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The Reproductive Biology of Spotted Seatrout, *Cynoscion nebulosus*, Along the Mississippi Gulf Coast

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Spotted seatrout, *Cynoscion nebulosus*, were collected from the barrier islands, Biloxi Bay and St. Louis Bay areas along the Mississippi Gulf Coast during April–Sep. 1998 and March–Sep. 1999. Female spotted seatrout reached 50% sexual maturity at 230 mm standard length (SL) (age 1), and 80% of age-1 spotted seatrout captured were sexually mature. Spotted seatrout have a 5-mo spawning season in Mississippi, ranging from mid-April to mid-Sep., although the onset of the season may vary annually depending on temperature. Histological analysis showed spotted seatrout are capable of spawning multiple times throughout the reproductive season, and batch fecundity was estimated from 51 fish undergoing final oocyte maturation (FOM). Batch fecundity (BF) was significantly ($P < 0.001$) positively related to SL and ovary-free body weight (OFBW); the equation best describing the BF–size relationship was BF = $(554.2 \cdot \text{SL}) - 88{,}398$ ($r^2 = 0.25$). Relative BF was significantly different among months ($P = 0.041$), with June values higher than those in Aug. Overall, mean relative BF was 165.7 ± 13.9 eggs/g OFBW. The FOM and postovulatory follicle methods gave similar estimates of overall spawning frequency of once every 4–5 d. However, there were significant differences ($P < 0.001$) in spawning frequency among areas; spotted seatrout from the barrier islands and St. Louis Bay areas spawned more frequently (mean, every 4 d) than fish from Biloxi Bay area (mean, every 15–18 d). Salinity, depth, and submerged habitat are not different among the areas, but there is greater shoreline development in the Biloxi Bay area. Differences in the reproduction of spotted seatrout among estuaries need to be considered when developing regional management plans for the species.

The spotted seatrout, *Cynoscion nebulosus,* supports important recreational fisheries throughout its range (New York to Tampico, Mexico; Hoese and Moore, 1998) and is quite abundant along the coastal areas of the Gulf of Mexico. Unlike most other members of the family Sciaenidae, spotted seatrout appear to spend their entire life within a single estuary (Helser et al., 1993). Mitochondrial DNA analysis suggests that spotted seatrout are subdivided into discrete subpopulations throughout their range (Gold et al., 1999). Thus, subtle differences in the life history of this species may occur among estuaries throughout its range. A solid understanding of these differences is important for development of useful regional fisheries management plans, such as the recently compiled spotted seatrout regional management plan for the Gulf of Mexico (Gulf States Marine Fisheries Commission, 2001).

Aspects of the reproductive biology of spotted seatrout have been described from Chesapeake Bay (Brown, 1981), Georgia (Mahood, 1975), Florida (Moody, 1950; Klima and Tabb, 1959; Tabb, 1961), Mississippi (Overstreet, 1983), Louisiana (Hein and Shepard, 1979), and Texas (Pearson, 1929; Miles, 1951; Brown-Peterson et al., 1988). However, with the exception of the most recent work by Brown-Peterson et al. (1988), these historical accounts of reproduction in spotted seatrout do not discuss multiple spawning, batch fecundity, or spawning frequency. Although Overstreet (1983) described the reproductive seasonality of spotted seatrout along the Mississippi Gulf Coast, estimates of batch fecundity and spawning frequency were not included. Most recent work on reproduction in spotted seatrout has concentrated on spawning behavior and locations (Saucier and Baltz, 1992, 1993) and reproductive physiology (Smith and Thomas, 1991; Laidly and Thomas, 1997). Therefore, up-to-date knowledge on the reproductive biology of spotted seatrout throughout much of its range is lacking.

Because of the continued importance of spotted seatrout to the recreational fishery in Mississippi (Gulf States Marine Fisheries Commission, 2001), a comprehensive study of the reproductive biology of spotted seatrout along the coast of Mississippi is warranted. In this report, we describe the size and age at sexual maturity and gonadal development, as well as
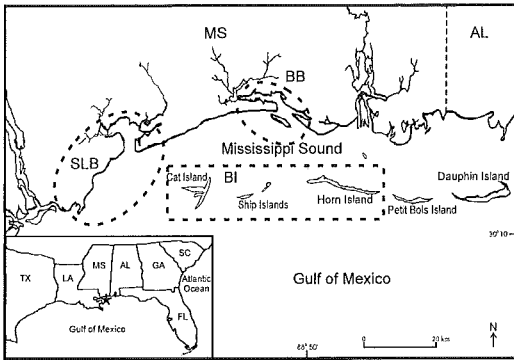
Fig. 1. Sampling areas for spotted seatrout along the Mississippi Gulf Coast. BI = Barrier Islands; BB = Biloxi Bay; SLB = St. Louis Bay.

provide estimates of the batch fecundity and spawning frequency of spotted seatrout from several areas along the Mississippi Gulf Coast. Our results are discussed in light of potential differences in reproduction among areas in Mississippi.

MATERIALS AND METHODS

Sample collection.—Spotted seatrout were captured with variable mesh gill nets (5–10-cm stretch mesh in 1.3-cm increments) from the Mississippi Gulf Coast barrier islands, Biloxi Bay, and St. Louis Bay areas from April through Sep. 1998 and March through Sep. 1999 during weekly sampling events. The barrier islands (BI) included Horn, Ship, and Cat islands; the Biloxi Bay area (BB) included Davis Bayou, Old Fort Bayou, Back Bay, and the Biloxi Bay; and the St. Louis Bay area (SLB) included St. Louis Bay and the mouth of the Pearl River (Fig. 1). Salinity (ppt) and water temperature (C) were recorded for each sampling episode. All fish were captured in the morning between 0600 and 1100 hr and immediately placed on ice for transport to the laboratory. In the laboratory, total length (TL, mm), standard length (SL, mm), and wet weight (W, g) were recorded for each fish, gonads were excised and weighed to the nearest 0.1 g (GW), and otoliths were removed for aging. The gonadosomatic index (GSI) was calculated for each fish as GSI = $[GW/(W - GW)] \times 100$.

