Reproductive biology of red drum, *Sciaenops ocellatus,* from the neritic waters of the northern Gulf of Mexico*

Charles A. Wilson
David L. Nieland
Coastal Fisheries Institute, CCEER
Wetland Resources Building, Louisiana State University
Baton Rouge, LA 70803-7503

Abstract.—The reproductive biology of red drum, *Sciaenops ocellatus*, in the northern Gulf of Mexico is described from examination of 3,351 specimens sampled from March 1986 through September 1992. The sex ratio of the spawning population, as manifest in purse seine collections, was essentially 1:1. Gonosomatic indices and ovarian histology demonstrated an 8-9 week spawning season from mid August to early October. Both sexes achieved >50% maturity at age 4; however, at 50% maturity males were somewhat smaller than females (660–670 mm vs. 690–700 mm, 3.4–3.5 kg vs. 4.0–4.1 kg). Simultaneous observations of oocytes in all stages of maturation throughout the spawning seasons confirmed group-synchronous oocyte maturation and multiple batch spawning. Batch fecundity of 51 females (age 3–33 yr) ranged from 0.16 million to 3.27 million ova per batch (mean=1.54 million ova) and was positively correlated with fork length, gonad-free body weight, eviscerated body weight, and age. Seasonal spawning frequencies estimated from the proportion of mature females with postovulatory follicles varied widely from once every 3 days to once every 80 days. More plausible spawning frequencies (2–4 d) were obtained if proportions of females exhibiting oocyte yolk coalescence and oocyte hydration, indicative of imminent spawning, were included in estimates of this variable.

Manuscript accepted 18 March 1994.
Fishery Bulletin 92:841–850.

Red drum, *Sciaenops ocellatus* (family: Sciaenidae), has been a prime target species for both recreational and commercial fishermen in the northern Gulf of Mexico. As conflicts over allocation of a purportedly declining population escalated in the mid 1980's, management of the red drum offshore spawning stock became an imperative. However, basic to the formulation of any management strategy is the need for sound biological information, including the various aspects of the species' reproductive biology. Most of the literature on red drum reproduction (see Murphy and Taylor [1990] for a review) has been derived from studies of juveniles and itinerant adults in estuarine waters. Little is known of the reproductive biology of adult "bull" red drum that assemble into large schools in the northern Gulf and constitute the spawning stock for the species in this area.

Overstreet[1] first reported on various aspects of the biology, including reproduction, of schooling red drum based on specimens gathered from the purse-seine fishery for the species. Fitzhugh et al. (1988) added to this body of knowledge by describing ovarian development in specimens similarly taken from the purse-seine fishery. They further provided the first documentation of feral red drum as group synchronous, batch spawners (Wallace and Selman, 1981) in which clutches of newly matured ova are spawned periodically throughout the spawning season. Thus all previous estimates of red drum fecundity in the wild, based on numbers of vitellogenic oocytes present in the ovary, were rendered invalid.

The present study is a continuation and an expansion of the work begun by Fitzhugh et al. (1988) and was undertaken in conjunction with two studies of red drum age and growth (Beckman et al., 1988; Wilson et al.[2]). Our specific objectives were 1) to verify the sex ratio of the spawning population; 2) to ascertain the duration of the spawning season; 3) to determine age, length, and weight at sexual maturity; and

---

*Contribution LSU-CFI-93-4 of the Coastal Fisheries Institute, CCEER, Louisiana State University.

[1] Overstreet, R. M. 1983. Aspects of the biology of the red drum, *Sciaenops ocellatus*, in Mississippi. Gulf Res. Rep. (Suppl. 1), p. 45–68. Gulf Coast Res. Lab., Ocean Springs, MS.

[2] Wilson, C. A., D. L. Nieland, and A. L. Stanley. 1993. Variation of year-class structure and annual reproductive output of red drum *Sciaenops ocellatus* and black drum *Pogonias cromis* from the northern Gulf of Mexico. Final Report for 1991–1992 to U. S. Department of Commerce, Marine Fisheries Initiative (MARFIN) Program, NA90AA-H-MF724. LSU-CFI-93-3, 37 p. and 16 figs.

4) to estimate batch fecundity and spawning frequency of red drum from the neritic waters of the northern Gulf of Mexico.

Methods and materials

Red drum were sampled in the neritic waters of the northern Gulf of Mexico (Mobile Bay, Alabama westward to Galveston Bay, Texas) from March 1986 through September 1992, a period spanning seven spawning seasons. Various aspects of the reproduction of those specimens taken from March 1986 through November 1986 have been previously reported by Fitzhugh et al. (1988). The availability of red drum during this study was sporadic and generally limited by federal and state restrictions on both the commercial and recreational fisheries in the Gulf of Mexico. Although the vast majority of specimens were taken by purse seine, the strategies used to locate red drum schools for capture varied among years. Prior to the closure of the Exclusive Economic Zone to all red drum harvest in 1986, specimens came from the commercial purse-seine fishery. Red drum collected from July 1986 through 1988 were taken concurrently with a National Marine Fisheries Service tag-recapture investigation. Their methodology simulated a commercial purse-seine fishery and used spotter airplanes to locate schools at the surface. Since August 1989 most red drum were taken incidentally in the directed purse-seine harvest of blue runner, *Caranx chrysos,* detected visually at the surface.

The above samples were supplemented with specimens from sportfishing tournaments, from incidental catches of vessels targeting snappers (Lutjanidae), and from gillnet and haul-seine catches. These sources were sampled as circumstances allowed to permit tracking of ovarian development and gonosomatic indices during those months when specimens taken by purse seine were not available.

