 min (transect A) versus 34 min (transect B).

Results

Courtship-associated sounds (calls) of red drum could clearly be detected by ear on the towed array recordings. Although nonbiological sounds (e.g., flow noise and ship sounds) picked up by the hydrophones were relatively loud, the dominant frequency of those sounds was around 250 Hz, about 100 Hz higher than the 150-Hz dominant frequency of red drum calls, and could be separated by spectral analysis. The drumming of red drum that were close to the hydrophones (i.e., the primary data collected for this analysis) was also substantially louder than the background noise and other biological sounds (Figure 1) and was clearly recognizable by ear.

Red drum calls were detected along most sections of all five transects (Figures 3–5), although data for the later part of San Jose Island transect B were lost due to an audiotape malfunction. All transects ran essentially parallel to the coast at a distance of 2–4 km from shore. The segment of Port Aransas transect A that goes straight offshore from the Aransas Pass jetties extends approximately 11 km from shore at a depth of about 20 m. This segment of the transect showed very little drumming, which indicated that spawning activity did not extend that far offshore; however, data supporting this contention are obviously limited. Nevertheless, our subsequent sampling effort was concentrated on the 10-m contour; the deeper portion of Port Aransas transect A (beyond 4 km from shore) was excluded from further analysis.

Transect segments were dominated by the absence of red drum calls. There was a total of 765 min of observations over all transects. Of those, 460 min (60%) contained no red drum calls, 249 min (33%) contained calls with low drumming rates (<16 calls/min), and only 56 min (7%) contained calls with high drumming rates (≥ 16 calls/min). Based on an average towing speed of 125 m/min (7.4 km/h) and a 200-m detection width, the 460 min that lacked calls results in coverage of 11.5 km^2 compared with a 1.4-km^2 coverage for high-rate drumming. The most intense drumming activity occurred between 1830 and 2130 hours. Little drumming was heard after 2130 hours at Matagorda Island or San Jose Island transect A. Low and high drumming rates were distributed throughout this time period without any temporal pattern.

There were extensive areas along each transect where no close drumming was heard and where most drumming rates were low. Calls were detected in both extensive clusters and in isolated occurrences along the transects. Drumming activity was not uniformly distributed along transects. High drumming activity was concentrated along one segment of the Matagorda