Aging analysis.—The left sagittal otolith from each fish was thin sectioned (0.4 mm), polished, and examined for annual opaque rings by techniques modified from Murphy and Taylor (1994). The number of opaque rings was

determined by two independent readers. Each fish was first assigned a biological age based on the date of capture and the number of opaque rings observed on the otolith. To keep fish grouped by cohort, all fish within the same year class (i.e., spawned between April and Sep. of the same year) were considered to be the same cohort and were assigned the age in years they would achieve during the calendar year they were captured.

Histological analysis and spawning frequency.—A small portion of ovarian or testicular tissue was removed for histological analysis from the mid-portion of the right or left gonad of each fish, placed in an individually labeled cassette and preserved in 10% neutral buffered formalin (NBF) for a minimum of 1 wk. Tissues were rinsed in running water overnight, dehydrated and embedded in paraffin, sectioned at 4 μm, and stained with hematoxylin 1 and eosinY by standard histological techniques. Maturity classes were assigned after histological inspection; ovarian maturity classes were modified from Brown-Peterson et al. (1988) and were defined as immature, early developing, mid developing, late developing, ripe, spent, and regressed. Testicular maturity classes followed Grier and Taylor (1998). Ovarian atresia was staged following Hunter and Macewicz (1985b). Females were considered to be sexually mature when they were in the early developing or later ovarian maturation classes.

Monthly spawning frequency estimates were made for females in the late developing and ripe classes on the basis of the percentage of females with ovaries containing (1) 0–24 hr postovulatory follicles (POF) or (2) oocytes undergoing final oocyte maturation (FOM). POF were staged following Hunter and Macewicz (1985a) and oocytes undergoing FOM were staged as in Brown-Peterson et al. (1988). The percentage of fish in the late developing and ripe maturity classes with ovaries containing either FOM or POF was calculated for each month. This value represents the percentage of the fish in the population that are about to spawn (FOM) or have just spawned (POF). For both the POF and the FOM methods, spawning frequency determinations followed the procedure of Hunter and Macewicz (1985a). Spawning frequency (d) was determined by dividing 100% (representing all the fish in sample) by the percentage of fish in the sample with FOM or POF in the ovaries.

Batch fecundity analysis.—A small portion of fresh ovarian tissue from all females in the late

developing class was cleared in a solution of ethanol:NBF:glacial acetic acid (6:3:1) and inspected under a dissecting microscope for evidence of FOM (Brown-Peterson et al., 1988). Females undergoing FOM were used for fecundity analysis. A 2–5-g portion of ovarian tissue was weighed to the nearest 0.1 g and placed in modified Gilson's solution (Bagenal, 1966) for 3–12 mo. The volumetric method was used to determine batch fecundity (Bagenal and Braum, 1971). Ovarian tissue was rinsed in running water overnight, and all oocytes were teased from the tissue and suspended in 250–600 ml of water. Six replicate 1-ml subsamples were removed, and all oocytes >350 μm, representing oocytes undergoing FOM (Brown-Peterson et al., 1988), were counted. Typically, 40–70 oocytes >350 μm were counted in each replicate. Fecundity is expressed as both batch fecundity (mean number of eggs/batch) and relative fecundity [mean number of eggs/gram of ovary-free body weight (OFBW)].

Statistical analysis.—All GSI values were arcsine–square root transformed prior to analysis (Sokal and Rohlf, 1995). All data were tested for normality and homogeneity of variance. Data that violated the assumptions of parametric statistics were analyzed by nonparametric statistics. Linear regression was used to examine the relationship between GSI and gonad-free body weight so that GSI could be used as an index of reproductive preparedness. A two-way ANOVA was used to test for differences in female GSI values (for GSI $\geq$ 1.5) as well as temperature between months and years. If the interaction term between month and year was significant, Student's t-test was used to compare monthly mean values between years for each month. Variation across months within a year was not of interest in this study. The relationship between batch fecundity or relative fecundity as the dependent variable and SL, OFBW, or age as the independent variable was analyzed with linear regression. Differences in relative batch fecundity among months was examined by Kruskal–Wallace (KW) ANOVA. If a significant H value was found, we separated mean ranks with pairwise Mann–Whitney (MW) U-tests, the results of which were adjusted by the sequential Bonferroni procedure (Rice, 1989). Differences in spawning frequency among areas was tested with chi-square. All statistics were computed with SPSSW 10 or Systat 9.0 (SPSS, Inc., Chicago, IL). Results were considered significant if $P < 0.05$.

RESULTS

Number and distribution of samples.—A total of 549 spotted seatrout were captured during the sampling period. Although nets were set at each sampling location three to four times a month throughout the sampling period, the actual number of monthly collections of spotted seatrout at each location varied from a low of zero (all locations at various months) to a high of four (May 1998 at BB, June 1998 at BI, and April 1999 at SLB). The mean numbers of collections each month for each location over the 2-yr sampling period were 1.14 (BI) and 1.57 (BB and SLB). During April 1998, March 1999, and Sep. 1999, samples were obtained from only one of the three locations; samples were obtained from two or three locations during all other months.

Size and age at maturity.—Of the 117 males that were captured, all were sexually mature, including the smallest individual at 201 mm SL, representing an age-1 fish. Thus, estimates of minimum size and age at attainment of sexual maturity could not be determined for male spotted seatrout from Mississippi. Only 3% of the 432 females captured were sexually immature, but these fish were used to estimate the length and age at 50% sexual maturity. Size-at-maturity estimates suggest that female spotted seatrout in Mississippi reach 50% maturity at 230 mm SL and 1 yr. The smallest female that had obtained sexual maturity was 225 mm SL (age 1), and all females larger than 260 mm SL were mature. Age-at-maturity estimates indicate that 80% of age-1 female spotted seatrout were mature. Additionally, 62% of the mature age-1 females showed evidence of recent spawning in the form of POF or FOM.