Protocols for the collection of morphometric data (fork length [FL] in mm, total weight [TW] in kg, eviscerated body weight [BW] in kg), processing of ovaries for histological examination, and enumeration of oocyte maturation stages from histological slides (Wallace and Selman, 1981; Fitzhugh et al., 1988) are given in Nieland and Wilson (1993). Histological slides were also scanned for the presence of yolk coalescence, and for postovulatory follicles and atretic follicles. Ages of individuals were estimated from sagittal otoliths as described in Beckman et al. (1988). Their methodology assumed a biologically reasonable hatching date of 1 October; however, for our purposes age estimates were calculated with 1 August as the arbitrary red drum hatching date. This modification allows all members of a cohort to be assigned the same integer year age.

Sexual maturity of females captured during the spawning season was defined as the progression of oocyte maturation to vitellogenesis (Brown-Peterson et al., 1988; Nieland and Wilson, 1993). Milt flow from the central lumen of the testes produced by gentle squeezing indicated sexual maturity in males similarly taken during the spawning season (Pearson, 1929; Brown-Peterson et al., 1988; Murphy and Taylor, 1990; Nieland and Wilson, 1993).

Only those red drum females captured by purse seine were included in calculations of spawning frequency and batch fecundity. Batch fecundity was estimated gravimetrically from fresh ovarian weights for 51 females exhibiting overt macroscopic and microscopic hydration of oocytes with the hydrated oocyte method (Hunter and Goldberg, 1980; Hunter et al., 1985). Seasonal spawning frequencies were estimated with two different methods after examination of 572 ovaries collected during the spawning seasons. The postovulatory follicle method (Hunter and Goldberg, 1980; Hunter and Macewicz, 1985; Hunter et al., 1985; Brown-Peterson et al., 1988; Nieland and Wilson, 1993) uses the number of mature females with postovulatory follicles to determine a spawning fraction or that proportion of the female spawning population that spawned the previous day. The inverse of the spawning fraction, the spawning frequency, is the average number of days over which each reproductively active female will spawn once. The spawning frequency estimates of Fitzhugh et al. (1993), referred to as the "time-calibrated" method, are based on a time-course of final oocyte maturation for black drum, *Pogonias cromis,* and another sciaenid species, the spotted seatrout, *Cynoscion nebulosus,* (Brown-Peterson et al., 1988). This methodology calculates proportions of day-0 females (imminent spawners evidenced by oocyte yolk coalescence or hydration) and day-1 spawners (previous spawners evidenced by postovulatory follicles) in the female spawning population. The average of the proportions of day-0 and day-1 females yields a spawning fraction which is inverted to produce spawning frequency as defined above. Note that females spawning on consecutive days will be classified as both day-0 and day-1 individuals. Also those females evidencing oocyte atresia states 2 (atresia of ≥50% of vitellogenic oocytes) and 3 (atresia of 100% of vitellogenic oocytes) (Fitzhugh et al., 1993) were not included in either estimate of spawning frequency. Both conditions, usually encountered at the end of the spawning season, indicate a zero probability of future spawning and an effective exit from the spawning population (Hunter and Macewicz, 1985).

The temporal persistence of postovulatory follicles in red drum ovaries was investigated in two captive red drum that were induced to spawn by means of photoperiod manipulation and gonadotropin injection (Nieland, Wilson, and Thomas, unpubl. data). Postovulatory follicles at 16-hour postspawning showed definite signs of degeneration, yet were recognizable as such and resembled those seen in many wild caught females. However, postovulatory follicles at 24-hour postspawning were extremely degenerate and had assumed an aspect much like that of an atretic follicle. Such a condition was rare in feral specimens; thus, all identifiable red drum postovulatory follicles were assumed to be less than 24 hours old. Postovulatory follicles seen in histological material were classified as early, late, or very late based on their degree of degeneration.

Relative investment of energy to reproduction of red drum was assessed with gonosomatic indices (GSI) calculated as GSI = (gonad weight/BW) × 100 (Nieland and Wilson, 1993). Calculations of mean monthly GSI exclude immature individuals of both sexes (Wilk et al., 1990; Nieland and Wilson, 1993). Because the increase in ovary mass, which occurs concomitantly with oocyte hydration, does not reflect energy to be expended in reproduction, females with hydrating oocytes were also excluded from calculations of mean monthly GSI. The Statistical Analysis System (SAS Institute Inc., 1985) was used for analysis of variance (ANOVA), maximum-likelihood analysis (PROBIT), and linear regression (GLM). Significance level for statistical analyses was 0.05 unless indicated otherwise.

Results

A total of 3,351 red drum (1,585 males, 1,765 females) were sampled for reproductive analysis. Of these, both the intact gonad weight and BW necessary for calculation of GSI were available for 2,859 mature and 341 immature specimens. Data on ovarian histology were compiled for 1,379 mature females and 123 immature females. Age at time of capture for 3,316 red drum for which otoliths were available ranged from 1 to 36 years for males and from 1 to 39 years for females. Proportions of the younger age classes were particularly high during our 1992 sampling when 327 of 504 individuals were age 6 or less. Total weight and FL ranges among all specimens were 0.7–19.2 kg and 399–1,115 mm, respectively.

Sex ratio

Sex ratios for red drum were highly variable among source and gear categories and between mature and immature individuals within these categories (Table 1). Among all specimens and all mature specimens, females were predominant; however, immature males exceeded immature females in number by two to one. Females also outnumbered males among all mature individuals taken by sportfishing, among mature individuals caught incidentally with lutjanids, and among those captured with haul seine. Conversely, males were more common among all purse-seine specimens, all immature specimens, and immature specimens taken by all methods except for sportfishing. Sex ratios were not statistically different from 1:1 for all mature red drum captured with purse seines, for all taken incidentally with lutjanids, and for those caught in gill nets.