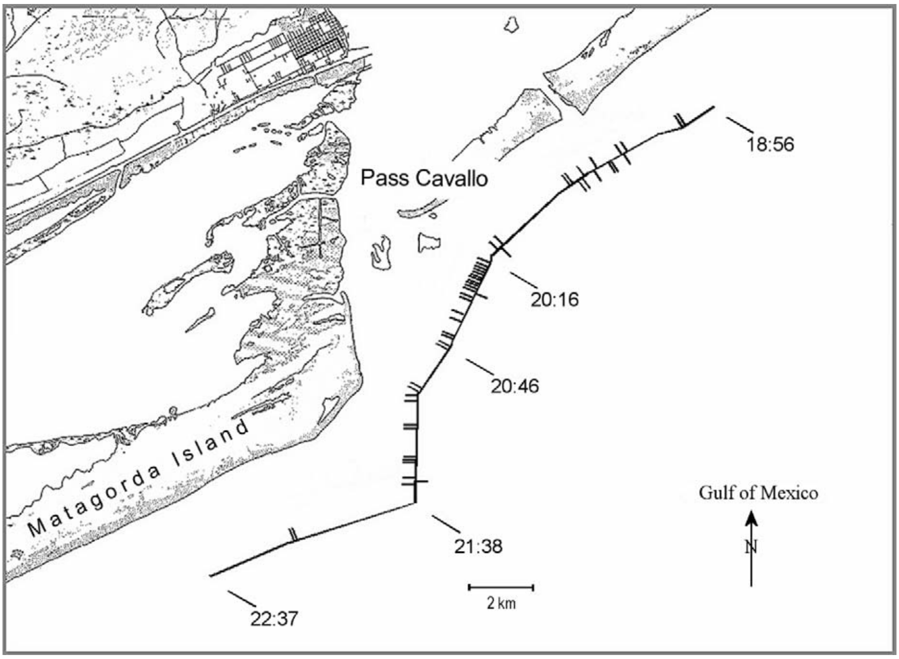

FIGURE 3.—Map of the Texas coast, showing the cruise track of a towed array of eight hydrophones along Matagorda Island (solid line) and locations of drumming red drum (hash marks attached to the cruise track). Hash marks above or to the left of the cruise track indicate sites of low drumming activity; those below or to the right of the cruise track indicate sites of high drumming activity. Survey start and stop times (and, for clarity, some intermediate times) are indicated.

Island transect (Figure 2), in two segments along San Jose Island transect A (Figure 3), and in one segment of the Port Aransas transect A (Figure 4). One segment of high drumming activity on the northeast end of San Jose Island transect A spanned 5 min of towing time and covered 600 m. The other, farther to the southwest on that transect, spanned 17 min of towing time and covered 2.1 km. Only 6 of the 17 min in this segment included low-rate drumming, and only 3 min were without drumming. Despite the appearance of clumping or contagion in the distribution of drumming activity along the transects, the null hypothesis of random distribution of calls among sections could not be rejected ($\chi^2 = 86.4$; critical value = 14.06; df = 7; $P > 0.05$).

Low drumming activity was widespread over all transects and occurred as both relatively isolated events and concentrations spanning several kilometers. Areas of no drumming were also interspersed throughout all transects, but there were several extensive areas of no drumming (spanning 2–3 km) on the Matagorda Island transect, San Jose Island transect A, and Port Aransas transect B. Several of the extensive segments that lacked drumming occurred after 2130 hours and may be more representative of the daily decline in drumming activity than of an absence of spawning activity at that location. Others, however, occurred during peak spawning time.

The spatially overlapping segments of Port Aransas transects A and B, surveyed on consecutive days, show extensive drumming throughout the inlet during both surveys (Figures 6, 7). There was a substantial difference in the intensity of drumming between the 2 d. On the first day, twenty-four 1-min segments were recorded; 17 of these (71%) contained drumming, and 7 (29%) showed high drumming activity. On the second day, thirty-four 1-min segments were recorded; 23 (72%) of these segments included drumming, of which only 2 (6%) had high-rate drumming activity. Both transects showed an approximately 600-m-long area of no drumming near the beach line (the areas were offset by about 200 m in the two surveys). However, there was ample evidence from hand-held hydrophone surveys of drumming in this region of the inlet at other times (my unpublished data).

Temperature and salinity varied little among transects within a year or even among years (Table 1) and showed no relationship to calling activity. With the exception of the dredged and jettied Aransas Pass, the ocean bottom throughout the study area is essentially homogeneous, being virtually flat and composed of fine muddy sands.

