

Abstract.—Commercial and recreational catches of red drum *Sciaenops ocellatus* were sampled from Tampa Bay and Mosquito/upper Indian River Lagoon, Florida, between August 1981 and March 1983. Males matured at smaller sizes and younger ages than did females. Males matured when they were 350–799 mm FL (ages 1–3), and females matured when 550–899 mm (ages 3–6). In 1981 and 1982, red drum spawned between August and November, with peak spawning occurring in September–October. Histological evidence suggested that spawning occurred in nearshore Gulf of Mexico waters, in passes, and in the estuary. Ages determined from thin sections of otoliths were validated by length-frequency and marginal-increment analyses for fish ages 1–3 and by observations of oxytetracycline-marked fish for ages 5, 12, 16, and 18. Growth was rapid through age 4 or 5 but then slowed markedly. Growth rates of males and females were similar on each coast. Estimates for the von Bertalanffy growth equation parameters K and t_0 were not significantly different between coasts; however, L_{∞} was significantly greater on the Atlantic coast. Therefore, predicted lengths of Atlantic fish were greater at all ages. Maximum observed lengths were 980 mm on the Gulf coast and 1110 mm on the Atlantic coast. Maximum observed ages of sampled fish were 24 years on the Gulf coast and 33 years on the Atlantic coast. The range of 95% confidence intervals for estimates of total annual mortality rate on the Gulf coast was 87–98% for ages 2–4; on the Atlantic coast, the range was 50–76% for ages 2–6.

Reproduction, Growth, and Mortality of Red Drum *Sciaenops ocellatus* in Florida Waters

Michael D. Murphy
Ronald G. Taylor

Florida Marine Research Institute, Department of Natural Resources
100 8th Avenue SE, St. Petersburg, Florida 33701

The red drum *Sciaenops ocellatus* is an estuarine-dependent sciaenid found in nearshore waters (usually <22 m deep) from northern Mexico to Massachusetts (Yokel 1966, Lux and Mahoney 1969, Ross et al. 1983); it is occasionally found north of Chesapeake Bay (Yokel 1980). Red drum support important recreational and, until recently, commercial fisheries in most coastal areas of the U.S. south Atlantic and Gulf of Mexico (Mercer 1984). These fisheries have recently undergone strict management in Florida to reduce growth and recruitment overfishing (Swingle et al. 1984, Goodyear 1987).

Despite the importance of the red drum, little is known about its life history in Florida. While the spawning season and size at maturity have been described for red drum in Texas (Pearson 1929, Miles 1951, Matlock 1985) and Mississippi (Overstreet 1983), the spawning season in Florida has been inferred only from larval collections taken along the Gulf coast (Springer and Woodburn 1960, Yokel 1966, Jannke 1971, Peters and McMichael 1987). Age and growth have been described for juvenile and adult red drum in U.S. south Atlantic waters (Bearden 1967, Theiling and Loyacano 1976, Music and Pafford 1984, Daniel 1988) and in the northern and western Gulf of Mexico (Pearson 1929; Simmons and Breuer 1962; Rohr 1964, 1980; McKee 1980; Doerzbacher et al. 1988). In Florida, larval and juvenile age and growth have been studied in Tampa Bay

(Peters and McMichael 1987), but only limited data are available on early growth in other areas (Kilby 1955, Roessler 1967).

This paper describes reproduction, age, growth, and mortality for red drum on the Gulf and Atlantic coasts of Florida. Weight-length and length-length relationships are also presented.

Methods and materials

From August 1981 through March 1983, monthly samples of red drum were collected from commercial and recreational catches in two coastal areas of Florida: (1) Tampa Bay (27° 40'N, 82° 35'W) on the Gulf coast, and (2) Mosquito/upper Indian River Lagoon (28° 40'N, 80° 40'W) on the Atlantic coast. Fish were captured using a variety of gear, including trammel nets, gill nets, hook-and-line, and haul seines. Fork length (FL) in millimeters was measured on all fish in the catch. Each month on both coasts, a random subsample was taken, and up to ten fish per length interval (<300, 400–499, 500–699, 700–899, and >899 mm) were measured for total length (TL) and standard length (SL), weighed for whole weight (W) to the nearest ounce (later converted to grams), and sampled for gonads and otoliths (sagittae). Gonads were preserved in the field in Davidson's or Zenker's fixative (Humason 1972), soaked in water for 24 hours in the laboratory, and then stored in 70% ethanol. A

Table 1
Reproductive classes of red drum gonads of each sex.