Seasonality

Gonosomatic indices and ovarian histological data indicated a potential 8–9 week red drum spawning season beginning in mid August and extending into October. Minimal GSI values for mature individuals were found from January to July, averaging 0.26 for males and 0.81 for females during these months (Fig. 1). Abrupt escalation of male and female GSI in August signalled potential, if not certain, spawning activity. Maximum GSI values were achieved in September followed by a return to near minimum levels

Table 1

Number of specimens sampled by sex and sex ratios for all, mature, and immature red drum collected in the northern Gulf of Mexico from March 1986 through September 1992 by source or gear of capture. No immature individuals were taken by haul seine or gill net.

Source or gear	Females	Males	Sex ratio (Female:Male)
All sources and gears	1,766	1,585	1:0.90
Mature	1,642	1,364	1:0.83
Immature	124	221	0.56:1
All purse seine	1,247	1,362	0.92:1
Mature	1,152	1,212	0.95:1*
Immature	95	150	0.63:1
All sportfishing	383	102	1:0.27
Mature	369	87	1:0.24
Immature	14	15	0.93:1*
All incidental with lutjanids	54	69	0.78:1*
Mature	39	13	1:0.33
Immature	15	56	0.27:1
Haul seine	43	11	1:0.26
Gill net	39	41	0.95:1*

* Not significantly different from 1:1 (chi-square test, df=1, $P<0.05$).

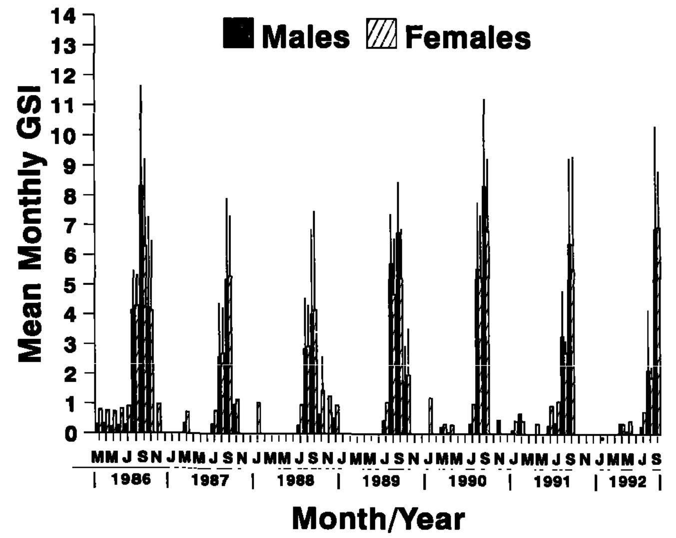

Figure 1

Mean monthly gonosomatic indices for mature male (n=1,306) and female (n=1,553) red drum from the northern Gulf of Mexico. Sample sizes for months during which red drum were available varied from 1 to 110 for males and from 1 to 183 for females. Absence of vertical bar for either sex indicates that no specimens were sampled during the month and year indicated below. Narrow vertical bars at tops of GSI bars indicate +1 standard deviation (SD) from mean value (plotted only for those months when SD>0.5).

in October. Our data, collected over more than six years, demonstrated a single annual GSI maximum (ranging from 4 to 8) in each sex.

Red drum ovarian tissues undergo an annual cycle of oocyte maturation and recrudescence coincident with the female GSI cycle. Over the entire study duration, oogonia and primary growth oocytes were present in varying numbers in all ovary samples but were virtually ubiquitous from January through June (Fig. 2). Recrudescence and maturation of primary growth oocytes to the cortical alveoli and vitellogenic stages, indicative of preparation for spawning, was seen in July. Maximum numbers of maturing vitellogenic and mature hydrated oocytes were found during August and September. Declines in numbers of cortical alveolar and vitellogenic oocytes and concomitant increases in numbers of primary growth oocytes occurred in October suggesting the cessation of spawning activity at this time. Although we have few data from November and December, primary growth oocytes are assumed to constitute nearly 100% of the oocyte population during these months.

Among all spawning seasons, the onset of spawning activity, evidenced by the first observation of yolk coalescence (late vitellogenesis) or postovulatory follicles in ovarian histological samples, ranged from 14 August to 18 August. Atretic states 2 and 3, indicative of cessation of spawning, became increasingly common from late September through early October. When we were able to extend our sampling in 1987 and 1988, 100% atresia of vitellogenic oocytes was realized by the end of October indicating completion of spawning at this time.

Age, length, and weight at maturity

The onset of sexual maturity in both male and female red drum in the northern Gulf of Mexico is variable with respect to age. Estimates of percent maturity at age are comparable and increase at much the same rate for both sexes, the only major discrepancies occurring at age 2 and age 5 (Table 2). Greater than 50% maturity is achieved in both sexes at age 4. All males and all females are mature at age 5 and age 6, respectively.

Sexual maturity in red drum is similarly unrelated to size of the individual (Table 2). Fork length and TW minima among mature female red drum were 598 mm (age 4, 4.18 kg) and 3.43 kg (age 3, 675 mm). Maximum-likelihood analysis (PROBIT analysis, Murphy and Taylor, 1989) of 10 mm increments and of 0.10 kg increments indicated 50% maturity is achieved at 690–700 mm and 4.00–4.10 kg. All females greater than 810 mm and 6.10 kg were mature.

Male red drum from the northern Gulf of Mexico mature at somewhat lesser length and weight than do females; however, sex-specific percent maturities at size become roughly equivalent at 750–700 mm and 5.00–5.49 kg (Table 2). Fork length and TW minima for mature males were 593 mm (age 5, 2.56 kg) and 2.35 kg (age 2, 615 mm). Fifty percent maturity (maximum-likelihood analysis as above) occurred at 660–670 mm and 3.40–3.50 kg and all males greater than 810 mm and 5.40 kg had matured.