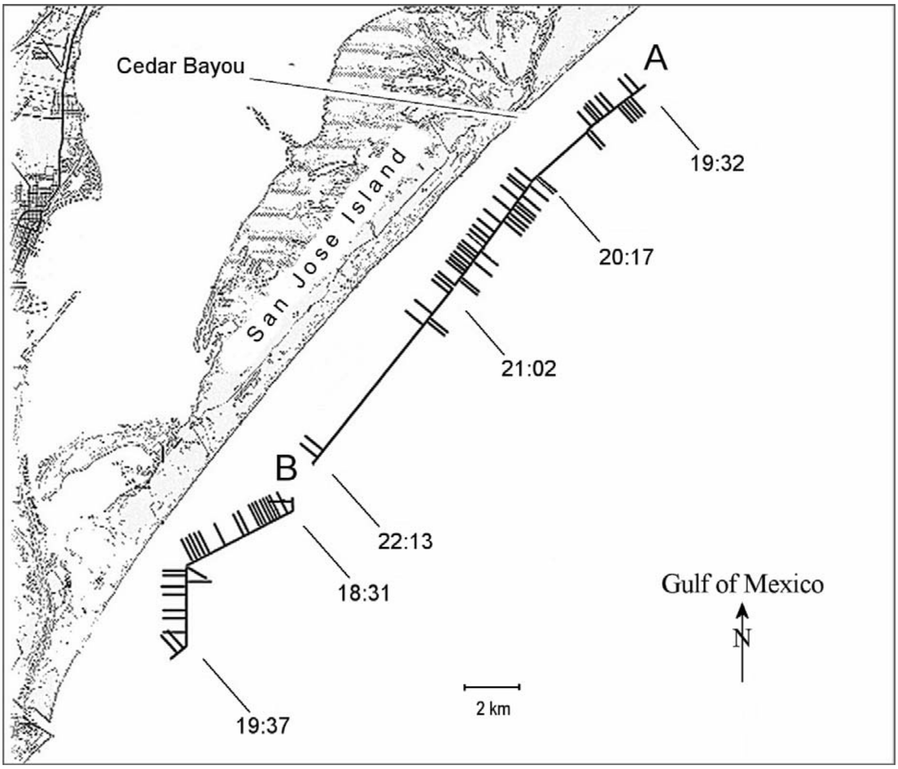

FIGURE 4.—Map of the Texas coast, showing two cruise tracks (A and B) of a towed array of eight hydrophones along San Jose Island, where red drum sound production was monitored (see Figure 3 caption for details).

Discussion

There are various ways of interpreting drumming sounds produced by male red drum. There are at least three possibilities: (1) the drumming male will engage in spawning at that location on that evening, (2) the drumming male is calling from a potential spawning site but will spawn at that site on that day only if joined (or selected) by a cooperative female, or (3) the drumming male may move to another place before engaging in spawning. Luczkovich et al. (1999) observed instances of red drum drumming without finding eggs, and Johnson and Funicelli (1991) found red drum eggs without hearing drumming. In both cases, short-term observations were made in shallow water with a hand-held hydrophone and the observers may have disturbed the fish or missed part of the spawning process. Connaughton and Taylor (1995) observed that drumming activity in weakfish occurred earlier in the evening at a shallow listening station than at deeper stations but were unable to determine whether the same fish moved between stations or different fish were drumming at different times. For this discussion, it is assumed that drumming at a given location roughly equates to spawning at that location, but the issue needs more investigation.

The distribution of drumming males indicates that some, if not most, spawning takes place among widely distributed individuals as opposed to highly aggregated groups. The null hypothesis of random distribution of drumming activity along the transects could not be rejected based on χ^2 analysis, suggesting that male red drum were neither uniformly distributed (possibly territorial) nor highly aggregated. Furthermore, it was clear from listening to the tapes that most of the low drumming rates were produced by a single fish. Only 7% of the 1-min summaries recorded high drumming rates, and even these typically consisted of only a few individuals. It is significant to note, however, that there were at least two extensive areas of multiple drumming fish. Both areas were in the vicinity of Cedar Bayou, a relatively small but historically persistent tidal inlet. One of these groups spanned a linear distance of over 2 km and its breadth was undetermined. The drumming rate (up to 40 calls/min) indicated that several red drum were calling simultaneously within the roughly 200-m detection range of the hydrophones, and this density was consistent over most of the 2-km stretch. Thus,

