REPRODUCTIVE BIOLOGY OF THE SPOTTED SEATROUT, *CYNOSCION NEBULOSUS*, IN SOUTH TEXAS[1]

NANCY BROWN-PETERSON,[2] PETER THOMAS,[3] AND CONNIE R. ARNOLD[3]

ABSTRACT

The spotted seatrout, *Cynoscion nebulosus*, spawns from April through the end of September in shallow bays in South Texas. All females were sexually mature at 300 mm SL and males at 200 mm SL. Histological examination of the testes showed that spermatogenesis began in January and continued until September, although spermatozoa remained in the testes until November. Spermatogenesis was more active in the peripheral lobules of the testes than in the central lobules during the latter half of the spawning season. The sequence and timing of final oocyte maturation (FOM) was investigated for the first time in this species. Lipid coalescence began at dawn and germinal vesicle migration started by midmorning. By early afternoon, oocytes were hydrated and spawning occurred at dusk.

Evidence of multiple spawning was examined. Morphological and histological data showed that oocytes were continually recruited from March through the end of September, and the percentages of vitellogenic and fully yolked oocytes did not decline during the spawning season. An average of only 15.5% of the vitellogenic oocytes underwent FOM and hydration during a single spawn. Postovulatory follicles were found in many fish with mature ovaries throughout the reproductive season. Laboratory studies showed that this species is capable of repeated spawns. Batch fecundity was best predicted by ovary-free body weight of the fish and averaged 451 ± 43 eggs/g ovary-free body weight. Estimates of spawning frequency ranged from every other day to once every three weeks.

The spotted seatrout, *Cynoscion nebulosus*, supports important commercial and recreational fisheries throughout its range (Chesapeake Bay, Virginia to Tampico, Mexico; Tabb 1966). Whereas aspects of the reproductive biology of this sciaenid species have been documented throughout its range (i.e., Chesapeake Bay: Brown 1981; Georgia: Mahood 1975; Florida: Moody 1950, Klima and Tabb 1959, Tabb 1961; Mississippi: Overstreet 1983; Louisiana: Hein and Shepard 1979; Texas: Pearson 1929, Miles 1950, 1951), a comprehensive study of reproduction in spotted seatrout does not exist for any area. An extensive knowledge of the reproductive life history of a species is necessary to understand certain aspects of its reproductive physiology and endocrinology. Most previous studies have concentrated on the size at sexual maturity and the extended spawning season of this species (Pearson 1929; Moody 1950; Tabb 1961; Mahood 1975). A protracted spawning season is generally characteristic of multiple spawners (Nikolskii 1969). In addition, Overstreet's (1983) histological data suggest that *C. nebulosus* may be a multiple spawner. However, the possibility that spotted seatrout are multiple spawners has not been thoroughly discussed in the literature, and previous estimates of fecundity (Sundararaj and Suttkus 1962; Overstreet 1983) have not considered the multiple spawning nature of *C. nebulosus* or have included estimates of batch fecundity.

In the present study, the reproductive biology of *C. nebulosus* in South Texas was investigated, and particular attention was given to evidence for multiple spawning and estimates of batch fecundity and spawning frequency. The spawning season, spawning sites, time of spawning, and percentage of running ripe fish were documented. In addition, the temporal pattern of final oocyte maturation was determined. The histological appearance of the gonads was examined, and particular attention was given to the presence of postovulatory follicles in ovarian tissue, an indicator of multiple spawning in the northern anchovy, *Engraulis mordax* (Hunter and Goldberg 1980). The size-frequency distribution of vitellogenic oocytes was examined, since this can indicate multiple spawning (deVlaming 1983). Batch fecundity was determined and spawning frequency

[1]Contribution No. 696, University of Texas at Austin, Marine Science Institute, Port Aransas, TX 78373.

[2]Marine Science Institute, University of Texas at Austin, Port Aransas, TX; present address: Florida Department of Natural Resources, Indian River Lagoon Aquatic Preserves, 4842 S. U.S. Highway 1, Fort Pierce, FL 34982.

[3]Marine Science Institute, University of Texas at Austin, Port Aransas, TX 78373.

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was estimated from both field-caught and laboratory fish.

MATERIALS AND METHODS

Collection of Samples

Spotted seatrout were collected in Redfish Bay or Lydia Ann Channel near Port Aransas, TX, U.S.A. at depths of 1–3 m (Fig. 1). Fish were captured using a 300 m gill net (82 mm stretch) or a 300 m trammel net (outer panels, 178 mm stretch; inner panel, 89 mm stretch) over shallow beds of turtle grass, *Thalassia testudinum* or shoal grass, *Halodule wrightii*, bordered by a 1–2 m drop-off into a channel. Fish <300 mm SL were captured with hook and line in 1–2 m of water.

Samples were collected weekly or twice monthly from March 1982 through early May 1985. No samples were taken in November and December 1983, October and December 1984, and February 1985. During 1982, samples were collected at dusk only; in 1983, 1984, and 1985, samples from dawn, midday, and midnight were also taken. During each sampling period, salinity and temperature were recorded as well as the time of capture.

Analysis of Fish and Gonads

Total length (TL) and standard length (SL) were measured to the nearest mm for each specimen and total body weight (WT) was determined to the nearest 10 g. Gonads were removed and weighed to the nearest 0.1 g (gonad weight, GW) and the gonadosomatic index (GSI) was calculated, using the formula: $GSI = (GW/WT) \times 100$.

Reproductive stage of the gonads was assessed macroscopically using the criteria in Table 1. The macroscopic criteria used were similar to those used by Overstreet (1983) and Macer (1974). A small portion of tissue was removed from the anterior or midsection of one gonad from each fish and preserved in Davidson's fixative for histological analysis (Jones 1966). Tissues were dehydrated and embedded in paraffin. Seven micron sections were cut and stained with Harris' hematoxylin and counterstained with eosin. Reproductive stage of each sample was assessed microscopically using the criteria in Table 1. Fish with