We observed no instances of decreased or arrested gonadal development among older individuals. Red drum of both sexes appear to be fully capable of reproductive activity from the onset of maturity until death.

Batch fecundity

Fitzhugh et al. (1988) reported significant ovarian location effects in their estimates of red drum batch fecundity. To test the precision of our estimates within individuals, replicate samples (30–60 mg) of ovarian tissue from each of six ovarian regions (anterior, medial, and posterior of both right and left lobes) were removed from six hydrated females captured

26 September 1988. Numbers of hydrated oocytes per gram of ovarian tissue were calculated for each sample (n=72). Nested ANOVA showed significant variation only among individuals; no location effects were demonstrated (Table 3). All individual batch fecundities herein are means of estimates made from three different randomly selected regions as defined above.

Batch fecundity estimates were generated for a combined sample of 51 red drum captured by purse seine during the 1986 (previously reported by Fitzhugh et al. (1988)), 1987, 1988, 1989, and 1991 spawning seasons. All displayed overt macroscopic and microscopic manifestations of oocyte hydration throughout the length and diameter of the ovarian lobes and were captured during the late afternoon or early evening hours (1600–1900 h). No sufficiently hydrated females were encountered in 1990 and 1992.

Age, FL, batch fecundity ranges, and numbers of hydrated specimens examined by year of capture are given in Table 4. Regression analyses of batch fecundity against FL (r^2=0.58), gonad-free body weight (r^2=0.46), age in year (r^2=0.43), and BW (r^2=0.43) are of reasonable predictive value (Fig. 3). Significant positive relations (P>0.0001) were indicated between batch fecundity and nontransformed values of the four independent variables. The relatively low r^2 values for the regressions appear to result from individual varia-

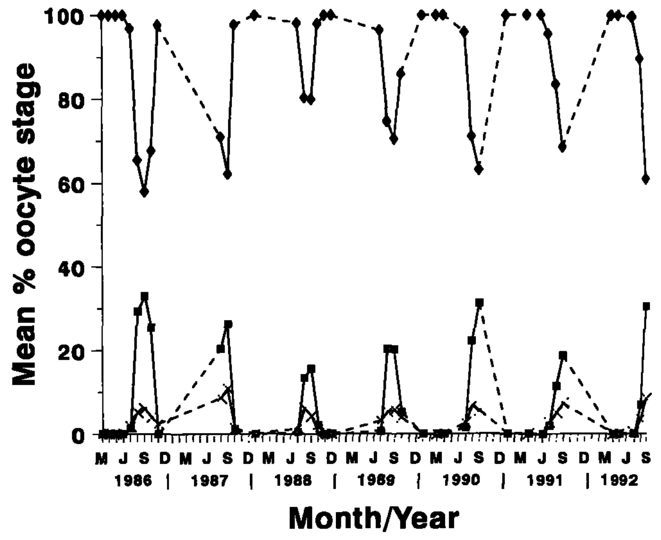

Figure 2

Monthly mean percent occurrence of primary growth (diamonds), cortical alveoli (crosses), and vitellogenic (squares) oocytes in ovaries of red drum from the northern Gulf of Mexico. Total sample size is 1,379; for months during which female red drum were available, sample size ranged from 1 to 160. Dashed lines span months during which specimens were unavailable. Ranges of standard deviations (SD) during August–October were 3.4–18.3 for primary growth oocytes, 0.0–3.4 for cortical alveoli oocytes, and 2.2–13.1 for vitellogenic oocytes.

Table 2

Percent maturity and numbers sampled (in parentheses) of female and male red drum at age, fork length, and total weight. Specimens included are those taken by all gears during August through October of 1986–1991 and August and September 1992. Total sample sizes are 1,262 females and 1,137 males.

Class	Female	Male
Age (years)		
1	0 (0)	0 (0)
2	0 (8)	13 (24)
3	28 (81)	30 (148)
4	71 (75)	73 (88)
5	88 (68)	100 (77)
≥6	100 (1,011)	100 (787)
Fork length (mm)		
<550	0 (7)	0 (15)
550–599	8 (13)	8 (25)
600–649	0 (26)	22 (68)
650–699	24 (42)	48 (82)
700–749	82 (65)	91 (98)
Fork length (mm)		
750–799	95 (129)	97 (178)
800–849	99 (216)	99 (280)
≥850	100 (764)	100 (391)
Total weight (kg)		
<3.00	0 (45)	13 (96)
3.00–3.49	8 (24)	35 (54)
3.50–3.99	33 (18)	60 (40)
4.00–4.49	75 (28)	84 (31)
4.50–4.99	83 (23)	90 (52)
5.00–5.49	94 (33)	97 (39)
5.50–5.99	95 (60)	100 (55)
6.00–6.49	98 (59)	100 (79)
≥6.50	100 (963)	100 (678)

tion within classes. Exclusion from the regression analyses of those specimens captured during October, based on the possibility of declining output toward the end of the spawning season as suggested by Fitzhugh et al. (1988), produced r^2 values ranging from 0.23 to 0.39.

Table 3

Nested analysis of variance on numbers of hydrated oocytes per gram ovary weight among ovarian regions (six total-three per lobe), between ovarian lobes (right and left), and among six female red drum captured 26 September 1988 from the northern Gulf of Mexico. MS=mean square.