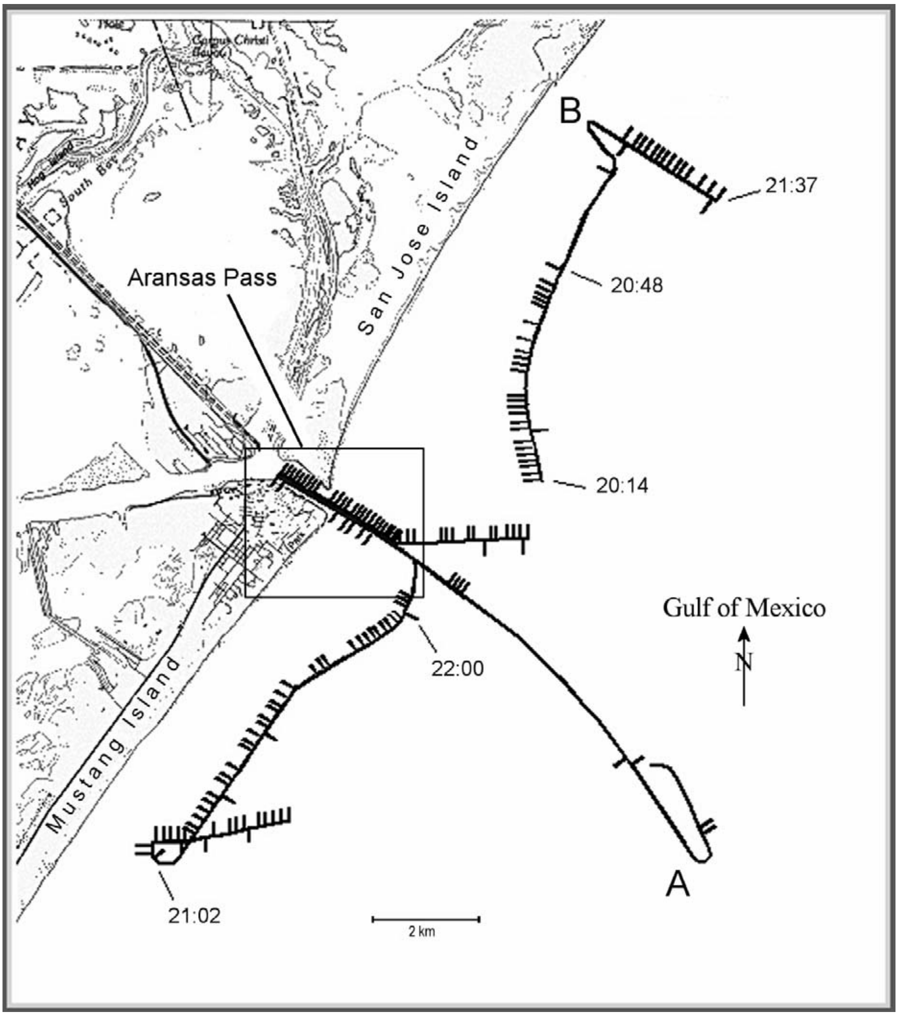

FIGURE 5.—Map of the Texas coast, showing two cruise tracks (A and B) of a towed array of eight hydrophones near Port Aransas, where red drum sound production was monitored (see Figure 3 caption for details). Box indicates the Aransas Pass tidal inlet section.

while drumming activity was widely distributed, there was some evidence of aggregation of males along some segments of the transects.

Most sciaenids are not vocal at times other than the spawning season (Mok and Gilmore 1983; Connaughton and Taylor 1995). While it is being assumed here that the distribution of drumming activity equates to the distribution of spawning activity (and, as a corollary, that a lack of drumming indicates a lack of spawning), the actual relationship between male drumming activity and actual spawning is not clear. Guest and Lasswell (1978), in a single observation of spawning by captive red drum, noted that males drummed consistently from dusk (1900 hours) until some period after actual spawning (2145 hours) but were quiet during multiple, brief bouts of nudging a female's urogenital opening. One of these nudging bouts resulted in three males spawning with a single female without sound production. Captive weakfish exhibited similar behavior in producing sounds almost continuously during courtship, except during brief periods of nudging and gamete release (Connaughton and Taylor 1996). Bremner et al. (2002) found that captive haddock *Melanogrammus aeglefinus* produced sounds throughout courtship up until the moment of gamete release, when calling ceased. These same haddock, maintained in pairs or triplets (with two males), produced courtship sounds even on days when the female did not release