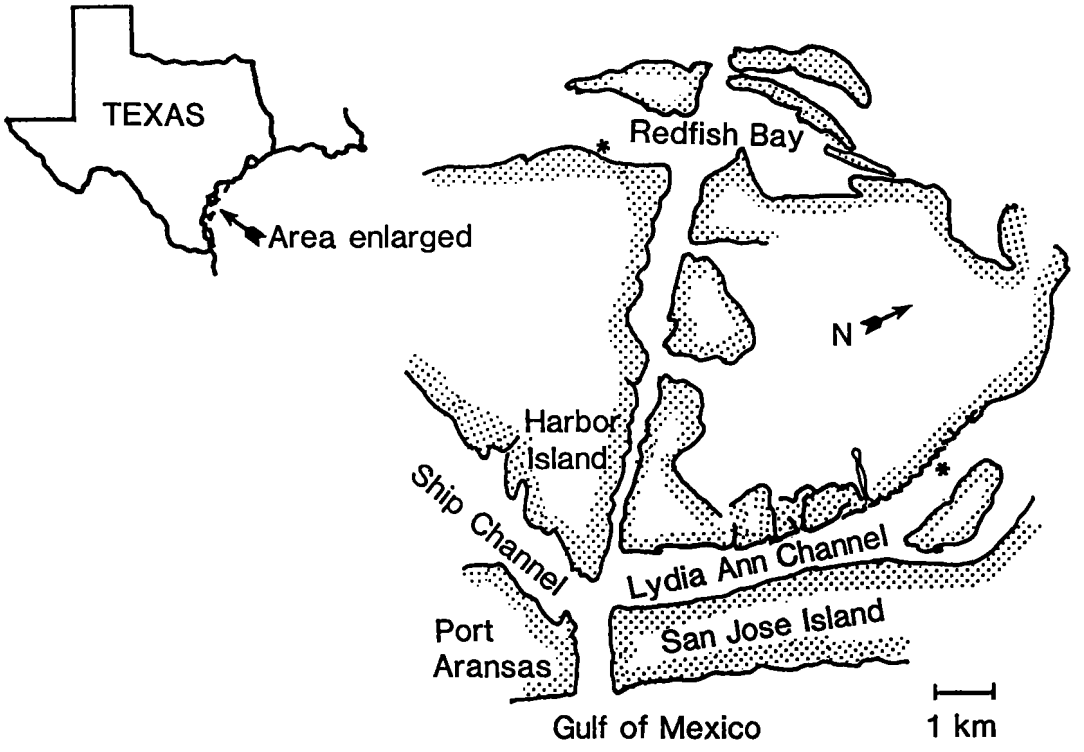

FIGURE 1.—Location of spotted seatrout sampling sites in South Texas. Asterisks denote sampling sites.

mature gonads were considered sexually mature. The microscopic criteria used were similar to those described by Yamamoto (1956), Hyder (1969), and Macer (1974). The percentages of each stage of oocyte, atretic structures, and postovulatory follicles were determined from histological slides of the ovaries of females >305 mm SL by counting all the oocytes in three randomly selected fields of view. An oocyte was counted if >50% of the cell was in the field of view. Two hundred and fifty to 500 oocytes were counted for each histological specimen.

A small portion of tissue (<0.5 g) was removed from the center of each ovary of females >305 mm SL collected in 1984 and 1985, placed in clearing solution (6 parts ethanol, 3 parts formalin, 1 part

TABLE 1.—Criteria used to describe gonadal reproductive stages of male and female spotted seatrout collected in South Texas.

Stage	Sex	Macroscopic appearance	Microscopic appearance
Immature	F	Ovary small, thin, light pink, slight vascularization. GSI range: 0.39–0.55.	Only primary oocytes present; no atretic oocytes. Lamellar margin thin.
	M	Testes small, thin, light grey, appearance similar to mesentery.	Only primary spermatogonia present.
Regressed	F	Ovary small, light pink, vascularization more obvious than in immature fish. GSI range: 0.39–1.16.	Primary chromatin nucleolar and early perinuceolar stage oocytes. Some atretic oocytes. Lamellar margin thicker than immature, more convoluted.
	M	Testes small, thin, white, slightly larger than immature fish. GSI range: 0.04–0.20.	Primary and secondary spermatogonia present.
Early developing	F	Ovary similar to regressed fish but slightly larger. GSI range: 0.80–1.26.	Appearance of late perinucleolar oocytes and primary cortical alveoli stage oocytes. No atretic oocytes present.
	M	Testes similar to regressed fish but slightly larger. GSI range: 0.16–0.48.	Many secondary spermatogonia and primary spermatocytes.
Developing	F	Ovary visably enlarged, light yellow, highly vascular, approximately 60% of the length of the body cavity. GSI range: 0.95–2.6.	Oocytes in secondary cortical alveolar stage and yolk granule stage. Many oocytes still in primary cortical alveolar stage. Early yolk globular stage present.
	M	Testes thickened, creamy white, no free milt expelled when cut. GSI range: 0.21–0.68.	All stages of spermatogenesis present, with few primary spermatogonia and free spermatozoa. Primary and secondary spermatocytes predominate.
Mature	F	Ovary large, brilliant yellow orange, oocytes visible to naked eye, vascularization prominent. Ovaries 80–90% length of body cavity. GSI range: 2.5–9.6.	Oocytes in yolk globular stage most common. Yolk and oil globules begin to encroach on nucleus. Largest oocytes range from 300 to 375 μm.
	M	Testes creamy white, thicker, more firm and elongated than developing testes. A small amount of milt expelled when cut. GSI range: 0.54–1.42.	No primary spermatogonia present, some secondary spermatogonia. Secondary spermatocytes and spermatids most numerous. Spermatozoa in central lobules.
Ripe	F	Oocytes hydrated, ovary looks clear, takes up almost entire body cavity, highly vascularized. GSI range: 12.5–19.9.	Many hydrated oocytes, irregularly shaped, eosinophilic. Other oocytes in yolk granular and yolk globular stages.
	M	Testes white, swollen, milt does not flow with light pressure, but flows freely when cut. GSI range: 1.07–1.62.	Spermatozoa, spermatids and secondary spermatocytes predominate. Few to no spermatogonia. Central lobules filled with spermatozoa.
Running ripe or spawning	F	Hydrated oocytes expelled with little to no pressure, ovary fluid, fills almost entire body cavity. GSI range: 7.7–17.6.	Same as ripe ovaries but fewer hydrated oocytes. Atretic and postovulatory follicles may be present.
	M	Testes creamy white, milt freely flowing with slight pressure. GSI range: 1.41–3.84.	Same as ripe fish, but spermatozoa evident in sperm ducts.
Partially spent	F	Ovary looks similar to mature condition but more flacid; occupies smaller percentage of body cavity. GSI range: 2.0–5.3.	Similar to mature ovary, except atretic oocytes in several stages of degeneration always evident. Postovulatory follicles occasionally present.
	M	Tests looks the same as running ripe but smaller. GSI range: 0.85–1.77.	No spermatogonia, few primary spermatoocytes. Most active spermatogenesis in peripheral lobules. Spermatozoa partially filling lobules and abundant in sperm ducts.
Spent	F	Ovary flacid but still highly vascularized, no longer than 50% of body cavity, pinkish in color. GSI range: 1.33–2.63.	Massive atresia of all remaining vitellogenic oocytes. Many primary and chromatin nucleolar oocytes present. Lamellar membrane highly convoluted.
	M	Testes flacid, width reduced, white. GSI range: 0.13–0.80.	Spermatozoa present in some lobules. Most lobules small, with only primary and secondary spermatogonia.

glacial acetic acid), and vigorously shaken for 30 seconds. Within a few minutes the cytoplasm cleared and the germinal vesicle could be easily observed microscopically. Ovarian fragments were taken from females collected at the spawning site over a 24-h period, placed in clearing solution and then examined under low-power magnification to determine the stage of final oocyte maturation.

Oocyte Size-Frequency Distributions and Estimates of Batch Fecundity

To determine fecundity and the frequency distribution of oocyte diameters, a 2–15 g piece of tissue was removed from the midsection of the ovaries of 57 fish and weighed to the nearest 0.01 g. The tissues were placed in a modified Gilson's solution (Bagenal 1966) for 3–12 months and periodically shaken to separate the oocytes from connective tissues. Ovaries containing hydrated oocytes were examined after three months since hydrated oocytes of spotted seatrout began to disintegrate when left in Gilson's solution for a longer period of time.