Source of Variation	df	MS	*F*-value	*P*>*F*-value
Individuals	5	42,580,790	69.86	0.0001
Lobes	6	242,773	0.33	0.9155
Ovarian regions	24	2,290,678	0.78	0.7318
Error	36	4,266,679		
Total	72	49,380,920		

Table 4

Age, fork length (FL), and batch fecundity (BF) ranges for red drum *Sciaenops ocellatus* from the northern Gulf of Mexico by year of capture. *n*=number of specimens.

Year	*n*	Age range (yr)	FL range (mm)	BF range (ova × 10^6)
1986	8	6–21	800–964	0.75–2.54
1987	2	20–33	933–1005	1.65–1.67
1988	6	9–30	820–950	1.87–3.22
1989	23	3–24	697–999	0.16–3.27
1990	0	—	—	—
1991	12	5–25	760–924	0.57–3.13
1992	0	—	—	—
Total	51	3–33	697–1005	0.16–3.27

Table 5

Comparison of red drum seasonal spawning frequencies (SF, expressed as average days between successive spawnings) estimated with the postovulatory follicle (POF) method of Hunter and Macewicz (1985) and the time-calibrated (TC) method of Fitzhugh et al. (1993). Day-0 females are those evidencing yolk coalescence or hydration of oocytes; day-1 females are those with postovulatory follicles from previous day's spawning. All specimens collected by purse seine from 13 August through 8 October.

		POF method		TC method		
Year	Mature females	Females with POF	SF	Day-0 females	Day-1 females	SF
1986	39	14	2.8	24	14	2.1
1987	79	17	4.6	36	17	3.0
1988	155	14	11.1	65	14	3.9
1989	91	17	5.4	36	17	3.4
1990	57	1	57.0	28	1	3.9
1991	80	1	80.0	51	1	3.1
1992	71	1	71.0	2	1	47.3
Total	572	65	8.8	242	65	3.7

Spawning frequency

Red drum spawning frequencies estimated with the postovulatory follicle method were highly variable among years (Table 5) ranging from one spawning event every 2.8 days in 1986 to one spawn every 80.0 days in 1991. A total of 65 of 572 sexually mature females captured during the 1986–1992 spawning seasons evidenced postovulatory follicles for a seven season average spawning frequency of 8.8 days. Spawning frequencies calculated with the time-calibrated method (Table 5) showed less variation and gave more plausible estimates. Except for the 1992 spawning season, when sampling was limited to three dates during the spawning season (28 August, 3, 12 September), spawning frequencies of one spawn every 2–4 days were predicted.

Discussion

Aspects of red drum reproductive biology in the Gulf of Mexico have been variously inferred from visual observation of gonadal development, from larval and juvenile abundances and lengths, and from histological documentation of ovarian development. Given both the disparities and subjectivity inherent among, and even within, these methodologies and the expanse of the Gulf of Mexico, it is not surprising that published accounts of red drum reproduction vary widely and, perhaps, geographically. We agree with West (1990) that histological methods produce the most accurate and most reliable results in assessing ovarian development and predicting reproductive variables. We also stress that our findings should not be broadly applied to red drum populations throughout the Gulf of Mexico.

The sex ratio of the 2,364 mature individuals taken by purse seine is undoubtedly most reflective of the offshore spawning stock of red drum in the northern Gulf of Mexico. Given that most of our specimens taken by purse seine were captured either just prior to or during the spawning season and considering the substantial sample size, our data establish a 1:1 sex ratio in schools of prespawning and spawning red drum. This supports