Spawning season and gonadal development.—Regression analysis indicated that female GSI could be predicted by OFBW ($r^2 = 0.024$, $P = 0.004$) for GSI > 1.5, indicating that GSI is not independent of female size. Although female GSI did significantly increase with body size regardless of reproductive condition, we used GSI as an indicator of reproductive condition on the basis of the low r^2 value of the relationship.

Spotted seatrout have a 5-mo reproductive season in Mississippi (mid-April through mid-Sep.; Fig. 2) on the basis of GSI values, although annual variations can shorten the season by as much as one 1 mo. The onset of the reproductive season varied between 1998 and 1999. Mean GSI values for both male and fe-
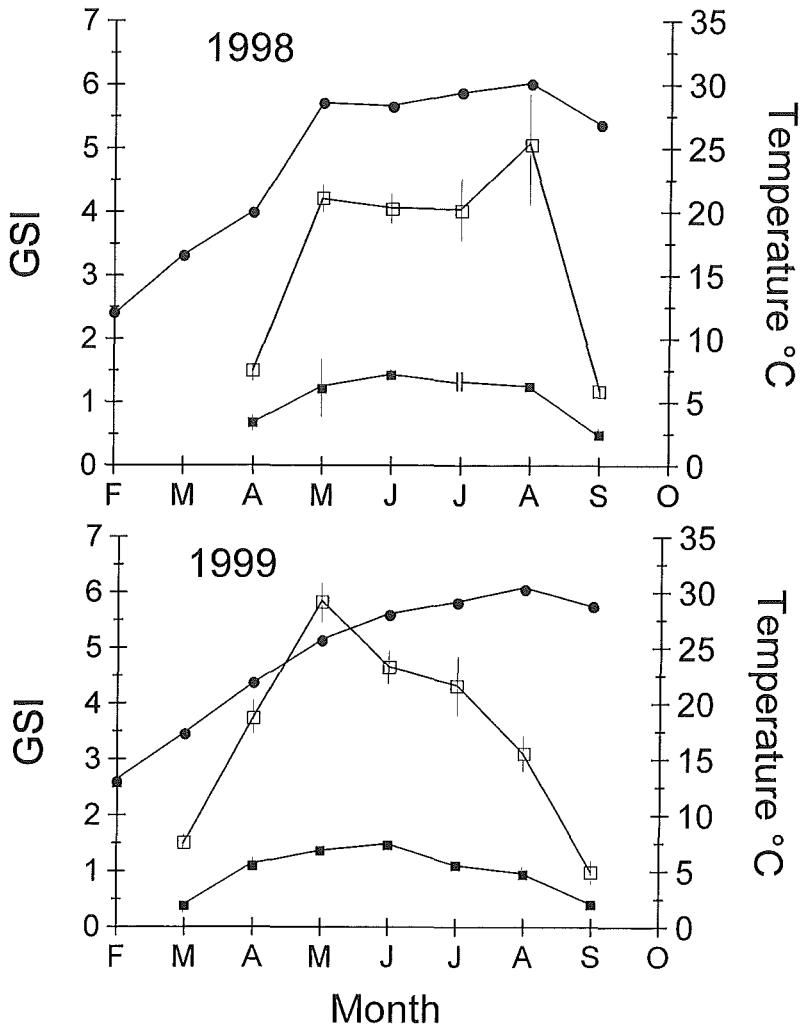
Fig. 2. Gonodosomatic (GSI) and temperature values ($\bar{x} \pm 1$ SEM) for spotted seatrout from the Mississippi Gulf Coast by year. ● = temperature; □ = female; ▨ = male.

male fish were low in late April 1998 (Fig. 2A) and appeared similar to values observed in late March 1999 (Fig. 2B). During 1998, GSI of both males and females increased rapidly between late April and early May, whereas a rapid increase in GSI values between late March and early April was evident in 1999.

Male GSI values remained relatively stable from May through Aug. 1998 and declined sharply in Sep. (Fig. 2A). Male GSI values increased rapidly between March and April 1999, peaked in June, and declined slowly thereafter, with a rapid drop in Sep. (Fig. 2B). ANOVA was not performed on male GSI values because of the small sample sizes during many months.

Female GSI values exhibited a small peak in May and a larger peak in Aug. 1998 before pre-

cipitously declining in Sep. (Fig. 2A). In contrast, during 1999, female GSI values increased rapidly between March and April, reached a peak in May, and declined thereafter, with a precipitous drop in Sep. (Fig. 2B). There was a significant interaction term ($F_{5,335} = 3.042$, $P = 0.011$) in our analysis of GSI by month and year. Additionally, Levine's test ($F_{11,324} = 1.96$, $P = 0.031$) indicated the data mean values were not homogeneous. However, because ANOVA is robust (Sokal and Rohlf, 1995) and we had a large sample size, we felt it appropriate to use these results. Female GSI values were significantly higher in 1999 than 1998 in April (Student's t = 4.99, df = 39.4, $P < 0.001$) and May (Student's t = 3.45, df = 16.2, $P = 0.001$), whereas GSI was significantly higher in 1998

TABLE 1. Testicular maturation classes for spotted seatrout from the Mississippi Gulf Coast during 1998 and 1999. Values expressed as percentages.

Testicular maturation class	March		April		May		June		July		Aug.		Sep.	
Year: N:	1998 0	1999 2	1998 6	1999 20	1998 2	1999 11	1998 21	1999 2	1998 0	1999 9	1998 1	1999 3	1998 23	1999 2
Regressed	—	0	0	0	0	0	0	0	—	0	0	0	9	0
Early maturation	—	100	100	45	0	9	0	0	—	0	0	33	0	0
Mid maturation	—	0	0	55	50	91	38	0	—	78	0	33	0	0
Late maturation	—	0	0	0	50	0	62	100	—	22	100	34	13	0
Regression	—	0	0	0	0	0	0	0	—	0	0	0	78	100

than 1999 in Aug. (Student's $t = 2.18$, df $= 16.2$, $P = 0.044$).