The volumetric method was used to estimate fecundity (Bagenal and Braum 1971). The oocyte samples were suspended in 500–1,500 mL of water and three replicate 0.5 or 1 mL subsamples were taken. All the oocytes >30 μm were counted, and those >80 μm in diameter (the growing oocytes) in each sample were measured to the nearest 15 μm using an ocular micrometer. A total of 556–1,110 growing oocytes were measured in each sample. The number of resting oocytes (oocyte diameter 30–80 μm) was determined by diluting the original oocyte suspension 1:10, and counting three replicate subsamples. Altogether, the frequency distributions of oocytes from 48 fish were analyzed (3 in developing stage; 9 in mature, spawning not imminent stage; 14 in mature, just prior to spawning stage; and 22 in running ripe stage). Fecundity was calculated following Macer's (1974) formula and expressed as relative fecundity of number of eggs per gram ovary-free body weight. Batch fecundity (BF) is defined as all oocytes >350 μm which were undergoing final oocyte maturation that formed a distinct batch, and all hydrated oocytes. This definition of batch fecundity is in agreement with Hunter and Macewicz's (1985) statement that oocytes undergoing final oocyte maturation may be included as hydrated oocytes when hydration occurs very rapidly.

Spawning of Fish in the Laboratory

Four female and two male spotted seatrout were maintained in a 30,000 L recirculating system. The tank, filtration system and feeding regime of the fish has been described previously (Arnold et al. 1976). The salinity ranged from 25 to 30‰. Spawning was induced by increasing the temperature and photoperiod from wintertime settings of 13°C, 9L:15D to 26°C and 15L:9D (Arnold et al. 1976). The filter boxes were checked daily for the presence of buoyant, newly fertilized eggs.

Statistical Analysis

Simple linear regression, oneway analysis of variance, and analysis of covariance were computed for the data using SPSS packaged programs (SPSS 1981).

RESULTS

Size at Maturity

Some female spotted seatrout were sexually mature after they reached 231 mm SL and >90% of the females had reached sexual maturity at 271 mm SL (Table 2). By 300 mm SL, all female spotted seatrout were sexually mature. Fish 300 mm SL or larger made up 85.4%, and immature fish comprised 6.5%, of all the females sampled.

Male spotted seatrout reached sexual maturity at a much smaller size than females. The size at

TABLE 2.—Number and percentage of mature female and male spotted seatrout by 10 mm size categories collected in South Texas, April 1982–May 1985. Maturity was judged by histological and macroscopic inspection.

Standard length (mm)	Female		Male	
	N	% mature	*N*	% mature
201–210	5	0	5	100
211–220	4	0	4	100
221–230	4	0	1	100
231–240	4	50	3	100
241–250	6	83	3	67
251–260	6	100	5	100
261–270	5	80	7	100
271–280	11	91	10	100
281–290	14	100	11	100
291–300	24	96	20	100
301–310	60	100	40	100
311–320	94	100	68	100
321–330	115	100	80	100
>330	945	100	507	100
Total	1,297		764	

which most male spotted seatrout attain sexual maturity could not be determined, since the smallest fish collected by the sampling methods (200 mm SL) were all sexually mature (Table 2).

Season and Time of Spawning

Histological and macroscopic examination of the gonads (see Table 3 and Figure 3) and mean GSI values (Fig. 2) show that spotted seatrout have an extended reproductive season in South Texas. Mean GSI values of males and females increased by April 1982–85 and remained elevated through the end of September. A 5°C increase in water temperature at the sampling sites to 23°C during the first week of April 1982–85 was paralleled by an increase in GSI to 2.1 in males and 4.5 or greater in females. The pattern of seasonal changes in mean GSI values of males was relatively consistent during the three-and-a-half years of sampling. Mean GSI values began to increase in mid-February, reached a maximum of 1.9–2.4 by April, and slowly declined during the spawning season until they dropped rapidly to regressed levels of 0.2 by the first half of October (Fig. 2). The seasonal patterns in mean GSI values of females were also similar from 1982 to 1985. In all four years, mean GSI increased in April and subsequently declined in May. In 1982–84, mean GSI increased again later in the season prior to the final decrease to regressed levels in October (Fig. 2). Thus, mean GSI values appear to be bimodal, with one period of peak spawning activity in April, and the second period of peak spawning activity varying between August 1982 and July 1983 and 1984.

Male and female spotted seatrout in spawning condition (males with freely flowing milt, females with ovulated oocytes) were consistently captured during a 2-h period around dusk over shallow (1 m) beds of *Thalassia testudinum* or *Halodule wrightii* bordered by a channel 2 m deep. The salinity at the spawning sites ranged from 20 to 37‰. Although actual spawning was not observed, collection of newly fertilized eggs from the spawning area at dusk confirmed that spawning was taking place (Holt and Holt[4]). Spawning fish were not captured over beds of scattered *H. wrightii* or *T. testudinum* that were not immediately adjacent to a channel. Females with freely

[4]S. A. Holt and G. J. Holt, University of Texas at Austin, Marine Science Institute, Port Aransas, TX 78373, pers. commun. 1983.

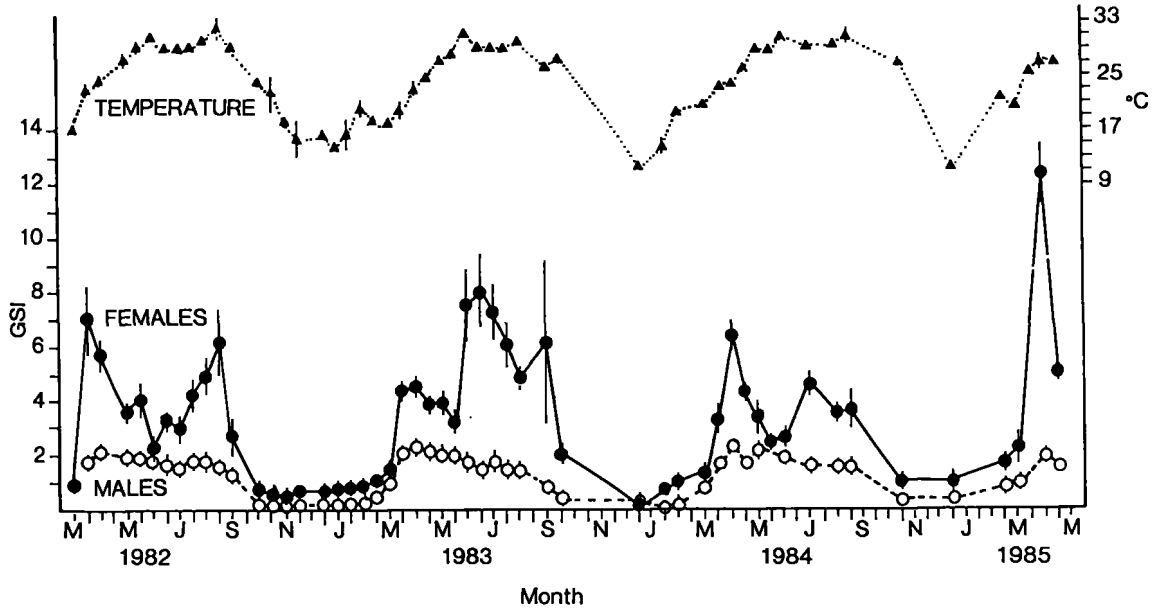

FIGURE 2.—Bi-monthly mean water temperature and mean gonadosomatic index (GSI) of male and female spotted seatrout collected in South Texas from March 1982 to May 1985, including ±1 SE of the mean. Sample size for each data point: 3–61 for females (sample size <15 in only 9 cases) and 2–52 for males (sample size <9 in only 9 cases).

flowing oocytes were only captured at dusk and milt appeared to flow more freely in males at dusk than at other times of the day.