Class	Female	Male
1. Immature	Few folds of ovigerous lamellae; few or no primary oocytes; oogonia predominate; diameter of ovary <3.0 mm.	Only spermatogonia present; no evidence of tubule development.
2. Developing or Resting virgin	Ovigerous lamellae fill lumen of entire gonad; abundant primary oocytes; oogonia present at periphery of lamellae. Lamellae contain abundant primary oocytes; few, if any, oogonia present; absence of atretic oocytes; tunica thickened.	Early spermatogenesis; few scattered cysts of primary spermatocytes; peripheral tubules differentiating lumen not developed.
3. Maturing	Early vitellogenesis; oogonia, primary oocytes, and oocytes with yolk vesicle present.	Mid-spermatogenesis; spermatogonia, cysts of spermatocytes and a few spermatids present along tubules.
4. Mature	Late vitellogenesis; oogonia, primary oocytes, and oocytes with yolk vesicles and yolk globules present.	Late spermatogenesis; few spermatozoa collecting in tubules and central lumen.
5. Gravid	Maturation. Oogonia, primary oocytes and oocytes with yolk vesicles, globules, and migrating nuclei present.	Reduced number of spermatogenic cysts; efferent ducts filled with spermatozoa; lumen of central duct partially filled with spermatozoa.
6. Spawning or Partially spent	Amorphous, hydrated oocytes present; oogonia, primary oocytes, and oocytes with yolk vesicles, yolk globules, and migrated nuclei present; fragments of ruptured oocytes scattered throughout; collapsed, empty follicles present; yolk remnants usually present in connective tissue and lamellae; tunica greatly thickened.	Efferent ducts filled with spermatozoa; spermatozoa in main collecting duct; distal portions of a few efferent tubules empty and somewhat thickened; spermatogonia absent.
7. Spent	Oogonia and primary oocytes present in budding ovigerous lamellae; ovary with "empty" areas; "plugs" of unshed oocytes present; atretic oocytes scattered throughout, usually in association with blood vessels.	No spermatogonia or spermatocytes present; efferent tubules empty; lumen of central collecting duct with few sperm; testis greatly reduced in size; tunic of previous spawners thickened and convoluted.
8. Recovering	Prolific recrudescence of ovigerous lamellae with myriad oogonia and primary oocytes; only gamma and delta atretic oocytes present in the lamellae. Tunica thickened and convoluted.	Network of efferent tubules lined with spermatogonia; numerous PAS leucocytes present in central sinus; tunica thickened and convoluted.

6-mm-thick sample from the central portion of one lobe of each gonad was embedded in paraffin, sectioned to 6- μ m thickness, stained with Mayer's haematoxylin (Humason 1972) and eosin Y, and mounted for microscopic examination. Additionally, sections of vitellogenic ovaries fixed in Zenker's fluid were sectioned to 8- μ m thickness and stained with Heidenhain's azan (Humason 1972).

Eight classes of maturity (Table 1) were distinguished based on the histological criteria of Wallace and Selman (1981) and Hunter and Macewicz (1985) for oogenesis and Grier (1981) and Grier et al. (1987) for spermatogenesis. Recognition of oocyte atresia and rejuvenation was important in determining whether a fish had previously spawned. Atretic oocytes were recognized by degeneration of the zona radiata, nuclear membrane, and yolk globules (Moe 1969, Wallace and Selman 1981,

Hunter and Macewicz 1985). "Rejuvenation" is defined as the development of oocytes that were held in an advanced perinuclear stage of development since the previous spawning season. These clutches of oocytes in postspawn, recovering females exhibited a characteristic dual cytoplasmic banding (Yamamoto 1956, Howell 1983).

Length at maturity was determined by grouping fish by coast and sex into 50-mm intervals, determining the percentage that were mature (\geq class 4) within each interval, and estimating the length at which 50% of the fish were mature by interpolating between interval midpoints. Oocyte diameters, measured with an ocular micrometer, were used to define the spawning season. Only oocytes whose nuclei were included in the cross section were measured, because these have been shown to represent true oocyte diameters (Foucher and

Beamish 1980). A total of 100 oocytes in a randomly chosen lamella were measured in each female gonad to calculate mean oocyte diameters within subsamples. To further delineate the spawning season and characterize variation in egg size, ten of the largest oocytes from each section were also measured (DeMartini and Fountain 1981), and their mean was plotted against the collection date.