The water temperature profile differed between the 2 yr (Fig. 2); temperature increased dramatically between April and May 1998 and then remained relatively steady until a decrease in Sep. In contrast, water temperature steadily increased from Feb. through Aug. 1999 and decreased slightly in Sep. February water temperatures were similar in both years, but March 1999 was warmer than March 1998 (Fig. 2). Mean water temperatures in early 2000 were slightly warmer than the previous 2 yr and increased from 14.2 ± 0.6 C in Feb. to 19.1 ± 0.9 C in March. There was no significant difference in water temperature from 1998 through 2000 for Feb. ($F_{2,18} = 0.609$, $P = 0.557$) or March ($F_{2,18} = 3.12$, $P = 0.069$). There was a significant interaction for water temperature between month and year for 1998 and 1999 ($F_{5,50} = 2.99$, $P = 0.023$), indicating the seasonal patterns were not the same. However, the only significant difference between years was in May (Student's $t = 3.56$, df $= 66$, $P = 0.01$), with mean temperatures in 1998 2.9 C warmer than in 1999.

Histological analysis of ovarian and testicular tissues confirmed the pattern seen with GSI values. All males sampled during late April 1998 and late March 1999 were in the early maturation class (Table 1), and none had spermatozoa in the ducts. However, all males captured during the remainder of the reproductive season during both years were in spawning condition. During 1998, males progressed from the mid maturation to the regression class from May through Sep. (Table 1). In 1999, a high percentage of males remained in the mid maturation class from April through Aug. No male was found in the late maturation class until June in 1999, and by Sep. all were in the regression class (Table 1). Active spermatogenesis occurred in the testis throughout the sampling period, although spermatogenesis was noticeably reduced in fish in the late maturation and regression classes in Aug. and Sep. of both years.

During late April 1998, only 13% of females had reached the late developing class, indicative of spawning readiness, and none was in the ripe class. In contrast, 63% of females were in spawning condition (late developing and ripe classes) by mid-April 1999 (Table 2). Additional data collected from March 2000 showed that the majority of females were in the late developing class by late March (Table 2), although there was no evidence of spawning during March 2000. Thus, the beginning of the spawn-

TABLE 2. Ovarian maturation classes for spotted seatrout from the Mississippi Gulf Coast during 1998, 1999, and 2000. Values expressed as percentages.

Ovarian maturation class	March			April		May		June		July		Aug.		Sep.	
Year: N:	1998 0	1999 2	2000 12	1998 8	1999 79	1998 80	1999 66	1998 53	1999 28	1998 20	1999 19	1998 12	1999 31	1998 25	1999 8
Immature	—	0	8	0	10	2	2	0	0	0	0	0	6	0	25
Early developing	—	50	17	38	16	6	2	0	0	0	0	0	0	0	0
Mid developing	—	50	17	37	8	19	3	2	4	0	5	0	0	0	0
Late developing	—	0	50	13	47	65	63	89	86	90	79	83	74	12	12
Ripe (FOM[a])	—	0	0	0	16	6	30	9	10	10	16	0	0	0	24
Spent	—	0	0	0	0	0	0	0	0	0	0	0	14	24	12
Regressed	—	0	8	12	6	2	0	0	0	0	0	0	6	60	50

[a] FOM = final oocyte maturation.

ing season in Mississippi appears to vary from early April (1999 and 2000) to early May (1998). Most of the females captured from May through Aug. 1998 and 1999 were in the late developing or ripe class. A few females remained in reproductive condition as late as mid-Sep. 1998 and 1999.

Histological evidence showed that female spotted seatrout in Mississippi are capable of spawning multiple times during the reproductive season. The ovaries of females in the late developing class contained oocytes in a variety of developmental stages (Fig. 3A). The presence of POF and vitellogenic oocytes in ovaries in the late developing class (Fig. 3B) indicated a recent spawning event and the potential for additional batches of oocytes to be released. Similarly, spotted seatrout ovaries undergoing FOM (Fig. 3C) contained oocytes about to be spawned as well as vitellogenic oocytes that could be released in later spawning events. Female spotted seatrout from all three collection areas in Mississippi were found with ovaries containing 24-hr POF or oocytes undergoing FOM from May through Aug. 1998 and April through Aug. 1999. Only a single female in each year was found with ovaries containing POF or undergoing FOM in Sep.

Batch fecundity.—A total of 51 females, ranging from 255 to 545 mm SL and from 1 to 5 yr, were used for batch fecundity analysis. Fecundity values of fish captured in all locations from June through Sep. 1998 and April through July 1999 were combined for analysis because of small sample sizes. Batch fecundity (BF) was significantly, positively correlated with both OFBW ($F_{1,50} = 14.3$, $P < 0.001$) and SL ($F_{1,50} = 16.2$, $P < 0.001$). SL was a better predictor of BF ($r^2 = 0.25$) than was OFBW ($r^2 = 0.22$), although BF varied greatly with fish size. The relationship between BF and SL (Fig. 4) is described by the equation: BF = (554.2·SL) − 88,398. Overall, batch fecundity ranged from a low of 12,633 eggs for a 308-mm SL fish in Aug. 1998 to a high of 354,000 eggs for a 507-mm SL fish in April 1999.

There was a significant relationship between relative BF and SL ($r^2 = 0.081$, $P = 0.042$), suggesting the effects of fish size were not completely removed from relative fecundity values. Mean monthly relative BF varied from a high of 231.1 ± 34.4 eggs·g^{-1} OFBW in June to a low of 84.9 eggs·g^{-1} OFBW in Sep. (Table 3). Overall mean relative BF for all specimens was 165.7 ± 13.9 eggs·g^{-1} OFBW. September relative fecundity values were eliminated from subsequent analyses because of small sample size.