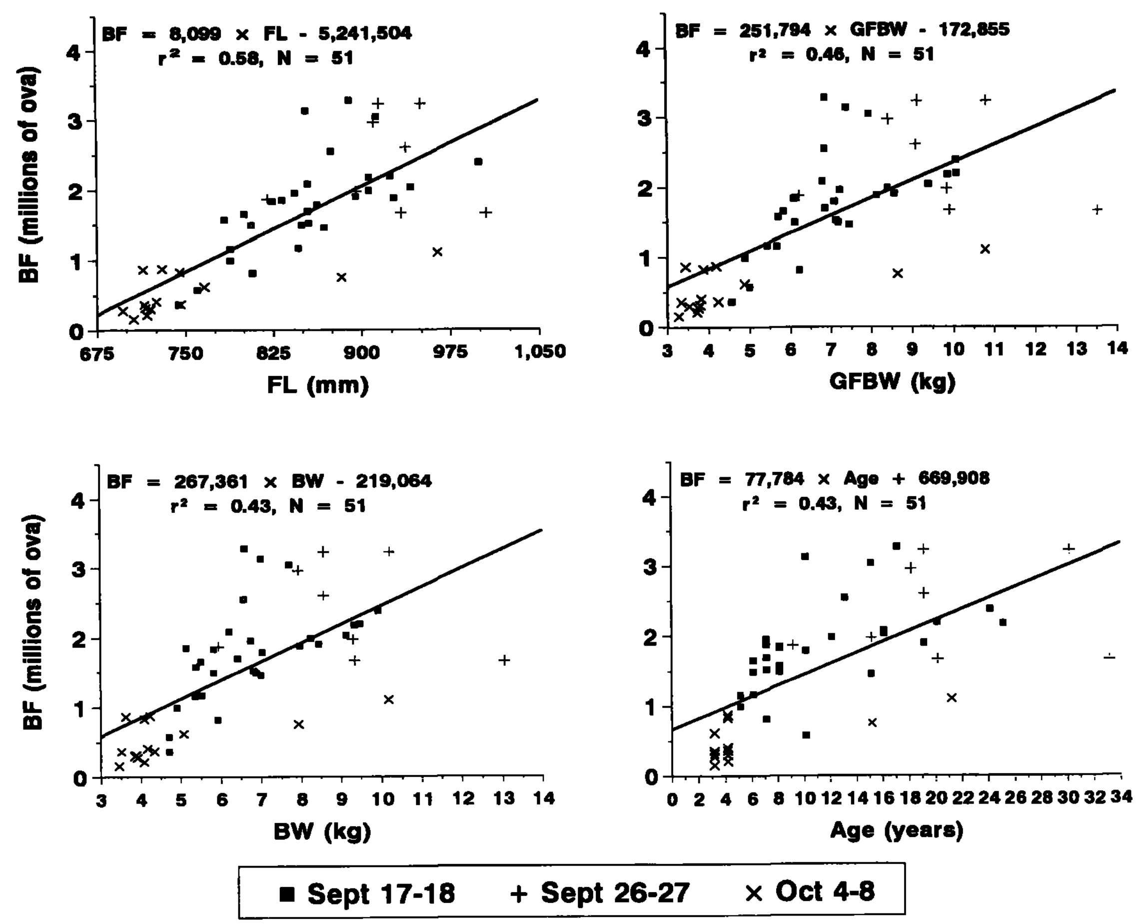

Figure 3

Regressions of eviscerated body weight (BW), fork length (FL), gonad-free body weight (GFBW), and age versus estimated batch fecundity for red drum from the northern Gulf of Mexico. Squares denote specimens captured on 17 September 1986 and 18 September 1991, pluses on 26 September 1988 and 27 September 1987, and crosses on 4 October 1989 and 8 October 1986. *n*=total sample size.

and further validates the use of a 1:1 ratio by Comyns et al. (1991) in their estimation of red drum spawner biomass in the north-central Gulf of Mexico.

For immature red drum, males significantly outnumbered females across all source and gear categories except among the few specimens randomly encountered at sportfishing tournaments. This numerical dominance of immature male red drum in offshore waters may indicate a predisposition for emigration from estuarine habitats at younger age than females which is reflected in the somewhat lesser age and size at maturity seen in males.

Previous accounts of red drum seasonality in the northern Gulf of Mexico have relied on inferences drawn from postspawning capture of larvae and juveniles and, to a lesser extent, from visual assessment of ovaries and testes. The red drum spawning season has been variously estimated with these methodologies as September to December (Boothby and Avault, 1971), August to November (Sabins, 1973), and from early September to early October (Comyns et al., 1991). However, our delineation of a mid-August to early October red drum spawning season is in accord with other studies that used histological techniques. Within our study area, analyses of red drum oocyte maturation by Overstreet[1] in Mississippi and by Fitzhugh et al. (1988) in Louisiana both demonstrated that red drum spawning is initiated in August and continues into October. Murphy and Taylor (1990) found spawning red drum from August to mid-November 1981 and from August to mid-October 1982 in the Tampa Bay, Florida area. The concordance among these estimates, drawn objectively and directly from histological data, demonstrates the effectiveness of this technique in assessing onset and duration of spawning seasons.

Determining the combination of environmental factors which are the impetus for an August-October red drum spawning season is beyond the scope of this study. However, temperature data gathered at a weather buoy located approximately 28 km south of Biloxi, MS (lat. 30.1°N, long. 88.8°W) indicate that seasonal mean sea surface temperatures ranged from 27.3° to 28.8°C and that daily mean sea surface temperatures varied from 23° to 31°C during periods of active spawning (National Climatic Data Center, Asheville, North Carolina). Similar temperatures have proven to be optimal in the spawning, hatching, and rearing of red drum in the laboratory (Arnold et al., 1977; Roberts et al., 1978; Holt et al., 1981; Arnold, 1988; Henderson-Arzapalo, 1992).

Estimates of age and size at maturity for red drum in the Gulf of Mexico, based largely on visual assessment of gonadal development, show extensive variation. In his study of red drum in Texas waters, Pearson (1929) perhaps originated the long held and widely applied belief that few red drum of either sex mature either before age 5 or before attaining 10 lb (4.5 kg) and 700 mm. Among red drum populations in Texas waters, maturity has been reported at 425 mm (Gunter, 1950), 625 mm (Miles[3]), age 4 and 29.5 inches (750 mm) (Miles[4]), and age 3 to 5 (Holt et al., 1981). For red drum off Mississippi, Overstreet[1] provided only a tabular compilation of the relation between standard length (SL) and gonad maturity stages. These data were interpreted by Murphy and Taylor (1990) to show 50% maturity in both sexes at about 700 mm SL. Murphy and Taylor also presented maturity schedules, which were based on histology of ovaries and testes and gross appearance of each, for red drum in Florida waters. They found fifty-percent maturity of males at 529 mm FL and all males mature at age 3; among females 50% and 100% maturity occurred at 825 mm FL and 6 years, respectively.

Given the maturity data cited above and that of the present study, one might infer the existence of geographical variation in maturity schedules among red drum populations in the Gulf of Mexico. We decline to discount this possibility. However, we suggest that differences in methods of maturity assessment and disparate definitions of maturity, especially in females, confound comparisons. West (1990) reviewed methods of assessing ovarian development in fishes and concluded that histology, though less efficient in both cost and time, is less subjective than, and preferable to, other methodologies.

For the purposes of the present study, we defined maturity in male red drum as the flow of milt from the central lumen of the testis during the August–October spawning season. The use of this subjective definition may account for some of the discrepancy in male maturity schedules between our study and that of Murphy and Taylor (1990).