Gonadal Development in Males

Testicular recrudescence began in January with the appearance of primary spermatocytes (Fig. 3), and by February the majority of the males were in the early developing or developing reproductive stage. In March, 89% of the males had testes containing free spermatozoa (Fig. 3), although only 27% were running ripe. Over 94% of all males captured from April until the end of August were running ripe. Spent males first appeared in August and all the males during October and November were either in the spent or regressed condition. In December, all males captured had regressed testes containing only primary and secondary spermatogonia (Fig. 3).

Histological observations revealed that the testes are the common unrestricted spermatogonia type, as described by Grier (1981). Spermatogenesis occurred throughout the entire testis during the majority of the year. However, from late February through early August, spermatogenesis was more advanced in the central lobules then in the peripheral lobules. By August there was no spermatogenic activity in the central lobules, although spermatogenesis continued in the peripheral lobules until mid-September. The only period of the year when there was no active spermatogenesis was from October through late January, although primary and secondary spermatogonia were present from October through the end of April (Fig. 3). Primary spermatocytes were common from late January until March, although they did not disappear from the testes entirely until the end of July. Secondary spermatocytes first appeared in mid-February, were common through the end of July and did not disappear until early September (Fig. 3). Spermatids and spermatozoa were present in the central lobules by late February, and from March through mid-August the central lobules were swollen with spermatozoa (Fig. 3). In late August and September many of the central lobules appeared to be partially empty of spermatozoa, although some spermatozoa were still present up to mid-November (Fig. 3). The peripheral lobules contained active spermatogenic cysts of primary and secondary spermatocytes during June and July and the lumens of these lobules began to fill with spermatozoa. The peripheral lobules were swollen with spermatozoa during August and September, but by mid-October no spermatozoa remained.

Gonadal Development in Females

Gonadal recrudescence was observed in a small percentage of the females captured in January and by March 94% of the females were undergoing ovarian development (Table 3). Fish with mature ovaries were found from March until the end of September, while running ripe fish were captured from April through the end of September (Table 3). Partially spent fish (females that appeared to have spawned at least once but still contained vitellogenic oocytes) were captured from May through the end of September. No com-

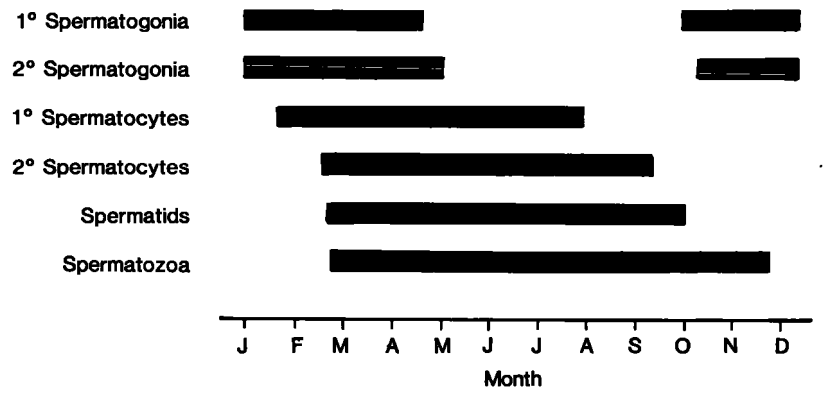

FIGURE 3.—Seasonal cycle of spermatogenesis in spotted seatrout collected in South Texas, as determined by histological and macroscopic observations. Data from April 1982 through mid-May 1985 are combined. 1° - primary, 2° - secondary.

TABLE 3.—Percentage of female spotted seatrout in seven reproductive stages by month, as assessed by histological and macroscopic examination of the ovaries. Data from April 1982 to May 1985 are combined. REG = Regressed, E DEV = Early Developing, DEV = Developing, MAT = Mature, RR = Ripe and Running Ripe, P SP = Partially Spent, SP = Spent.

		Percent in each reproductive stage						
Month	*N*	REG	E DEV	DEV	MAT	RR	P SP	SP
January	70	98	2					
February	51	55	43	2				
March	124	4	56	31	9			
April	372		4	6	78	12		
May	220			4	84	5	7	
June	104			1	56	19	24	
July	114		1		48	30	20	1
August	100				58	32	7	3
September	37	14			37	30	11	8
October	8	87						13
November	27	100						
December	51	98			2			
Total	1,278							

pletely spent fish were captured before July and few were captured during the remainder of the reproductive season.

Histological observations of fish with regressed ovaries collected from late September to mid-February showed only primary chromatin nucleolar and early perinucleolar oocytes. Atretic oocytes were present from September until mid-December; no atretic oocytes were observed from mid-December through the end of February. The appearance of late perinucleolar and primary cortical alveoli stage oocytes in late January, February, and early March represented the initial stages of ovarian recrudescence. Ovarian development was proceeding rapidly by early March and oocytes in the secondary cortical alveoli and yolk granule stages were common.

During the reproductive season, histological observations of the ovary showed a heterogeneous morphology. Oocytes in all stages of growth (from resting to the fully grown yolk globular stage) were distributed throughout the ovaries of all mature, running ripe, and partially spent fish collected from March through the end of September. Vitellogenesis was probably continuous from February until the end of September, as shown by the continual presence of large numbers of oocytes in the cortical alveoli and yolk granule stages. The relative percentages of three types of post cortical alveolar stage oocytes in fish in the mature reproductive stage did not change markedly from March through the end of September (Fig. 4). The percentage of oocytes in the yolk granule stage (diameter in histological preparations: 150–190 μm) varied from a low of 7.3% in June to a late season high of 16.1%, and averaged 13% of the total number of oocytes in the ovary. Yolk globular oocytes, the largest oocytes present (diameter: 200–375 μm), were most common. The percentage of oocytes in the yolk globular stage ranged from a high of 30.8% in April to an end-of-season low of 22.6% in September and averaged 26.9% during the reproductive season. In addition to the actively growing oocytes in the ovary, a small percentage of atretic oocytes was always found in fish with mature ovaries. Atretic oocytes are defined here as vitellogenic oocytes undergoing alpha stage atresia. The percentage of atretic oocytes ranged from a low of 2.2% in March to a midsummer high of 8% in July and averaged 5.4%. Additionally, postovulatory follicles (POF) were observed in the ovaries of fish captured from

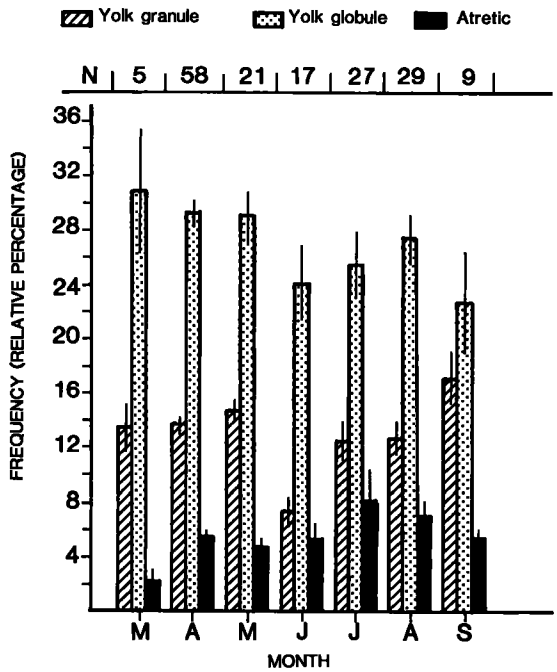

FIGURE 4.—Frequency of three different types of oocytes in female spotted seatrout ovaries in the mature reproductive stage (MAT, Table 3) as assessed by histological observation. Fish were collected from South Texas during the reproductive season. Frequency refers to the percentage of each type of oocyte relative to the total number of all types of oocytes counted. Data from April 1982 through the end of September 1983 are combined and the number (*N*) of individuals examined each month is indicated. Bars indicate mean percentage of oocytes ±1 SE of the mean. Yolk granule oocyte diameters ranged from 150 to 190 μm, and yolk globule oocyte diameters ranged from 200 to 375 μm in histological preparations. Atretic oocytes are defined here as oocytes in alpha stage atresia.