Otoliths were excised from subsampled fish, cleaned, and stored dry in vials. Sagittae were sectioned in the laboratory using a Beuhler Isomet Low-Speed Saw with diamond wafering blades. A 0.5-mm-thick section, cut through the core of the right sagitta, was mounted on a microscope slide with Coverbond Mounting Media. Each section was examined for age marks using a dissecting scope (32 \times) with reflected light. All sections were independently read once by two individuals; then, when necessary, a common reading was conducted. Determining age by simply counting annuli was not always possible because annulus formation occurs about 2–6 months after the anniversary of the actual hatching date (see “Age Determination and Growth” section). To assign ages accurately, we assumed a biologically realistic hatching date of 1 October (see “Spawning Size, Age, Season, and Location” section; Matlock 1984), and ages were incremented on this date. Observations of otolith sections from oxytetracycline (OTC)-marked fish served to directly validate opaque bands as annuli. Oxytetracycline-injected fish (intramuscular injection of 25 mg/kg body wt.) were held in outdoor ponds ($n = 4$) for subsequent recapture and examination after they were free for more than 1 year. All four fish were recaptured after 19 months.

Red drum captured by all gear types were included in the growth analyses. The von Bertalanffy (1957) growth equation, $FL = L_{\infty} (1 - \exp[-K(t - t_0)])$, was fit to observed age-length data by using the NLIN procedure (Marquardt option) of SAS (Vaughan and Kancirik 1982). Growth equation parameters are defined as follows: L_{∞} = the average fork length (mm) that a fish would achieve if it were allowed to grow indefinitely in accordance with the model; K = Brody's growth constant; t_0 = the hypothetical age at which a fish would have zero length, and t = age in years (Ricker 1975). The weight-length relationship was described by linear regression of \log_{10} -transformed data. Analysis of covariance was used to test for differences between regressions.

Age-length keys were applied to length frequencies to separate age groups and develop sample abundance data used to estimate total annual mortality rate (A):

$A = 1 - S$, where S is the annual survival rate. Age-length keys were developed for each season for combined samples captured by trammel net, hook-and-line, and haul-seine. Abundance of each age-group in the samples was then summed over all seasons during the study period. Total annual mortality rates were estimated from truncated age data that included all fully recruited age-groups with sample abundance of five or more fish. This procedure eliminated any bias inherent in the collection of large fish (Chapman and Robson 1960). Survival rates were calculated using the modified Heincke method (Seber 1973), Robson and Chapman (1961) estimates developed for truncated age data, and catch curves.

Results and discussion

Spawning size, age, season, and location

Males matured at smaller sizes (χ^2 -test, $p < 0.05$) and younger ages than did females on both coasts. Some Gulf coast males were sexually mature after they reached 400 mm, and some on the Atlantic coast were mature after they reached 350 mm (Table 2). Interpolated lengths at 50% maturity were 529 mm and 511 mm, respectively. Most males were mature at age 1 or 2, and all were mature by age 3 (see “Age Determination and Growth” section). Some Gulf coast females were sexually mature after they reached 600 mm, and some on the Atlantic coast were mature after they reached 550 mm. Lengths at 50% maturity were 825 and 900 mm, respectively. Some females were mature at age 3, and all were mature by age 6.

While results of previous investigations suggest that the size and age at which red drum mature may vary over its geographical range (Pearson 1929, Gunter 1950, Miles 1951, Overstreet 1983, Music and Pafford 1984), we show that there are also large maturational differences between sexes. Lengths at 50% maturity were about 300–390 mm smaller for males than females. In Mississippi, males and females began developing when they were 300–549 mm SL (358–629 mm FL); however, only after growing to 700 mm SL (792 mm FL) were more than 50% of the samples of either sex mature (Overstreet 1983). Female red drum in Texas matured during their fourth or fifth year, at about 750–850 mm TL (711–803 mm FL) (Pearson 1929, Miles 1951, Matlock 1985). A 755-mm TL (716 mm FL) male red drum sampled in Georgia had well-developed gonads and was apparently mature (Music and Pafford 1984).

Spawning peaked on both coasts of Florida from about September through October. Maximum oocyte diameters and the presence of eggs with yolk vesicles, globules, and migrating nuclei indicated that active

Table 2

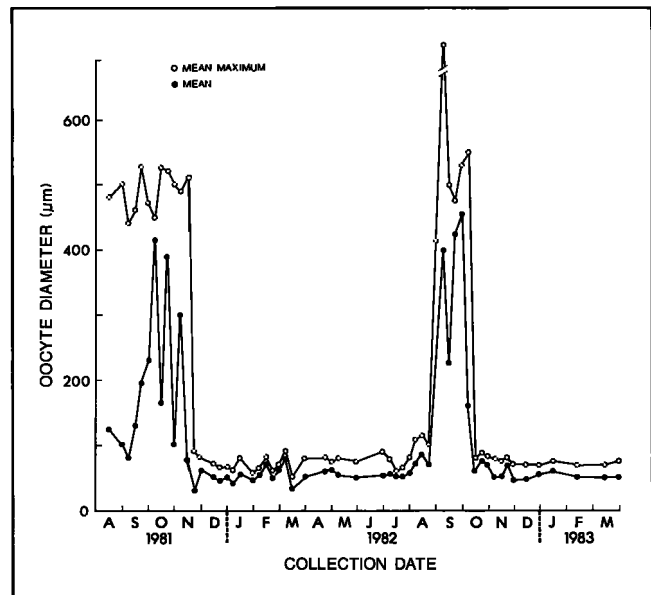
Percent of sampled red drum in each 50 mm FL length interval that were mature (\geq class 4) on the Gulf and Atlantic coasts of Florida. Numbers in parentheses are numbers of fish examined.