Because these data were not homogeneous by month (Levine's test, $F_{4,45} = 7.46$, $P < 0.001$), a KW test was used to detect a significant difference in ranked relative fecundity among months (H = 9.96, df = 4, $P = 0.041$). Pairwise MW U-tests, adjusted by the sequential Bonferroni method, showed that June relative fecundities were significantly higher than those in Aug. ($P = 0.003$). There were no significant differences ($P > 0.05$) in any other pairwise comparisons.

Batch fecundity significantly increased with increased age of spotted seatrout ($F_{1,50} = 6.59$, $P = 0.013$, $r^2 = 0.12$) although this was not a strongly predictive relationship because of large amounts of variability in BF at age. There was no significant relationship between relative BF and age ($F_{1,50} = 3.4$, $P = 0.07$, $r^2 = 0.065$). Mean BF was $66,200 \pm 8,400$ for age-1 fish and increased to 354,000 for age-5 fish (Table 4). ANOVA showed there was no significant difference in mean BF among ages 1–4 ($F_{3,50} = 2.2$, $P = 0.10$); age-5 fish were not included in this analysis because of small sample size.

Spawning frequency.—Spawning frequency varied monthly, annually, and by method of calculation for spotted seatrout in coastal Mississippi (Table 5). Spawning frequency was not calculated if no fish in the late developing ovarian class were captured (April 1998) or if there were low numbers of fish in the late developing class (N < 10; Sep. of both years). During 1998, the lowest spawning frequency was observed in May for both the POF (once every 27.7 d) and the FOM (once every 13.7 d) methods, whereas highest spawning frequencies were found in Aug. for both methods (every 2 d for POF method, every 6 d for FOM method). However, the sample size was small in Aug., so these numbers may not be an accurate representation of true spawning frequency. The overall spawning frequency for 1998 was calculated to be every 5.2 d for the POF method and every 10.7 d for the FOM method (Table 5). During 1998, spotted seatrout were consistently estimated to spawn less frequently by the FOM method.

Spotted seatrout appeared to spawn more frequently in 1999. During May, frequencies ranged from once every 1.9 d (FOM method) to once every 3.4 d (POF method). Spawning occurred less frequently in June 1999, ranging from every 9.1 d (FOM method) to 13.5 d (POF method). Overall, the spawning frequency in 1999 ranged from 3.3 d by the FOM method to 4.7 d by the POF method (Table 5). During April–June 1999, the FOM method
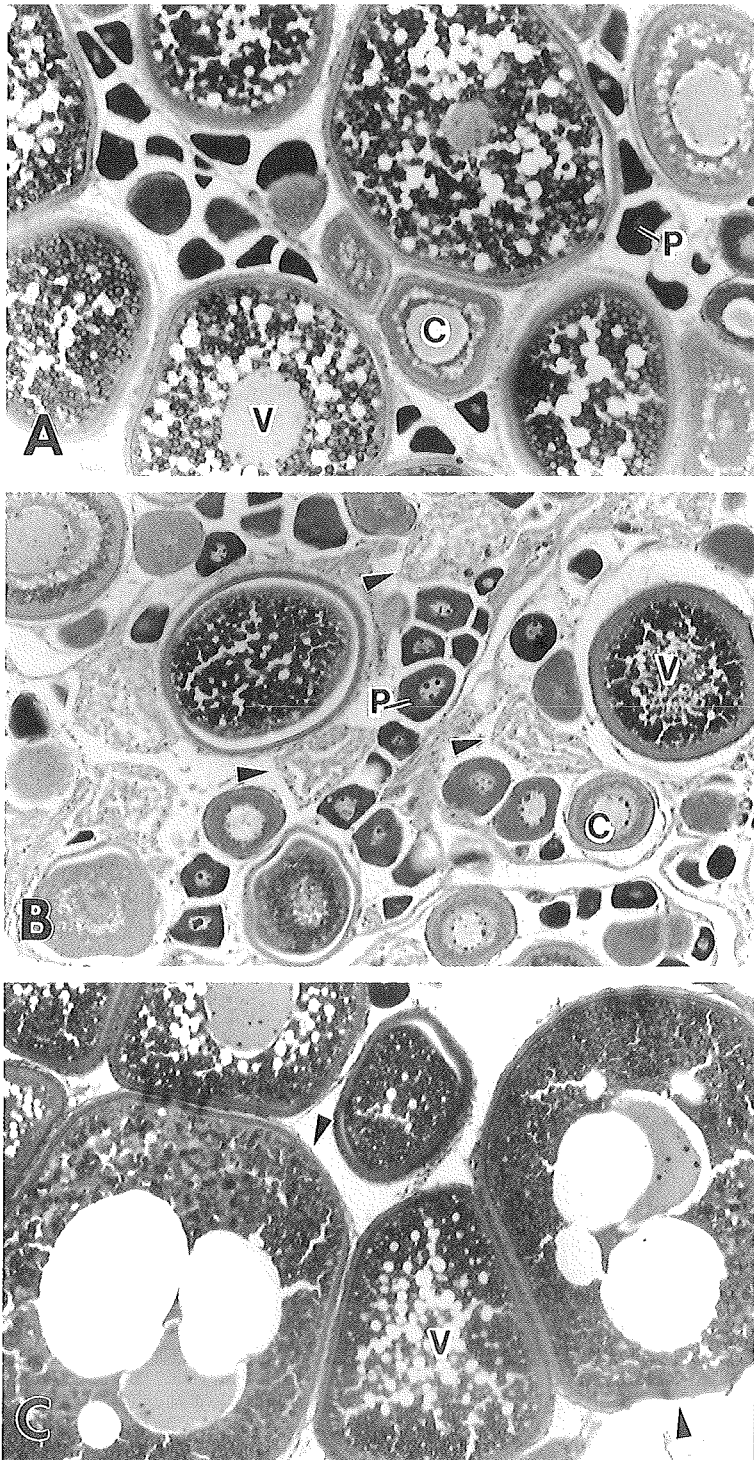
Fig. 3. Photomicrographs of ovarian tissue from spotted seatrout along the Mississippi Gulf Coast. V = vitellogenic oocyte; C = corticoli nucleolor oocyte; P = primary oocyte. (A) Ovary in late developing class. 124× magnification. (B) Ovary of a female in the late developing class with 24-hr postovulatory follicles (POF; arrows). 124× magnification. (C) Ovary of a female in the late developing class with oocytes undergoing final oocyte maturation (FOM, arrows). 128× magnification.
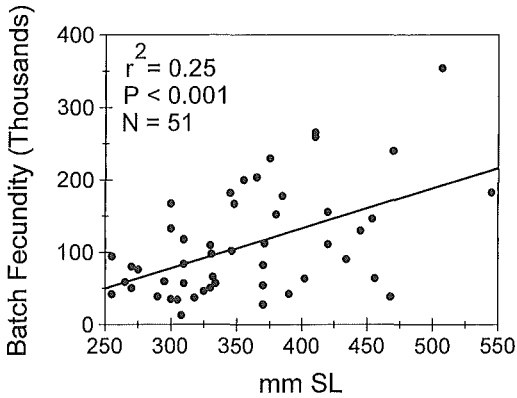
Fig. 4. Relationship between batch fecundity and standard length (SL) for 51 spotted seatrout from the Mississippi Gulf Coast. Data from all areas and all months are pooled.