April through September, although the percentage of POF relative to the total number of oocytes was always small (<5%).

The histological appearance of the zona radiata and follicle layers changed as the oocytes developed. The zona radiata (chorion) was thin and nonstriated in perinucleolar and cortical alveoli oocytes. The zona radiata started to take on its characteristic striated appearance when oocytes reached the yolk granular stage and became noticeably thicker and more striated as oocytes grew into the yolk globular stage. In contrast, the granulosa and thecal layers appeared to decrease in thickness as oocyte development proceeded. Oocytes in the perinucleolar and cortical alveoli stages had thick, well-developed granulosa and thecal layers. In yolk granular and yolk globular oocytes, both follicle layers were noticeably thinner and the thecal layer was not always continuous around the oocyte.

Frequency distributions of growing oocytes (diameters in Gilson's solution >80 μm; perinucleolar to hydrated stage oocytes) from ovaries of 48 fish were analyzed, and Figure 5 shows typical patterns in fish from four reproductive stages. In a fish captured in March with developing ovaries, growing and vitellogenic oocytes (oocytes during the phase of active vitellogenin uptake) ranging from 80 to 185 μm in diameter were present (Fig. 5A; 625 oocytes counted). Fish in the mature reproductive stage in which spawning did not appear to be imminent, as indicated by GSI values <4, had growing and vitellogenic oocyte diameters ranging from 100 to 320 μm (Fig. 5B; 556 oocytes counted), comprising 21% of the total number of oocytes >30 μm in the ovary. Fish just prior to spawning, as indicated by GSI values >7, had a distinct batch of oocytes with diameters >350 μm that were undergoing final oocyte maturation (Fig. 5C; 585 oocytes counted). However, there were no other distinct modes of vitellogenic oocytes. In running ripe fish, the batch of large oocytes hydrated to a diameter of 520 μm or greater (Fig. 5D; 1,110 oocytes counted). The results (Figs. 5A–D) clearly demonstrate that *C. nebulosus* has a continuous distribution of growing and vitellogenic oocytes. The oocyte frequency distribution of the vitellogenic oocytes <320 μm in diameter remaining in running ripe fish ap-

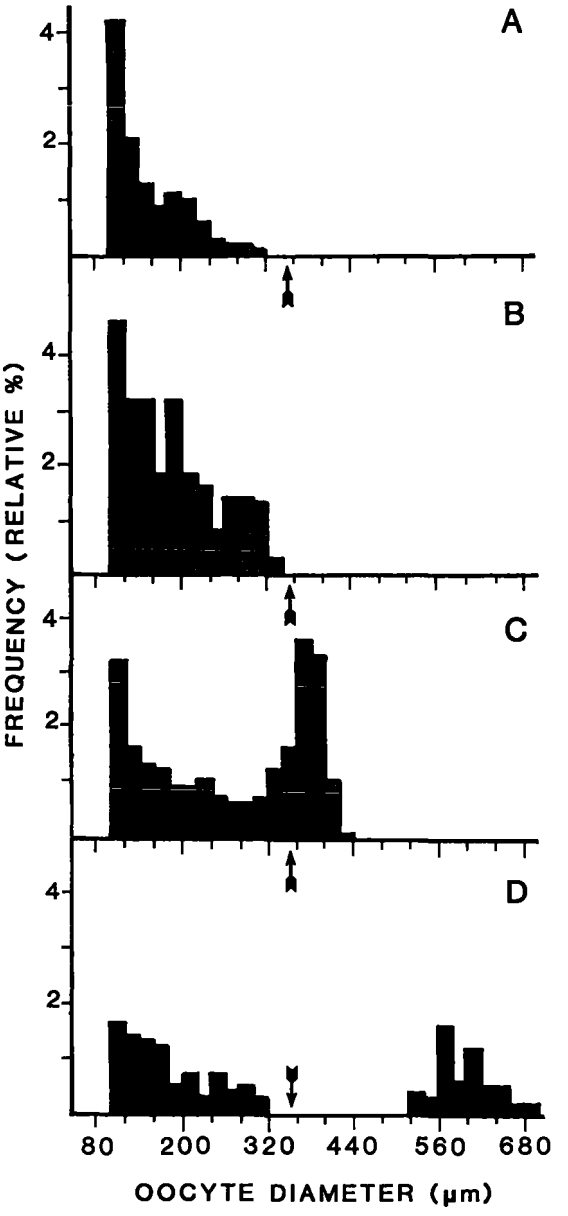

FIGURE 5.—Frequency distributions of growing oocyte diameters (>80 μm) in female spotted seatrout collected from South Texas. Growing oocytes comprised 21% of the total number of oocytes >30 μm in the ovary. Oocyte diameter refers to the diameters of oocytes after preservation in Gilson's solution. Frequency refers to the percentage of each size of oocyte relative to the total number of oocytes in the subsample. Each graph represents data from a single fish at a different reproductive stage. The arrow at 350 μm indicates the minimum size necessary for final maturation to occur. A. Developing stage in March, GSI = 1.6. B. Mature stage in which spawning is not imminent, GSI = 3.7. Fish in this stage were collected from April through the end of September. C. Mature stage just prior to spawning, GSI = 7.4. Fish in this stage were collected from April through the end of September. D. Running ripe stage, GSI = 17.6. Fish in this stage were collected from April through the end of September.

peared similar to the oocyte distribution in nonspawning fish (Fig. 5B, D). The percentage (21%) of growing and vitellogenic oocytes in the ovary remained constant throughout the reproductive season in fish in the mature and running ripe stages.

Final Oocyte Maturation

Final oocyte maturation (FOM) was highly synchronized in spotted seatrout and occurred only in oocytes >400 μm [5]. Figure 6A shows a photomicrograph of a histological section of a spotted seatrout ovary in the mature reproductive stage that was not undergoing final oocyte maturation. Many oocytes were in the yolk globular stage and appeared to be fully grown. The first readily observable stage of FOM in "cleared" oocytes was lipid coalescence (Fig. 6B). The oil droplets in the oocytes began to coalesce around the germinal vesicle (nucleus) and subsequently formed one to three large oil droplets. This stage was not always observed in histological preparations since many of the oocytes were not sectioned through their centers. The yolk globules remained discrete during lipid coalescence. After the lipids had coalesced, the germinal vesicle (GV) began to migrate to the periphery of the oocyte (germinal vesicle migration, or GVM). GVM could be seen in both histological sections (Fig. 6C) and in "cleared" oocytes (Fig. 6D). The oil droplet occupies the center of the oocytes shown in Figure 6C, D. Histological observation of this stage (Fig. 6C) showed that the yolk globules were not coalesced, the oil droplets had coalesced to form one or two large droplets and the GV had begun to lose its integrity and often appeared semicircular. At the completion of GVM, the nuclear (germinal vesicle) membrane broke down (GVBD) and the nuclear material intermingled with the cytoplasm of the oocyte. Hydration occurred shortly thereafter, followed by ovulation and spawning of the fully mature oocyte.