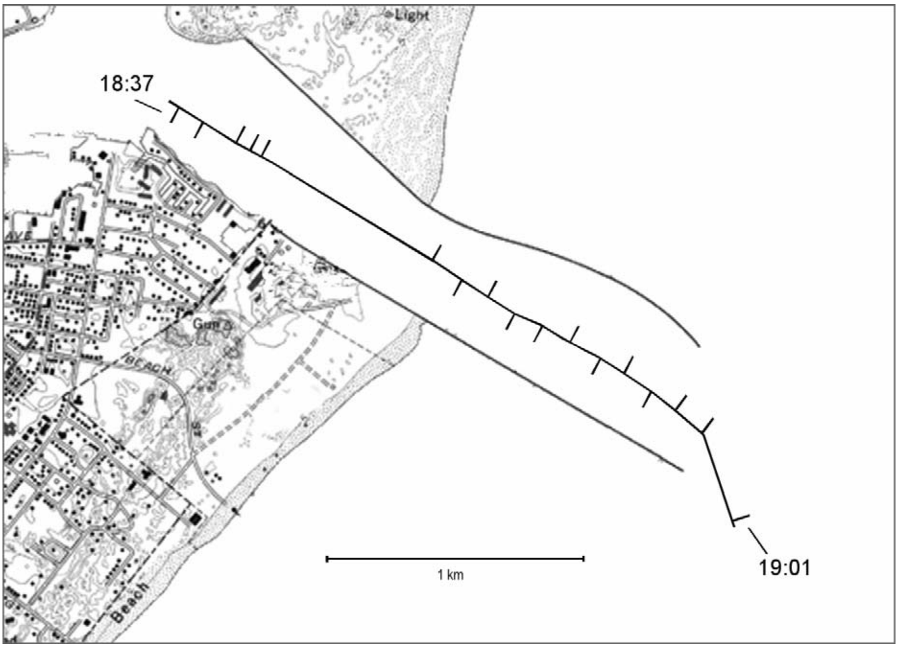

FIGURE 6.—Map showing detail of Port Aransas, Texas, transect A where it overlapped with transect B of a towed array of eight hydrophones used to monitor red drum sound production (Figure 5).