provided higher estimates of spawning frequency, whereas the POF method produced higher estimates in July and Aug.

Differences in both spawning frequency and salinity were apparent among the three capture locations (Table 6). Salinity was significantly higher at the barrier island site than at the Biloxi Bay or St. Louis Bay sites during 1998 ($F_{2,22} = 15.88$, $P < 0.001$), 1999 ($F_{2,23} = 31.36$, $P < 0.001$), and when data from both years were combined ($F_{2,48} = 43.73$, $P < 0.001$). During 1998, there was a significant difference in spawning frequencies among the three areas by the POF method ($\chi^2 = 22.4$, n = 66, $P < 0.001$), with fish in the Biloxi Bay region spawning less frequently (once every 27.8 d) than fish from the barrier islands (every 4 d) and St. Louis Bay (every 2.8 d) regions. Although the same pattern was evident during 1998 for the FOM method, there was

TABLE 4. Batch fecundity ($\bar{x} \pm$ SE) by age for spotted seatrout along the Mississippi Gulf Coast during 1998 and 1999.

Age	N	Mean batch fecundity
1	6	66,200 ± 8,400
2	28	98,400 ± 12,300
3	13	124,300 ± 18,900
4	3	153,400 ± 59,900
5	1	354,000

not a significant difference among areas ($\chi^2 = 5.0$, n = 30, $P = 0.082$). During 1999, a significant difference in spawning frequencies among areas was found by the FOM method ($\chi^2 = 34.5$, n = 46, $P < 0.001$), with fish from St. Louis Bay spawning more frequently than those from Biloxi Bay; no fish undergoing FOM was captured from the barrier islands (Table 6). Spawning frequency was also lower in Biloxi Bay during 1999 by the POF method, but the difference was not significant ($\chi^2 = 5.7$, n = 61, $P = 0.057$). When data from both years were combined, a significant difference in spawning frequency among areas was found by both the POF ($\chi^2 = 23.16$, n = 127, $P < 0.001$) and FOM ($\chi^2 = 31.13$, n = 76, $P < 0.001$) methods, with spotted seatrout captured in Biloxi Bay spawning less frequently than fish from the other two locations. Overall, spawning frequency in Biloxi Bay ranged from once every 14.5 to 18 d, compared with a spawning frequency of once every 4 d for the barrier islands and St. Louis Bay (Table 6).

DISCUSSION

The reproductive biology of spotted seatrout in coastal Mississippi is similar to that reported

TABLE 3. Relative batch fecundity ($\bar{x} \pm$ SE) by month for spotted seatrout along the Mississippi Gulf Coast during 1998 and 1999 expressed as number of eggs per gram ovary-free body weight.

Month	N	Relative fecundity[a]
April	8	128.8 ± 12.5 AB
May	23	160.6 ± 23.3 AB
June	8	231.3 ± 34.4 A
July	6	225.3 ± 33.5 AB
Aug.	5	87.8 ± 18.1 B
Sep.[b]	1	84.9
Overall	51	165.7 ± 13.9

[a] Small capital letters indicate significant differences (Mann-Whitney U-test, $P < 0.05$) in relative fecundity among months on the basis of ranked data.
[b] Sep. was not included in this analysis.

TABLE 5. Monthly spawning frequency in days for spotted seatrout from the Mississippi Gulf Coast during 1998 and 1999. Only fish in the late developing ovarian class were used for calculations.

Month	Monthly spawning frequency (d)[a]					
	1998			1999		
	N	POF	FOM	N	POF	FOM
April	0	—	—	47	5.2	3.6
May	55	27.7	13.7	62	3.4	1.9
June	48	3.7	9.6	27	13.5	9.1
July	20	3.3	10.0	17	4.2	5.7
Aug.	12	2.0	6.0	21	5.3	None
Overall	135	5.2	10.7	174	4.7	3.3

[a] N = number of fish in late developing class; POF = postovulatory follicles; FOM = final oocyte maturation; None = no fish with FOM.

TABLE 6. Spawning frequency in days for spotted seatrout from different regions along the Mississippi Gulf Coast during 1998 and 1999. Only fish in the late developing ovarian class were used for calculations.