Fork length (mm)	Gulf		Atlantic	
	Male	Female	Male	Female
200-249		0 (3)		
250-299	0 (7)	0 (4)	0(10)	0 (7)
300-349	0(21)	0(17)	0 (7)	0(17)
350-399	0(18)	0(24)	9(22)	0(22)
400-449	16(19)	0(16)	16(19)	0(32)
450-499	24(21)	0(24)	35(20)	0(28)
500-549	47(19)	0 (6)	56(25)	0(18)
550-599	81(27)	0(24)	70(20)	7(15)
600-649	88(43)	2(53)	85(20)	0(26)
650-699	85(36)	4(28)	82(38)	0(18)
700-749	100(36)	28(36)	93(27)	0(36)
750-799	100 (6)	36(14)	94(17)	7(14)
800-849	100 (3)	50 (2)	100 (6)	7(14)
850-899	100 (1)	100 (3)	100 (4)	0 (1)
900-949	100 (6)	100 (3)	100 (1)	100 (1)
950-999	100 (2)	100 (2)	100 (2)	100 (9)
1000-1049		100 (1)	100 (1)	100 (5)
1050-1099			100 (2)	
1100-1149				100 (1)

vitellogenesis occurred in August and September 1981, when the study began on the Gulf and Atlantic coasts, respectively (Fig. 1). Gonads were in spawning condition or were partially spent during September–October 1981. In 1982, active vitellogenesis began in August, and most spawning or partially spent individuals were collected in September. Mean and maximum oocyte diameters declined by mid-November 1981 and by mid-October 1982, indicating cessation of peak spawning (Fig. 1).

These results are consistent with the findings of previous studies (Pearson 1929, Mansueti 1960, Yokel 1966, Jannke 1971, Sabins 1973, Peters and McMichael 1987). However, spawning in Tampa Bay may have begun earlier than August in 1982 because larval and juvenile length-frequency distributions and otolith analyses of daily growth indicated that spawning had begun in mid-July (Peters and McMichael 1987). Apparently, spawning in mid-July did not occur in a large enough portion of the population to be reflected in our samples. Macroscopic analyses of adult gonads and analyses of gonosomatic indices have suggested that spawning takes place in Texas during October through February (Heffernan 1977) and that spawning off Mississippi takes place during summer (Overstreet 1983).

Ovarian histological features provided evidence that spawning occurs in the nearshore Gulf of Mexico, in

**Figure 1**

Mean and mean maximum oocyte diameters for red drum sampled from both Atlantic and Gulf coasts of Florida.

the vicinity of passes, and within estuaries. Ovaries of females captured in all three areas displayed either (1) advanced oocytes with migrating nuclei or hyaline oocytes released from the follicular layer, indicative of an imminent spawn (DeMartini and Fountain 1981), or (2) atretic bodies and postovulatory follicles (POF), indicative of a recent spawn (Yamamoto and Yoshioka 1964, Takita et al. 1983, Hunter and Macewicz 1985). A female captured 4.8 km off the Florida Gulf coast had numerous oocytes with migrating nuclei, and a male from the same site had spermatozoa filling the efferent duct of the testes, both of which suggest imminent offshore spawning. A large female red drum captured about 7 km within the mouth of Tampa Bay contained ovulated hydrated oocytes, POF, and several atretic oocytes. All of these artifacts indicate that she had recently spawned. Supporting the hypothesis that estuaries are also used as spawning sites is the fact that females ($n = 4$) that had POF or hyaline oocytes released from the follicle layer were found about 42 km within Tampa Bay, 35 km south of Ponce de Leon Inlet in Mosquito Lagoon, and 90 km north of Sebastian Inlet.