Final oocyte maturation occurred within 10 hours in spotted seatrout in the natural environment (Fig. 7). A total of 209 fish were collected over eight 24-h periods from April through August in 1984 and 1985. Forty-three percent of the fish collected between the hours of 0500 and 1500 were undergoing FOM. Lipid coalescence was first observed at dawn (0545), and GVM started at 0900. By 1430, all fish undergoing final maturation had hydrated oocytes and ovulation and spawning commenced at dusk (1830) and continued until 2100. None of the fish collected from 2100 to 0500 were undergoing FOM.

Batch Fecundity

The significant positive relationship ($P < 0.001$) between BF and ovary-free body weight can be best described by the following equation: $BF = 459WT - 56{,}066$, $r^2 = 0.56$ (Fig. 8), while curvilinear equations best described the relationship between BF and SL and TL. The coefficients of determination in all cases were <0.56.

A one-way analysis of variance showed that mean BF (number of eggs per gram ovary-free weight) did not vary significantly during the April through September spawning season. Mean relative batch fecundity was highest in September, lowest in May, and varied little during April, June, and July (Table 4).

A prominent batch of oocytes was present only in females that were in all stages of final oocyte maturation or were running ripe (Figs. 5C, D; 7). The average batch size calculated from 14 fish containing hydrated oocytes and no postovulatory follicles was 451 ± 43 eggs/g ovary-free body weight. This number averaged 15.5 ± 2.5% of the number of growing and vitellogenic oocytes in the ovary.

TABLE 4.—Monthly mean batch fecundity expressed as number eggs/g ovary-free body weight of spotted seatrout in South Texas. All means were not statistically different.

Month	N	Mean fecundity ±1 SE
April	19	477 ± 42
May	2	320 ± 72
June	3	435 ± 109
July	5	409 ± 76
August	3	361 ± 60
September	3	560 ± 79

Spawning Frequency

To estimate the spawning frequency of spotted seatrout in South Texas, the percentage of running ripe females captured monthly from April through the end of September in 1982 through 1985 was examined. Only fish captured at dusk and >305 mm SL were included in this analysis. The percentage of spawning females ranged from

[5] A 400 μm live oocyte equals a 350 μm oocyte preserved in Gilson's solution. Both measurements represent oocytes beginning FOM.

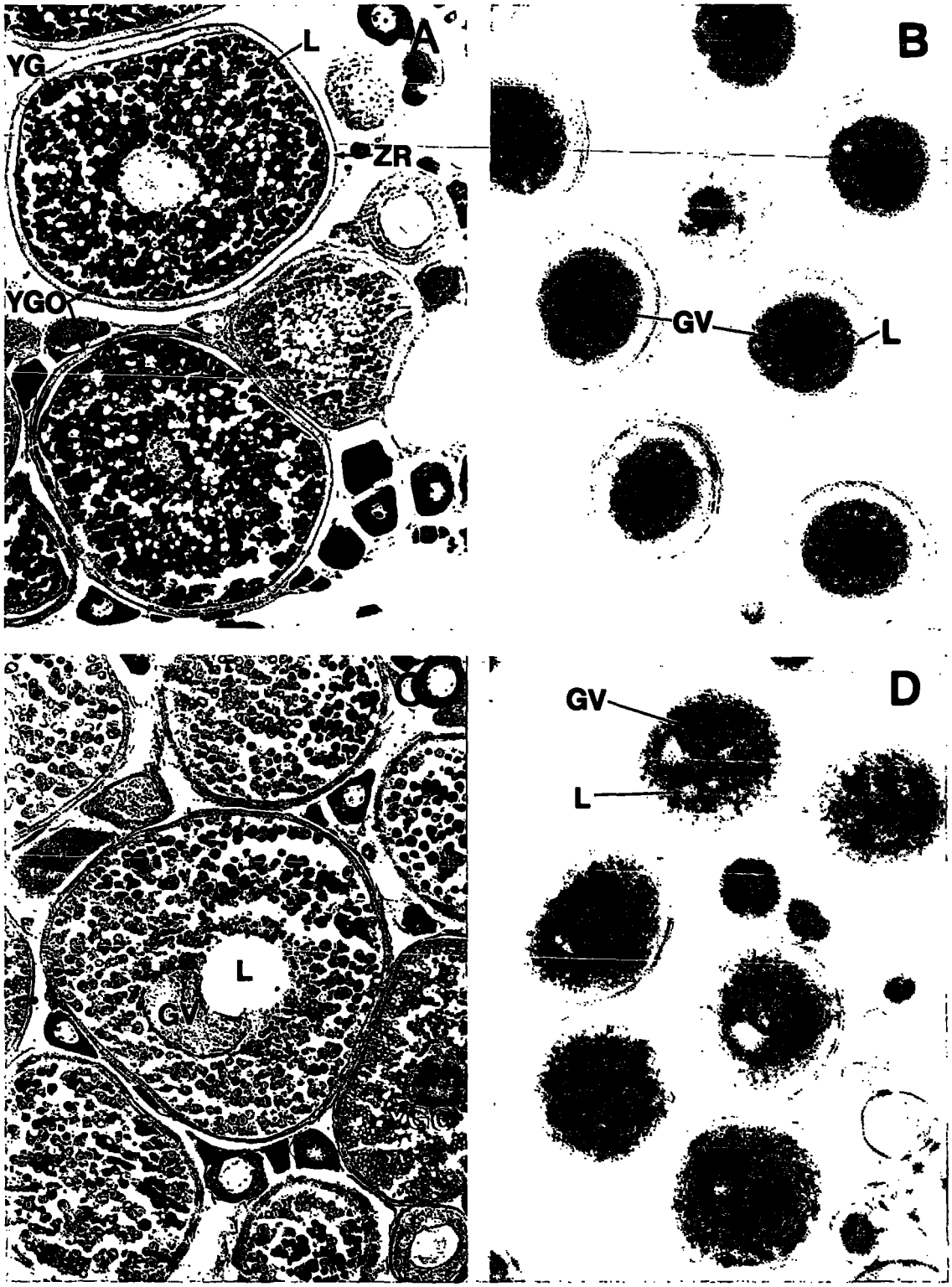
A
L
YG
ZR
YGO
B
GV
L
L
GV
D
GV
L

FIGURE 6.—Photomicrographs of oocytes from spotted seatrout in the mature reproductive stage collected from South Texas. A. Histological section of an ovary in the mature stage that is not undergoing final oocyte maturation (FOM). Oocyte development is continuous, with fully grown yolk globular oocytes co-occurring with oocytes in earlier stages of development (Magnification 120×). B. "Cleared" oocytes in the lipid coalescence stage, the first stage of FOM (magnification 40×). C. Histological section of an oocyte undergoing germinal vesicle migration (GVM). (Magnification 160×). D. "Cleared" oocytes in the GVM stage (magnification 40×). Key: GV = germinal vesicle or nucleus, L = Lipid droplets, YG = yolk globules, YGO = yolk globular oocyte, ZR = Zona radiata.