	Spawning frequency (d)[a]										
	Barrier Islands				Biloxi Bay				St. Louis Bay			
Year	‰	N	POF	FOM	‰	N	POF	FOM	‰	N	POF	FOM
1998	25.2 ± 1.0	48	4.0	9.6	11.5 ± 1.4	55	27.8	18.5	14.3 ± 3.1	33	2.8	6.6
1999	25.2 ± 0.8	11	3.7	None	11.8 ± 1.2	17	8.5	8.5	10.6 ± 1.4	143	4.5	3.0
Overall	25.6 ± 0.6	59	3.9	11.9	11.6 ± 1.0	72	18.0	14.5	11.7 ± 1.4	176	3.9	3.5

[a] ‰ = salinity ($\bar{x}$ ± SE); N = number of fish in late developing class; POF = postovulatory follicles; FOM = final oocyte maturation; None = no fish with FOM.

for other areas in the Gulf of Mexico (see Moody, 1950; Hein and Shepard, 1979; Overstreet, 1983; Brown-Peterson et al., 1988). Throughout their range, spotted seatrout have an extended reproductive season, are multiple spawners, and achieve sexual maturity at a relatively small size and young age. Female spotted seatrout from Mississippi may attain sexual maturity at a slightly smaller size than those from Texas; all Mississippi females were sexually mature by 260 mm SL, whereas 100% sexual maturity did not occur in Texas until 280 mm SL (Brown-Peterson et al., 1988). A previous study in Mississippi reported that 26% of females 189–219 mm SL were sexually mature, although 100% sexual maturity was not reached until 400 mm SL (Overstreet, 1983). Whereas the current study found the smallest sexually mature female to be 225 mm SL, the size when 100% of females reach sexual maturity was much smaller than previously reported. This apparent difference in size at first sexual maturity may be related to sample size; 8.7% of the females captured by Overstreet (1983) were 140–219 mm SL, whereas only 1% of females in the present study were in that size range. Although representation in the 220–299-mm SL size range was similar between studies [22% in Overstreet (1983) and 25% in the present study], we found 92% of the females to be sexually mature compared with 78% sexual maturity reported by Overstreet (1983). A decrease in size at sexual maturity is generally considered to relate to a decrease in population size (Rothschild, 1986); this situation should be examined closely in Mississippi spotted seatrout.

A greater percentage of age-1 female spotted seatrout appear to be sexually mature in Mississippi (80%) than in Texas (68%; Bumguardner et al., 1998). Whereas the potential of age-1 fish actually spawning was questioned in Louisiana (Sundararaj and Suttkus, 1962), data from Mississippi clearly show that 62% of the mature age-1 spotted seatrout contributed to the spawning stock, on the basis of the presence of FOM or POF in the ovaries. Although there is no evidence that fish younger than age 1 are reproductively active in Mississippi, Crabtree and Adams (1998) reported that some age-0 fish in Indian River Lagoon, FL, had hydrated oocytes and POF. However, assignment of ages varies among regions (S. VanderKooy, Gulf States Marine Fisheries Commission, pers. comm., Aug. 2000). Thus, some Mississippi fish assigned to the age-1 cohort group may not have actually reached their biological age 1.

The April or May through early Sep. spawning season documented in this study is similar to the May–Aug. (and occasionally Sep.) spawning season previously noted by Overstreet (1983). The spawning season in Mississippi, however, appears to be several weeks shorter than that for other areas in the Gulf of Mexico, which generally extends from early April through the end of Sep. (Gulf States Marine Fisheries Commission, 2001). The presence of preflexion larvae in Florida Bay as early as Feb. and as late as Dec. (Rutherford et al., 1989) suggests the potential of a 10-mo spawning season in that area. Thus, the duration of the spawning season appears to vary across areas and latitudes, a fact that could impact a region-wide management strategy. Indeed, Florida manages their spotted seatrout on a northwest/northeast/south region basis because of differences in reproduction, age, and growth within the state (Muller et al., 1997).

The initiation of the reproductive season appears to vary annually in Mississippi. Similar interannual differences in the reproductive season of spotted seatrout have been reported from Mississippi (Overstreet, 1983), Louisiana (Hein and Shepard, 1979), and Texas (Brown-Peterson et al., 1988) and is no doubt related to water temperature. Temperature prior to the actual spawning season can be important for initiation of gonadal recrudescence. Although there was no statistically significant dif-

ference in temperature in Feb. and March for 1998, 1999, and 2000, biologically, the difference between 16.5 C (March 1998) and 19.1 C (March 2000) may be significant for gonadal development. Similarly, although there was no statistically significant difference in mean water temperature between April 1998 and 1999 (Student's $t_{3,4} = 1.62$, $P = 0.192$), the 19.9 C temperature in April 1998 may be too low to sustain spawning of spotted seatrout. Gray et al. (1991) found that spotted seatrout have a significantly reduced spawning success at 20 C. Brown-Peterson et al. (1988) hypothesized, on the basis of field and laboratory observations, that spotted seatrout in south Texas were unable to successfully spawn at temperatures below 23 C. However, McMichael and Peters (1989) reported the occurrence of larval spotted seatrout in Tampa Bay at 20.4 C, suggesting successful spawning can occur below 23 C. The presence of spotted seatrout with ovaries containing POF or undergoing FOM in April 1999 in Mississippi, with mean water temperature of 21.8 C, also supports spawning at temperatures cooler than 23 C, although the majority of females with FOM and POF were found at temperatures above 23.0 C. Perhaps spotted seatrout in warm-temperate estuaries such as Tampa Bay and along the Mississippi Gulf Coast can spawn at lower temperatures than those from more subtropical locations such as south Texas and Florida Bay. However, temperatures above a minimal threshold are no doubt necessary to initiate and sustain spawning, which could explain the observed reproductive delay of 1 mo in 1998 when compared with 1999 and 2000.

Ovarian maturation patterns did not differ from those previously reported for Mississippi (Overstreet, 1983) and Texas fish (Brown-Peterson et al., 1988) and confirmed multiple spawning in spotted seatrout in Mississippi. The testicular maturation pattern of Mississippi spotted seatrout, indicating a decrease in spermatogenic activity toward the end of the reproductive season, was similar to that of Texas spotted seatrout (Brown-Peterson et al., 1988). Additionally, testicular maturation classes assigned to spotted seatrout were identical to those of common snook (Grier and Taylor, 1998), suggesting changes in the germinal epithelium and spermatogenesis are similar among perciform species.