Based on data from egg and larval collections made just inside passes, most investigators have concluded that red drum spawn principally in nearshore areas close to channels and passes (Pearson 1929, Miles 1950,

Simmons and Breuer 1962, Yokel 1966, Jannke 1971, Holt et al. 1985). Our data suggest that spawning may also occur over the nearshore continental shelf and in estuaries. Collections of mature or recently spent fish made in nearshore Gulf waters from just outside the barrier islands to depths of 69.5 m suggest that spawning takes place offshore in the Gulf of Mexico (Christmas and Waller 1973; Heffernan 1977; W.A. Fable, NMFS Panama City Lab., Drum seine observers trip report, 18–21 Aug. 1982. Memo 00.Sep.82*002148 to A.C. Jones, NMFS Miami Lab., 4 p.). Peters and McMichael (1987) reported that although most spawning in Tampa Bay occurred close to its mouth, some spawning probably took place in nearshore Gulf waters. Recent egg collections provide evidence that red drum spawn within Mosquito Lagoon (Johnson and Funicelli In press). Our collection of females in Mosquito Lagoon containing POF corroborate these findings and suggest that red drum found equally far within Tampa Bay may also be spawning within the estuary. Moreover, red drum movement was observed during a sonic tracking study in Mosquito Lagoon (Carr and Smith 1977, Carr and Chaney 1976) and little directed movement during the spawning season was noted.

Age determination and growth

Ages of red drum from 0 to at least 18 could accurately be determined using otoliths. Red drum sagittae showed clearly delineated, easily interpreted (100% agreement between counts) hyaline and opaque bands. Otoliths with 0–33 opaque bands were examined; they were taken from 1085 red drum (551 Gulf coast and 534 Atlantic coast) with size ranges of 225–1110 mm. Although ages of red drum were validated for only the first 18 years, we assumed, for age and growth analysis, that each opaque band represents an annual mark (annulus).

Minimally overlapping monthly length frequencies, a consistent marginal increment minima each year, and observations of oxytetracycline-injected fish supported the hypothesis that the opaque bands are annuli. Modal length progressions representing the 1978, 1979, 1980, and 1981 year-classes on the Gulf coast and 1980 and 1981 year-classes on the Atlantic coast could be followed in length frequencies (Figs. 2, 3). These length modes could be followed for fish up to 3 years-old and consistently agreed with lengths of fish having corresponding otolith-determined ages. The periodicity of the mean monthly marginal increment minima each winter (December–March) for fish having one or two opaque bands further suggests that opaque bands were deposited annually (Fig. 4). Opaque bands on fish older than age 3 are also probably annuli. Four adult red drum that were injected and held in outdoor ponds for

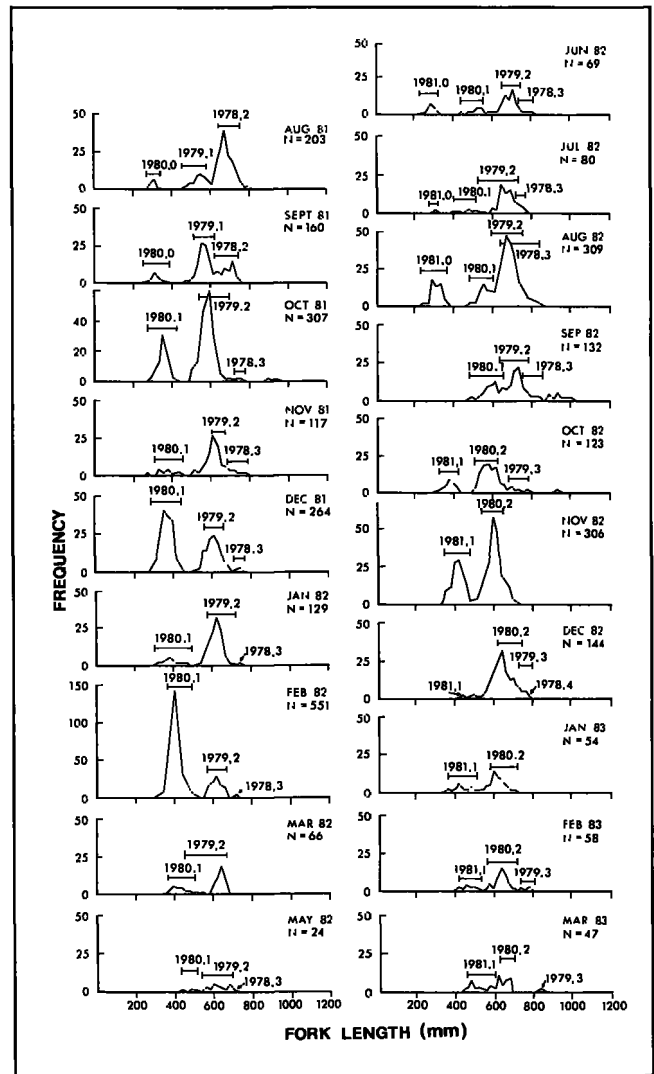


Figure 2

Monthly length frequencies for red drum from the Gulf coast of Florida. No collections were made in April 1982. Horizontal bars show length ranges for otolith-aged year-classes and are labeled for year-class and age in years.