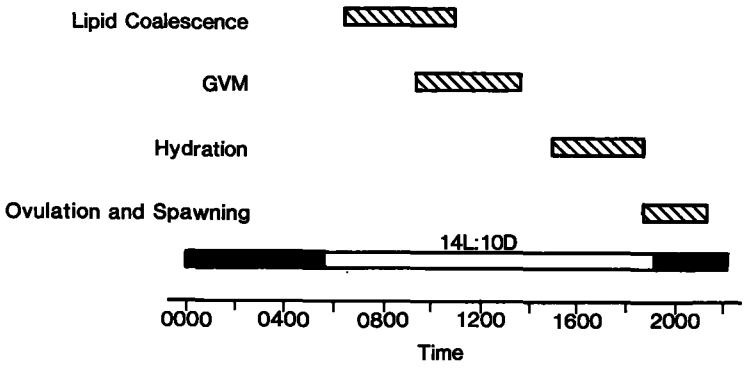

FIGURE 7.—Time-course of final oocyte maturation in spotted seatrout collected from South Texas. Lipid coalescence is the initial stage in final oocyte maturation. Data obtained from 46 fish undergoing final oocyte maturation in April and May 1985. GVM = germinal vesicle migration. 14L: 10D = hours of light and dark.

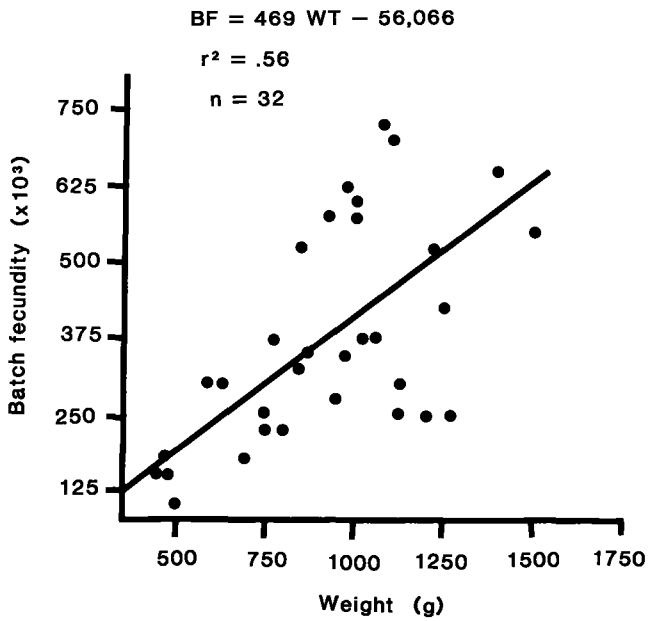

FIGURE 8.—Relation between batch fecundity (BF) and ovary-free body weight (WT) of spotted seatrout from April 1984 to May 1985. Thirty-three fish with oocytes >350 μm that were undergoing final oocyte maturation and formed a distinct batch of oocytes or had hydrated oocytes are included.

a low of 8% in May to a high of 45% in September (Table 5). An average of 27.5% of the females captured during the spawning season were running ripe, corresponding to an average spawning frequency of once every 3.6 days or 50 times during the 6-mo spawning period.

The spawning frequency was also estimated from females that were undergoing final oocyte maturation (FOM) between the hours of 0600 and 1400 in April, May, July, and August 1984 and 1985 (Table 5). For comparison, the actual percentage of running ripe females captured during the same months is also presented. An average of 42.8% of the females examined for final oocyte maturation from April through August were undergoing FOM. Therefore, average spawning frequency was once every 2.3 days, or 80 times during the 6-mo spawning season.

Spawning frequency was also estimated from the percentage of females captured with ovaries containing postovulatory follicles (POF). An average of 13.1% of the females captured had ovaries which contained POF ranging from 12 hours to 2 days old. This would correspond to a spawning frequency of once every 7.6 days or 24 times during the spawning season.

Finally, the spawning frequency of four female *C. nebulosus* in the laboratory under conditions of controlled temperature and photoperiod were examined (Table 6). The fish spawned from 1 to 10 times each month for 17 months, an average of 17 spawns per individual over a 12-mo period (Table 6). This would correspond to a spawning frequency of once every 21 days.

TABLE 5.—Percentage of spotted seatrout spawning (RR) or undergoing final oocyte maturation (FOM) in South Texas. Data on spawning fish collected April 1982–May 1985. Data on fish undergoing FOM collected April 1984–May 1985.

	Spawning fish 1982–85			Fish undergoing FOM 1984–85			
Month	*N*	# RR	% RR	*N*	# FOM	% FOM	% RR
April	256	42	16	33	14	42	37
May	140	11	8	21	10	48	13
June	101	20	20	—	—	—	—
July	82	33	40	7	3	43	52
August	101	36	36	8	3	38	—
September	20	9	45	—	—	—	—
Mean			27.5			42.8	25.5

TABLE 6.—Number of spawns and average water temperature by month for four female spotted seatrout contained in a 30,000 L tank in Port Aransas, TX, under conditions of controlled temperature and photoperiod, July 1974–November 1975. Experimental procedures described in Arnold et al. (1976).

Month	Number of spawns	°C
July	8	26.75
August	7	26.75
September	4	26.0
October	6	25.5
November	4	24.5
December	8	24.0
January	9	23.5
February	10	24.0
March	10	24.0
April	3	25.75
May	1	25.0
June	0	22.0
July	6	25.75
August	2	25.0
September	2	23.0
October	9	23.5
November	10	24.0
Total	99	
Average: 17 spawns/ 12 months/ female		

DISCUSSION

Sexual Maturity and Spawning Season

Male spotted seatrout reached sexual maturity at a smaller size than females which appears to be a fairly common phenomenon in spotted seatrout throughout its range (see Mercer 1984 for a review). Both male and female spotted seatrout in South Texas reached sexual maturity at a size similar to that reported for other groups of *C. nebulosus* along the Gulf Coast (Moody 1950; Klima and Tabb 1959; Overstreet 1983) and at a smaller size than along the East Coast (Tabb 1961; Brown 1981).

Running ripe females were captured only between one hour before and two hours after sunset in South Texas, suggesting a high degree of synchrony in spawning fish. Collections of newly fertilized eggs during a $2\frac{1}{2}$-h period after sunset (Holt et al. 1985) provides supporting evidence for this spawning synchrony.

Both histological data and GSI values showed spotted seatrout have an extended spawning season in South Texas. Gonadal recrudescence began in January in male and in February in female spotted seatrout. Spawning commenced in April and continued until the end of September. Other studies of *C. nebulosus* along the Gulf and East coasts of the United States have also reported long spawning seasons (Mercer 1984). Additionally, other sciaenids have extended spawning seasons (Merriner 1976; White and Chittenden 1977; DeVries and Chittenden 1982; Love et al. 1984),

suggesting a prolonged spawning season is a common reproductive strategy among sciaenids living in temperate and subtropical waters.

The duration of the spawning season may be related to water temperature. Perhaps this apparent association with temperature is related to the viability and development of spawned spotted seatrout eggs. Twenty-three degrees may be the minimum temperature necessary for successful spawning, as indicated by both the failure to capture running ripe fish at lower temperatures and by data from spotted seatrout induced to spawn under laboratory conditions (Arnold et al. 1976; Table 6). However, since spawning ceased in September when water temperatures were well above 23°C, possibly a decrease in photoperiod in combination with a decrease in temperature provides the necessary cue for termination of spawning. Hein and Shepard (1979) suggested photoperiod may be an important regulating factor in *C. nebulosus* spawning. Data from laboratory-spawned spotted seatrout (Arnold et al. 1976) also support this speculation.