Fecundity determinations in multiple spawning species such as spotted seatrout require accurate measurement of oocytes that are about to be spawned. Previous estimates of fecundity for Mississippi spotted seatrout (Overstreet,

1983) were based on the inaccurate method of counting all vitellogenic oocytes present in the ovary. Whereas BF is traditionally determined with hydrated oocytes, we estimated BF from oocytes undergoing FOM. Final oocyte maturation is a rapid process in spotted seatrout, starting no more than 12 hr prior to actual spawning (Brown-Peterson et al., 1988). Because accurate BF estimates can be made with oocytes undergoing FOM in species that have rapid FOM (Hunter and Macewicz, 1985a), the BF estimates provided here are comparable to fecundity estimates made by the traditional, hydrated oocyte method. The large variations observed in BF estimates among similar size and age fish probably represent normal variation in spawn size rather than a bias from the method used. The relationship between BF and fish size is often accompanied by large variations and subsequently low r^2 values, as reported for other sciaenids such as spotted seatrout from Texas (Brown-Peterson et al., 1988), weakfish (*Cynoscion regalis*; Lowerre-Barbieri et al., 1996), striped weakfish (*Cynoscion striatus*; Macchi, 1998), black drum (*Pogonias cromis*; Fitzhugh et al., 1993; Nieland and Wilson, 1993) and red drum (*Sciaenops ocellatus*; Wilson and Nieland, 1994). Nevertheless, the BF–SL relationship for Mississippi spotted seatrout has a lower r^2 value than previously reported for other sciaenids. The large variation in BF at size and age could be related to differential shrinkage of large oocytes due to unequal storage time in Gilson's solution prior to fecundity analysis. Alternatively, female spotted seatrout in Mississippi may exhibit a greater plasticity in spawn size than other sciaenids.

Spotted seatrout from Mississippi appear to be less fecund than those in other areas. The only significant difference in relative BF among months was between June and Aug. Thus, relative BF values for all months were combined, and the mean value for 51 fish of 165.7 ± 13.9 eggs·g^{-1} OFBW was used for comparison purposes. This value is much lower than relative BF values of 258 eggs·g^{-1} OFBW (Colura et al., 1988) and 451 ± 43 eggs·g^{-1} OFBW (Brown-Peterson et al., 1988) calculated for Texas fish. More recent work reports higher relative BF values, ranging from 156 to 656 eggs·g^{-1} OFBW in Indian River Lagoon, FL (Crabtree and Adams, 1998) to $1,089 \pm 529$ eggs·g^{-1} OFBW in coastal Texas (Bumguardner et al., 1998). The lower relative fecundity reported for Mississippi may be related to more stressful environmental conditions along the Mississippi Gulf Coast or to less food availability; environmental and nutritional factors

are known to affect fecundity values (Tyler and Sumpter, 1996). The mean salinity in each collection area in Mississippi was either below or above the 15–21‰ range that has been reported to be optimal for spotted seatrout spawning (Saucier and Baltz, 1993).

Overall spawning frequency estimates were similar between 1998 and 1999, although there were some differences between the POF and FOM methods used to estimate frequencies. Spotted seatrout throughout coastal Mississippi appear to spawn once every 3–5 d during a 5-mo reproductive season. This spawning frequency is similar to those from south Texas (every 2.3 d by the FOM method or every 7.6 d by the POF method; Brown-Peterson et al., 1988) and in the southern Indian River Lagoon, FL (every 3.2 d; Crabtree and Adams, 1998). Although the spawning frequency in Mississippi appears comparable to other areas, the potential annual fecundity is lower in Mississippi because of the shorter reproductive season and lower BF. For example, an average 2-yr-old fish in Mississippi could potentially spawn between 31 and 51 times during the reproductive season, releasing a total of 3,050,400–5,018,400 eggs during a single season. In contrast, an average 2-yr-old fish in Texas weighing 430 g could potentially spawn between 24 and 80 times, releasing a total of 4,480,480–14,601,600 eggs during the reproductive season.

The most interesting aspect of the current study was the significant difference in spawning frequency among areas. During both 1998 and 1999, fish captured from Biloxi Bay spawned less frequently than those from the barrier islands and St. Louis Bay, suggesting that Biloxi Bay is a less conducive spawning habitat and that Biloxi Bay has a minimal contribution to overall spawning by spotted seatrout in coastal Mississippi. Whereas salinity has been shown to be an important variable in spawning site selection (Saucier and Baltz, 1993), there was no significant difference in salinity between Biloxi and St. Louis bays, although there was a significantly higher spawning frequency in St. Louis Bay when compared with Biloxi Bay. Thus, salinity alone cannot explain the differences observed in spawning frequency among sites. The submerged habitat, consisting of a soft bottom and little to no submerged aquatic vegetation, is also similar between the two areas and thus cannot explain the observed differences in spawning frequency. Current velocity and depth have also been shown to be important variables in spawning site selection (Saucier and Baltz, 1993). Where-

as depth profiles are not particularly different among the three sampling locations, there is a difference in water movement as affected by wind action. Both the barrier island sites and the St. Louis Bay area are more open and receive considerable wind-related water movement; Biloxi Bay is more protected and may be less affected by winds. Additionally, shore-based development is minimal at both barrier island and St. Louis Bay areas, whereas there is little undeveloped shoreline along Biloxi Bay. The resulting reduction in available marsh habitat due to shoreline development has been shown to have a significant impact on a number of juvenile fish and invertebrate species in the area (Peterson et al., 2000) and may also affect adults dependent on aquatic vegetation as a spawning area, such as spotted seatrout. Perhaps the combination of winds and lack of shoreline development contribute to the increased spawning frequency at the barrier islands and in the St. Louis Bay area. Regardless of the explanation for these differences, this is the first time that differences in spawning frequency have been reported within a confined geographical area for spotted seatrout. Because such differences can dramatically affect annual fecundity, regional spawning frequencies should be considered when designing management plans for spotted seatrout.

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