19 months deposited one opaque band each between release (August 1986) and recapture (March 1988). These fish were 5, 12, 16, and 18 years-old when recaptured.

Otoliths have been used to determine the age of red drum (Miles 1951, Rohr 1964, Theiling and Loyacano 1976), but the use of opaque bands as an age determinant has never been adequately tested. Off Mississippi, annuli apparently form on otoliths during winter or spring (Rohr 1964). In Texas, where the validity of using scales to determine ages of red drum ≤ 4.5 years-old has been established (Matlock et al. 1987), annuli form on scales between February and April in

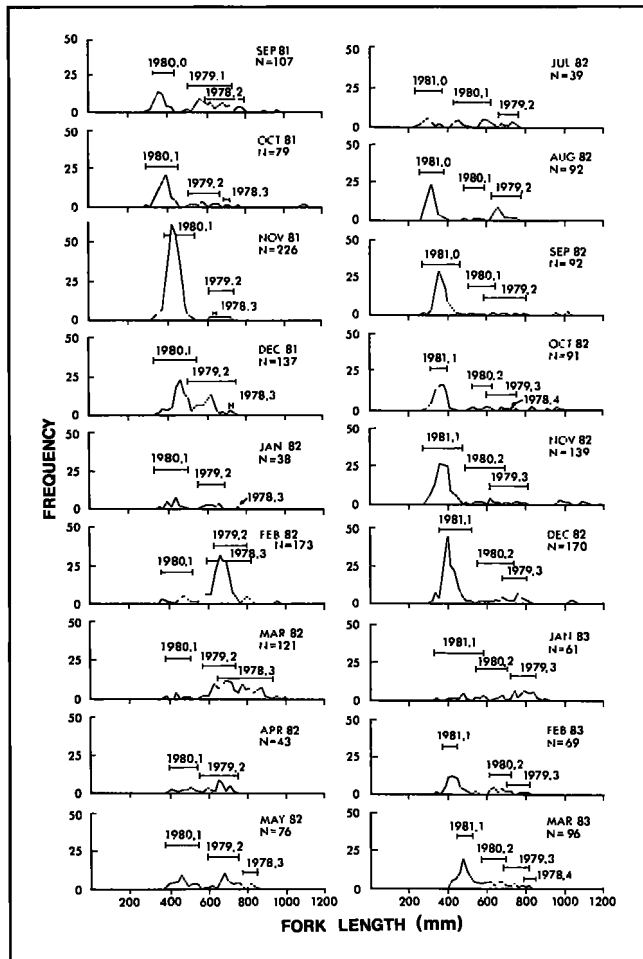


Figure 3

Monthly length frequencies for red drum from the Atlantic coast of Florida. No collections were made in June 1982. Horizontal bars show length ranges for otolith-aged year-classes and are labeled for year-class and age in years.

Matagorda Bay (Wakefield and Colura 1983), during winter in Aransas/Corpus Christi Bay (Pearson 1929), and as early as January in all Texas bays (Matlock et al. 1987). Red drum deposit a first annulus on otoliths and scales during their second winter, when they are about 14–18 months-old (Pearson 1929, Rohr 1964, Theiling and Loyacano 1976, Hysmith et al. 1983, Wakefield and Colura 1983, Matlock 1984, Matlock et al. 1987). Apparently, juvenile red drum that measure 40–100 mm during their first winter (Kilby 1955, Peters and McMichael 1987) do not form an annulus; our smallest specimen with an annulus was 379 mm.

Red drum grew rapidly until age 4 or 5, and then growth slowed markedly (Table 3; Fig. 5). For each coast, the average observed sizes of fish ages 1–3 were not significantly different between sexes (Student's *t*-test; $p > 0.10$ in all cases). However, in comparing