The seasonal pattern of mean GSI values during the spawning season was relatively consistent for both males and females over the $3\frac{1}{2}$-yr period, 1982–85 (Fig. 2). The bimodality of the female GSI data suggests the possibility of two peaks in spawning activity, although the timing of the second peak varies from year to year, thus demonstrating the need for several consecutive years of data. Bimodal spawning peaks have been previously reported for the species by Hein and Shepard (1979) in Louisiana, Stewart (1961) in Florida, and Brown (1981) in Chesapeake Bay, VA. However, mean GSI values should be used with caution when attempting to predict actual peaks in spawning activity (deVlaming et al. 1982).

Fecundity

Accurate annual fecundity measurements are difficult to determine for multiple spawning fishes with an extended spawning season. Methods of calculating annual fecundity from measurements of the total number of growing oocytes at the beginning of the spawning season (Bagenal 1966), or other approaches based on the total number of oocytes at the beginning of the spawning season minus egg retention at the end of the spawning season (Conover 1985), are inappropriate for multiple spawning species such as spotted seatrout which show continuous recruitment of oocytes during the reproductive season. Thus, the previous estimates of annual fecundity in spotted seatrout, which did not take continuous recruitment of oocytes into consideration and measured either total fecundity (Overstreet 1983) or fecundity of growing and vitellogenic oocytes (Sundararaj and Suttkus 1962), probably underestimated annual fecundity. Furthermore, BF has not previously been calculated for this species.

Although no monthly differences in BF were apparent (Table 4), sample sizes were too small to draw any definite conclusions from these data. The relatively low coefficient of determination (0.56) is similar to values reported by Conover (1985) for Atlantic silversides, *Menidia menidia*, another multiple spawning species. Perhaps a more accurate estimate of annual fecundity than previously reported for spotted seatrout can be obtained by multiplying BF by the number of spawns during the reproductive season. Unfortunately, as discussed later, estimates of spawning frequency vary considerably, so it is not possible to make an accurate estimation of the annual fecundity. However, available data indicate that average annual fecundity may be greater than 10 million eggs.

Multiple Spawning

Histological examination of the testes revealed that spermatogenesis ceased earlier in the central lobules, although they contained spermatozoa one-and-one-half months longer than the peripheral lobules. It is possible that the same central lobules act as storage areas for spermatozoa produced by the more spermatogenically active peripheral lobules during the second half of the spawning season, as suggested by Hyder (1969) for *Tilapia*. This may represent a strategy in multiple spawning fish with a prolonged spawning season that allows for a constant supply of spermatozoa while investing a minimal amount of energy into spermatogenesis.

Several lines of evidence indicate that female *C. nebulosus* also spawn several times during the reproductive season. The relatively high percentage of running ripe females, fish undergoing FOM and partially spent fish captured throughout the spawning season, and the absence of completely spent fish until the last third of the spawning season, suggest that an individual does not spawn all the vitellogenic eggs in the ovary at one time. Indeed, oocyte size-frequency analysis shows a continuous distribution of growing and

vitellogenic oocytes (Fig. 5) and fecundity estimates show that only about 15% of the growing oocytes undergo FOM prior to a spawn. Histological data shows that the percentage of vitellogenic oocytes in the ovary remains constant throughout the spawning season (Fig. 4), which suggests that new oocytes may be recruited into the vitellogenic phase as rapidly as mature oocytes are released. Convincing histological evidence of multiple spawning is the presence of postovulatory follicles (POF) from May through the end of September in ovaries containing many vitellogenic oocytes. Hunter and Goldberg (1980) characterized postovulatory follicles in laboratory-spawned *Engraulis mordax*, a multiple spawning fish, and found POF in all females that had spawned in the laboratory one or two days previously. Finally, laboratory studies also show that spotted seatrout are capable of multiple spawning under relatively constant environmental conditions (Table 6). Tucker and Faulkner (1987) also found that six female fish kept in raceways outdoors at the ambient summer temperature and photoperiod spawned repeatedly.

Spawning Frequency

It is especially difficult to determine the spawning frequency of wide-ranging, multiple-spawning marine fishes such as *C. nebulosus* that are not group-synchronous spawners. One method to estimate spawning frequency is to count the number of distinct batches of vitellogenic oocytes in the ovary (Shackley and King 1977). However, only one distinct batch of vitellogenic or hydrated oocytes can be distinguished in spotted seatrout ovaries at any one time (Fig. 5) and the reliability of this method has been questioned (deVlaming 1983). Therefore, three techniques were used to estimate spawning frequency in spotted seatrout.

Spawning frequency was estimated to be once every 3.6 days from the percentage of running ripe fish caught on the spawning grounds. Although this is probably an overestimate owing to sampling bias, the error may not be susbtantial, since the spawning grounds are also the feeding grounds for this species (Moody 1950) and many nonspawning individuals were captured. The time of sample collection did not significantly influence the estimate of spawning frequency. High spawning frequencies were also obtained (every 2.3 days) when fish were captured 6–12 hours prior to spawning and examined for signs of final oocyte maturation (Table 5). The spawning frequency of other sciaenids fishes has been estimated by this technique (DeMartini and Fountain 1981; Love et al. 1984). Additionally, Hunter and Macewicz (1985) suggested that this method produces a useful first approximation of spawning frequency.

The proportion of fish having POF in the ovary has also been used to determine spawning frequency (Hunter and Goldberg 1980; Alheit et al. 1984; Hunter and Macewicz 1985). Spotted seatrout were found to have POF throughout the spawning season, although the age of the POF was often difficult to determine. Furthermore, detailed laboratory studies have not been undertaken to accurately age POF in spotted seatrout. However, the once a week estimate of spawning frequency obtained using this method is similar to spawning frequencies reported for two other sciaenids, the queenfish, *Seriphus politus*, (DeMartini and Fountain 1981) and the white croaker, *Genyonemus lineatus*, (Love et al. 1984). Spawing frequency estimates from POF are probably more reliable than estimates based on the number of spawning fish since sampling bias is less likely to occur when capturing fish with POF.

Another method used to quantify spawning frequencies in various species is direct observation of spawning in the laboratory or in "controlled" field situations, such as impoundments (Gale and Deutsch 1985; Hubbs 1985; Heins and Rabito 1986). Spotted seatrout spawned an average of once every three weeks per individual under controlled temperature and photoperiod in the laboratory (Table 6). Tucker and Faulkner (1987) found that six female spotted seatrout kept outdoors at ambient temperature and photoperiod averaged one spawn per individual every 2.3 weeks. The same spawning frequency was noted for an individual female, although that same individual later spawned three times in four days (Tucker and Faulkner 1987). Thus, spotted seatrout appear to be capable of the high spawning frequencies estimated from field-caught fish with hydrated ovaries, although this frequency is probably not sustained throughout the entire spawning season. In general, the spawning frequencies in both laboratory studies are lower than those estimated from actual spawning fish in the field. However, it is unclear whether this is due to an overestimation of spawning frequency in the field or to a decline in spawning frequency owing to confinement in the laboratory.

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