However, for assessment of the maturity schedule of female red drum in the northern Gulf we employed a histologically objective benchmark definition: the presence of vitellogenic oocytes in the ovaries of individuals captured during the spawning season. Murphy and Taylor (1990) considered as mature only those females of class 4 (late vitellogenesis) or greater among their eight female reproductive classes in estimating an 825 mm FL at 50% maturity. This necessitated the categorization of out-of-season females (their class 2) and of in-season females evidencing early vitellogenesis (their class 3) as immature. The former would not have been included in our analysis of female maturity; the latter would have been classified as mature under our definition which precludes judgments between early and late vitellogenesis. A cautious re-interpretation of the tabular data in Overstreet[1] would yield greater than 50% maturity of females at 550–699 mm SL rather than the >700 mm SL as stated by Murphy and Taylor (1990). Applying our definition of maturity to Murphy and Taylor's data would perhaps produce a length at 50% maturity more in line with our estimate of 690–700 mm FL.

Group-synchronous maturation of oocytes (Wallace and Selman, 1981) and multiple, or batch, spawning has been demonstrated in several species of sciaenid fishes, including red drum (Fitzhugh et al., 1988). Among these are queenfish, *Seriphus politus* (DeMartini and Fountain, 1981); black croaker, *Cheilotrema saturnum* (Goldberg, 1981); white croaker, *Genyonemus lineatus* (Love et al., 1984); spotted seatrout (Brown-Peterson et al., 1988); and black drum (Fitzhugh et al., 1993; Nieland and Wilson, 1993). For these and other such species, the standing crop of oocytes of some arbitrary size or of vitellogenic oocytes gives little indication of the individual's seasonal fecundity. Rather fecundity is indeterminate and is the result of clutches of oocytes matured and spawned periodically over the length of the spawning season. Thus any estimate of seasonal fecundity must consider the length of the spawning season, the number of ova released in each spawning event (batch fecundity), and the periodicity of these spawning events (spawning frequency).

---

[3] Miles, D. W. 1950. The life histories of the spotted sea trout, *Cynoscion nebulosus*, and the redfish, *Sciaenops ocellatus*. Annu. Rep. (1949–1950), Tex. Game and Fish Comm. Mar. Lab., p. 66–103. Tex. Parks and Wildl. Dept., Austin.

[4] Miles, D. W. 1951. The life histories of the sea-trout, *Cynoscion nebulosus*, and the redfish, *Sciaenops ocellatus*: sexual development. Annu. Rep. (1950–1951), Tex. Game and Fish Comm. Mar. Lab., 11 p., 2 figs., and 3 tables. Tex. Parks and Wildl. Dept., Austin.

Prior to the confirmation of batch spawning in feral red drum by Fitzhugh et al. (1988), fecundity of wild caught specimens had been variously estimated as 0.5–3.5 million ova per season (Pearson, 1929; Holt et al., 1981; Miles[5]). Much greater potential fecundities (up to 94.5 million), based on volumetric and gravimetric estimates of oocytes available for spawning, were presented by Overstreet[1]. This potential for an immense seasonal reproductive output in wild red drum has been demonstrated in the laboratory where specimens have been manipulated to produce repeatedly a few hundred thousand to millions of ova per spawning event (Arnold et al., 1977; Roberts et al., 1978; Anonymous, 1979; Arnold, 1988). Other than the batch fecundity estimates for feral red drum presented by Fitzhugh et al. (1988) and those herein, only one other estimate has appeared in the literature. Comyns et al. (1991), from our data for September of 1986, 1987, and 1988, used a mean batch fecundity of 2.128 million ova in their computations of red drum spawner biomass in the north-central Gulf of Mexico.

Our seasonal estimates of spawning frequency are the first to be presented for red drum in the wild. Those seasonal frequencies (3–5 d) calculated for 1986, 1987, and 1989 with the postovulatory method and those (2–4 d) calculated for 1986–1991 with the time-calibrated method are believed to be most representative of the spawning population as similar spawning frequencies have been observed in the laboratory (Arnold et al., 1977; Arnold, 1988). However, spawning frequency is likely not constant over the course of the spawning season. Within-season spawning peaks coinciding with the new and full moon have been postulated by Peters and McMichael (1987) and Comyns et al. (1991) based on larval abundances. The irregularity of our sampling precluded our investigation of this phenomenon.

Given an 8–9 week spawning season, a mean batch fecundity of 1.54 million ova, and a spawning frequency of 2–4 days, an average red drum female could be expected to spawn some 20–40 million ova per season. Among sciaenid species, this estimate of annual fecundity is exceeded only by that of the black drum, a species of similar size which has an annual fecundity of 35–45 million ova (Nieland and Wilson, 1993). Females of both species are potentially long-lived (30–35 yr) and, thus, might produce up to a billion of ova during their lifetimes.

Acknowledgments

The authors gratefully acknowledge Daniel Beckman, Gary Fitzhugh, Brigitte Nieland, Robert Parker, Louise Stanley, Bruce Thompson, a host of graduate students and student workers, and personnel of the National Marine Fisheries Service for their assistance in field sampling. Phillip Horn, Ralph Horn, Harlon Pearce, and numerous fishing tournament organizations generously allowed us access to and use of their facilities. We especially thank Paul Morse, Jim Reahard, Jimmy Reahard, and the crews of the fishing vessels *Captain Grumpy* and *Mistake* for their help and hospitality. Permits for possession and transport of red drum, logistical and moral support were provided by the National Marine Fisheries Service, Louisiana Department of Wildlife and Fisheries, and Mississippi Bureau of Marine Resources. Major sources of funding for this research were the U.S. Department of Commerce Marine Fisheries Initiative (MARFIN) Program and the Louisiana Sea Grant College Program, a part of the National Sea Grant College Program administered by the National Oceanic and Atmospheric Administration, U. S. Department of Commerce. The Louisiana Sea Grant College Program is also supported by the State of Louisiana.

Literature cited

Anonymous.
1979. Redfish spawn produces 11.4 million fry. Texas Parks Wildl. 37(7):15.