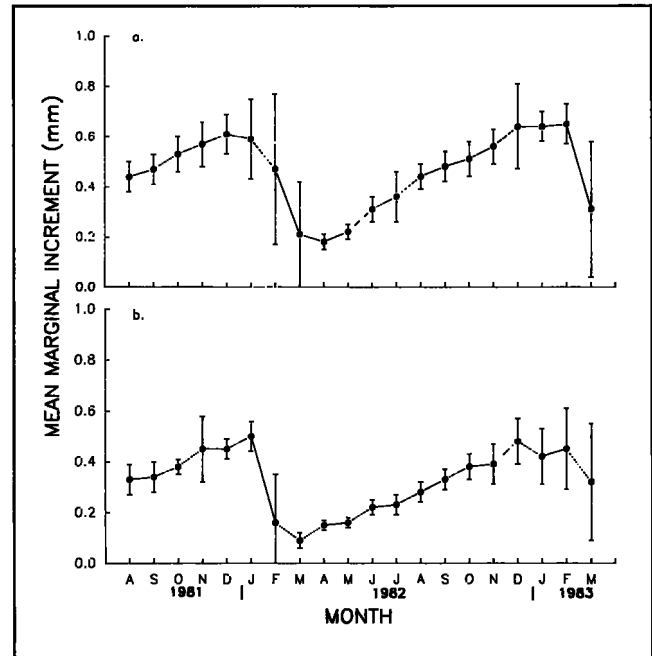


Figure 4

Mean monthly marginal increment (± 1 SD) for red drum in Florida waters with (a) one and (b) two annuli on otolith sections. Differences between coasts were not significant (ANOVA, $p > 0.05$), therefore pooled data are presented.

coasts, the average observed sizes were significantly larger ($p < 0.001$) at ages 1 and 2 on the Atlantic coast than they were on the Gulf coast. After age 2, growth appeared to be slower on the Atlantic coast; however, the variance for age 3 lengths was significantly greater (*F*-test; $p < 0.05$) on the Atlantic coast. Sample sizes of older age groups were too small to test for statistical differences.

Lengths predicted from the von Bertalanffy growth curve agreed with the average observed lengths of red drum on the Gulf and Atlantic coasts (Table 3; Fig. 5). Asymptotic length (L_{∞}) was significantly larger (Student's *t*-test, $p < 0.01$) on the Atlantic coast than on the Gulf coast, while the Brody's growth constant (*K*) and age at zero length (t_0) were not significantly different ($p > 0.05$). Therefore, predicted lengths were greater at all ages for Atlantic coast red drum than for Gulf coast fish. Our estimates of asymptotic length are generally greater than other reported values: 717 mm TL (680 mm FL), 835 mm TL (789 mm FL), and 803 mm TL (760 mm FL) for Lower Laguna Madre, Matagorda, and Galveston Bays in Texas, respectively (Wakefield and Colura 1983); 918 mm TL (865 mm FL) in Texas bays (Doerzbacher et al. 1988); and 950 mm TL (894 mm FL) in Mississippi Sound (Rohr 1980). This suggests that red drum grow larger in Florida or, as

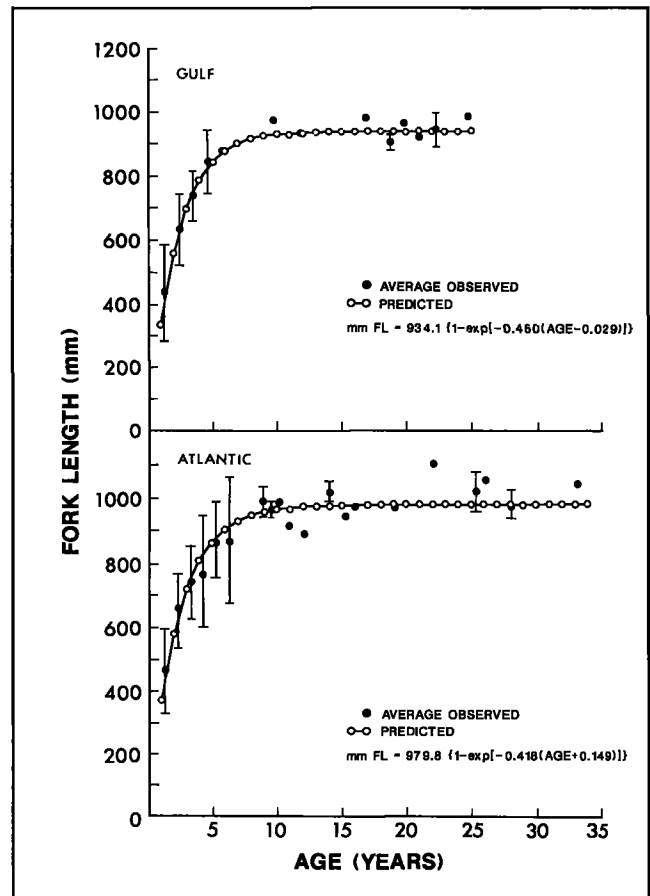
Table 3

Average observed and predicted fork lengths (mm) for red drum sampled from Gulf and Atlantic coasts of Florida. Sample sizes are in parentheses.