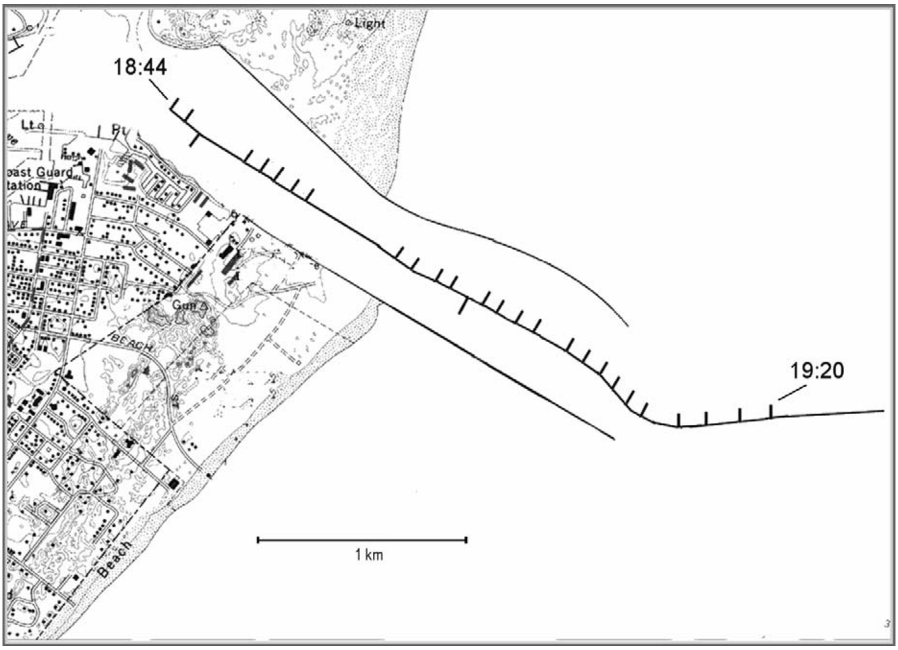

FIGURE 7.—Map showing detail of Port Aransas, Texas, transect B where it overlapped with transect A of a towed array of eight hydrophones used to monitor red drum sound production (Figure 5).

TABLE 1.—Mean seawater temperature (°C) and mean salinity (‰) measured along five cruise tracks of a towed array of eight hydrophones used to monitor red drum sound production along the Texas coast.

Transect	Date	Mean temperature	Mean salinity
Port Aransas A	11 Oct 1999	27.2	32.9
Port Aransas B	12 Oct 1999	27.2	32.9
Matagorda Island	3 Oct 2000	26.5	34.2
San Jose Island A	4 Oct 2000	26.8	33.8
San Jose Island B	28 Oct 2000	26.4	34.4

eggs. Taken as a whole, these results suggest that (1) during the spawning season, males produce courtship-related sounds almost continuously (at least during the evening for sciaenids) and (2) the absence of sound production in an area probably indicates an absence of spawning there.

The repeated survey in the Aransas Pass inlet reveals both similarities and differences in drumming activity between days at the same site. The primary difference was the intensity of drumming activity. Even though the spatial distribution and coverage of drumming along the transect was similar between days, there was a substantially greater proportion of high drumming activity on the first day. High drumming activity probably represents drumming by more than one fish during the 1-min segment rather than additional, or faster, drumming by one individual. It cannot be known whether that was the result of more fish in the area on the first day or simply more fish drumming on the first day.

There are no published data giving empirical evidence of the size or spatial configuration of red drum spawning aggregations. Most references to spawning locations are based on catches of eggs and larvae (Pearson 1929; Jannke 1971; Holt et al. 1985; and Murphy and Taylor 1990) and give spawning locations in general terms, such as "in coastal waters" or "near tidal inlets." Several studies on spawning activity in other sciaenid fishes have suggested that spawning takes place in dense, discrete aggregations and thus at discrete sites. Saucier and Baltz (1992) reported that they could locate spawning aggregations of spotted seatrout *C. nebulosus* in the Louisiana estuaries to within 15–20 m based on changes in sound amplitude recorded through a hand-held hydrophone (i.e., a single hydrophone deployed from a quiet, stationary boat). These authors characterized drumming aggregations as small, medium, and large, but they did not give estimates of the spatial extent of aggregations or the density or distribution of individual fish within the groups. Mok and Gilmore (1983) also used sound amplitude to characterize spawning aggregations of silver perch *Bairdiella chrysoura* in the Indian River Lagoon, Florida, as close and small or close and large. Those authors identified a close, large aggregation that extended over an area of at least 1 km of the Indian River Lagoon, and they identified several such aggregations throughout the Indian River Lagoon. Connaughton and Taylor (1995) and Luczkovich et al. (1999) also characterized loud sounds of the appropriate fundamental frequency as coming from large aggregations of spawning weakfish in the Delaware Bay, Delaware, and Pamlico Sound, North Carolina, respectively. All the data described above were collected by a single hydrophone deployed sequentially at multiple sites.