Arnold, C. R.
1988. Controlled year-round spawning of red drum *Sciaenops ocellatus* in captivity. Contrib. Mar. Sci., Suppl. to vol. 30:65–70.

Arnold, C. R., W. H. Bailey, T. D. Williams, A. Johnson, and J. L. Lasswell.
1977. Laboratory spawning and larval rearing of red drum and southern flounder. Proc. Annu. Conf. S.E. Fish and Wildlife Agencies 31:437–440.

Beckman, D. W., C. A. Wilson, and A. L. Stanley.
1988. Age and growth of red drum, *Sciaenops ocellatus*, from offshore waters of the northern Gulf of Mexico. Fish. Bull. 87:17–28.

Boothby, R. N., and J. W. Avault Jr.
1971. Food habits, length-weight relationship, and condition factor of the red drum (*Sciaenops ocellatus*) in southeastern Louisiana. Trans. Am. Fish. Soc. 100:290–295.

Brown-Peterson, N., P. Thomas, and C. R. Arnold.
1988. Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in South Texas. Fish. Bull. 86:373–388.

Comyns, B. H., J. Lyczkowski-Schultz, D. L. Nieland, and C. A. Wilson.
1991. Reproduction of red drum, *Sciaenops ocellatus*, in the northcentral Gulf of Mexico: seasonality and spawner biomass. *In* R. D. Hoyt (ed.),

Larval fish recruitment and research in the Americas, p. 17–26. Dep. Commer., NOAA Tech. Rep. NMFS 95.

DeMartini, E. E., and R. K. Fountain.
1981. Ovarian cycling frequency and batch fecundity in the queenfish, *Seriphus politus*: attributes representative of serial spawning fishes. Fish. Bull. 79:547–560.

Fitzhugh, G. R., T. G. Snider III, and B. A. Thompson.
1988. Measurement of ovarian development in red drum (*Sciaenops ocellatus*) from offshore stocks. Contrib. Mar. Sci., Suppl. to vol. 30:79–83.

Fitzhugh, G. R., B. A. Thompson, and T. G. Snider III.
1993. Ovarian development, fecundity, and spawning frequency of black drum *Pogonias cromis* in Louisiana. Fish. Bull. 91:244–253.

Goldberg, S. R.
1981. Seasonal spawning cycle of the black croaker, *Cheilotrema saturnum* (Sciaenidae). Fish. Bull. 79:561–562.

Gunter, G.
1950. Correlation between temperature of water and size of marine fishes on the Atlantic and Gulf coasts of the United States. Copeia 1950:298–304.

Henderson-Arzapalo, A.
1992. Red drum aquaculture. Rev. Aquat. Sci. 6:479–491.

Holt, J., A. G. Johnson, C. R. Arnold, W. A. Fable Jr., and T. D. Williams.
1981. Description of eggs and larvae of laboratory reared red drum, *Sciaenops ocellata*. Copeia 1981:751–756.

Hunter, J. R., and S. R. Goldberg.
1980. Spawning incidence and batch fecundity in northern anchovy, *Engraulis mordax*. Fish. Bull. 77:641–652.

Hunter, J. R., and B. J. Macewicz.
1985. Measurement of spawning frequency in multiple spawning fishes. *In* R. L. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, p. 79–94. Dep. Commer., NOAA Tech. Rep. NMFS 36.

Hunter, J. R., N. C. H. Lo, and R. J. H. Leong.
1985. Batch fecundity in multiple spawning fishes. *In* R. L. Lasker (ed.), An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*, p. 67–77. Dep. Commer., NOAA Tech. Rep. NMFS 36.

Love, M. S., G. E. McGowen, W. Westphal, R. J. Lavenberg, and L. Martin.
1984. Aspects of the life history and fishery of the white croaker, *Genyonemus lineatus* (Sciaenidae), off California. Fish. Bull. 82:179–198.

Murphy, M. D., and R. G. Taylor.
1989. Reproduction and growth of black drum, *Pogonias cromis*, in northeast Florida. Northeast Gulf Sci. 10:127–137.
1990. Reproduction, growth, and mortality of red drum, *Sciaenops ocellatus*, in Florida waters. Fish. Bull. 88:531–542.

Nieland, D. L., and C. A. Wilson.
1993. Reproductive biology and annual variation of reproductive variables of black drum in the northern Gulf of Mexico. Trans. Am. Fish. Soc. 122:318–327.

Pearson, J. C.
1929. Natural history and conservation of redfish and other commercial sciaenids on the Texas coast. U.S. Bur. Fish. Bull. 44:129–214.

Peters, K. M., and R. H. McMichael Jr.
1987. Early life history of *Sciaenops ocellatus* (Pisces: Sciaenidae) in Tampa Bay, Florida. Estuaries 10:92–107.

Roberts, D. E., Jr., B. V. Harpster, and G. E. Henderson.
1978. Conditioning and induced spawning of the red drum (*Sciaenops ocellata*) under varied conditions of photoperiod and temperature. Proc. World Maricult. Soc. 9:311–332.

Sabins, D. S.
1973. Diel studies of larval and juvenile fishes of the Caminada Pass area, Louisiana. M.S. thesis, Louisiana State Univ., Baton Rouge, 163 p.

SAS Institute.
1985. SAS user's guide: statistics, version 5 ed. SAS Institute Inc., Cary, NC, 956 p.

Wallace, R. A., and K. Selman.
1981. Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325–343.

West, G.
1990. Methods of assessing ovarian development in fishes: a review. Aust. J. Mar. Freshwater Res. 41:199–222.

Wilk, S. J., W. W. Morse, and L. L. Stehlik.
1990. Annual cycles of gonad-somatic indices as indicators of spawning activity for selected species of finfish collected from the New York Bight. Fish. Bull. 88:775–786.