The results presented here for red drum appear contradictory to the aforementioned studies. It is likely that experimental and analytical methods contributed to this difference. The primary difference is that the present data were taken from a continuously recording hydrophone moving through the environment as opposed to sequential recordings from multiple discrete locations. A second difference, and one afforded by the nature of the data, is that this analysis was based on the distribution of drumming individuals and not on drumming of the group. Despite the relatively loud background noise on the hydrophone at around 250 Hz, a "rumble" or "roar" at around 150 Hz (the fundamental frequency of red drum drumming) could frequently be heard on the tapes. This sound was heard in the presence and in the absence of drumming individuals. This is essentially the same sound described as a large-group sound by other authors. It is not clear whether the apparent difference between loose aggregations of spawning red drum described here and the description of dense spawning aggregations described in the literature for other sciaenids is real or merely a function of methodological and analytical differences, but additional research on mating systems in sciaenids and other coastal fishes is clearly warranted.

Red drum appear to form "spawning aggregations" in the technical sense of the word (Domeier and Collin 1997) in that they "gather (in an area) for the purpose of spawning, with fish densities or numbers significantly higher than those found in the area of aggregation during the nonreproductive season." Although adult red drum were not specifically examined for reproductive condition in this study, it is clear from collections of red drum eggs and larvae in the area (Holt et al. 1989; Rooker and Holt 1997) and the examination of gonadal condition of adult red drum taken in the recreational fishery at the Aransas Pass (personal observation) that red drum were spawning in the immediate vicinity of the study area. Density estimates for adult red drum in the area are not available, but the recreational fishery for mature red drum in the Aransas Pass tidal inlet and along coastal beaches exists only in September and October, and catches of large adult red drum in these areas are relatively rare in other months. The red drum spawning aggregation described here does not, however, appear to be a dense cluster of hundreds or thousands of individuals engaging in mass spawning events, as has been seen in some tropical reef species (e.g., brown surgeonfish *Acanthurus nigrofuscus*: Kiflawi et al. 1998); rather, the red drum aggregation is probably a loose association of individuals gathered in the same region. The red drum spawning aggregation may more closely resemble a large version of that described for red hind *Epinephelus guttatus* by Shapiro et al. (1993), who observed that pairs or small groups were scattered over a wide but well-defined area and typically engaged in pair or group spawning (one male spawning with one to several females).

Based on the distribution of sound production, red drum apparently spawn all along the nearshore region of the central Texas coast. This survey was not spatially comprehensive enough to fully delineate the spawning area, but it is clear that spawning activity is widespread and was not concentrated at inlets as suggested by earlier authors (Simmons and Breuer 1962; Jannke 1971). Areas of the coastline far removed from the inlets had relatively intense drumming activity, confirming the suggestions of Murphy and Taylor (1990) that spawning also occurs over the nearshore continental shelf. This wide distribution of spawning sites indicates that adult red drum populations, at least in Texas, are not acutely threatened by recreational fishing activity directed at spawning aggregations. Only a relatively small portion of the drumming males gather at easily accessible sites (such as inlet jetties) for spawning. Other spawning groups are distributed all along the coastline. If individual fish remain in the immediate vicinity of the spawning sites, much of the population is not particularly vulnerable to exploitation. The common snook *Centropomus undecimalis* presents an alternate behavioral–spawning model. Lowerre-Barbieri et al. (2003) showed that common snook form large spawning aggregations at tidal inlets along Florida's eastern coast that persist throughout the protracted summer spawning season. Only 20% or so of the females in an aggregation were ready to spawn on any given day, and it appeared that spawning fish dispersed from the school before actual spawning occurred. Acoustic tagging showed that individual fish left and rejoined the aggregation; one individual returned after an absence of 6 weeks. Virtually nothing is known of the movement of individual adult red drum. If red drum aggregate during the day and disperse in the evening to spawn, or if individuals move in and out of aggregations that are readily accessible to fishing, then the population may be at greater risk of exploitation. It should be noted that current Texas fishing regulations allow for the retention of only one adult red drum (>71.12 cm or 28 in) per licensee per year (or two if the first tag is returned) in an effort to protect spawning adults.

The full extent of the offshore spawning area of red drum is yet to be determined, and much remains to be learned about their reproductive strategies. The use of towed hydrophone arrays offers promise of an efficient means to achieve those goals.

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