Age (yr)	Gulf		Atlantic	
	Average observed	Predicted	Average observed	Predicted
0	296 (62)		335 (59)	
1	436(169)	337	462(192)	373
2	635(232)	557	655(166)	581
3	736 (65)	696	742 (66)	718
4	845 (5)	784	768 (14)	808
5	877 (1)	839	863 (5)	867
6		874	871 (5)	905
7		896		931
8		910	995 (2)	948
9	975 (1)	919	973 (2)	959
10		925	986 (1)	966
11		928	918 (1)	971
12	925 (1)	930	894 (1)	974
13		932		976
14		933	1028 (2)	977
15		933	954 (1)	978
16		933	960 (1)	979
17	968 (1)	934		979
18	898 (2)	934		979
19	957 (1)	934	975 (1)	979
20		934		980
21	918 (1)	934		980
22	960 (6)	934	1110 (1)	980
23		934		980
24	980 (1)	934		980
25			1038 (3)	980
26			1060 (1)	980
27				980
28			983 (2)	980
29				980
30				980
31				980
32				980
33			1050 (1)	980

noted by Matlock (1984), that the larger fish which predominately inhabit continental shelf waters were not adequately sampled in Texas and Mississippi. Matlock (1984) estimated the von Bertalanffy growth equation for red drum in Texas using data from Pearson (1929) and found what he considered a more reasonable estimate of L_{∞} of 1068 mm TL (1002 mm FL).

Length-at-age estimates of red drum in Florida were similar to those reported in past literature for red drum in Texas (Pearson 1929, Miles 1951, Simmons and Breuer 1962; Table 4). However, red drum in Florida appear to grow more rapidly than red drum in Mississippi (Rohr 1980), South Carolina (Thieling and Loyacano 1976), and those in a more recent study from

**Figure 5**

Average observed (± 2 SD or range if $n = 2$; see Table 3) and predicted mean lengths of red drum in Florida waters.

Texas (Wakefield and Colura 1983). However, as noted above the differences in length-at-age estimates could be attributed to a sampling bias toward smaller near-shore fish.

Mortality

Ninety-five percent confidence limits for estimates of total annual mortality rate ($1 - S$) using sample abundance data ranged 87–98% for red drum ages 2–4 on the Gulf coast and 50–76% for red drum between ages 2–6 on the Atlantic coast during 1981–83. Red drum were fully recruited by age 2. Sample size of fish older than 4 years on the Gulf coast and 6 years on the Atlantic coast fell below the suggested lower limit of five fish to ensure unbiased estimates (Chapman and Robson 1960). Mean estimates of total annual mortality rates were consistently greater for Gulf coast fish (Table 5).

Total annual mortality of red drum has been estimated for Everglades National Park in Florida and for Texas bay systems. In Everglades National Park, Rago

Table 4

Literature accounts of mean fork lengths at age for red drum. Fork lengths are in millimeters and were converted from TL or SL, if necessary, using the relationships in text.

Area, study, and method	Age (yr)									
	1	2	3	4	5	6	7	8	9	10
Texas										
Pearson (1929)										
Aransas/Corpus Christi Bays; length frequency	300	530	630	750	840					
Miles (1951)										
Aransas Bay; otoliths	380-423	575	630-684			826	871*	917-940		
Simmons and Breuer (1962)										
Lower coast; tag recapture	322	519	693							
Wakefield and Colura (1983)										
Lower Laguna Madre; scales	290	447	542							
Matagorda Bay; scales	255	399	526	605	660					
Galveston Bay; scales	275	439	547	619						
South Carolina										
Theiling and Loyacano (1976)										
otolith sections**	429	560	695	782	803	842	803			
Mississippi										
Rohr (1980)										
otoliths	356	522	638	717	772	810	839	853	867	875
Florida										
Present study										
Gulf coast; otolith sections	337	557	696	784	839	874	896	910	919	925
Atlantic coast; otolith sections	373	581	718	808	867	905	931	948	959	966

*A mixture of fish age seven and eight.

**Average size for age group from June through November.

Table 5

Pooled mean estimates and 95% confidence intervals of total annual mortality (A) for red drum ages 2-4 on the Gulf coast and ages 2-6 on the Atlantic coast.

Method	Total annual mortality			
	Gulf		Atlantic	
	A	95% CI	A	95% CI
Seber (1973)	0.92	0.91-0.94	0.65	0.59-0.70
Robson and Chapman (1961)	0.91	0.90-0.93	0.66	0.63-0.70
Catch curve	0.94	0.87-0.98	0.65	0.50-0.76

and Goodyear (1985) used tag-recapture days-at-large data to estimate a total annual mortality rate of 0.73 during 1984-85. Also based on tag-recapture data, total annual mortality rates in Texas bays were about 68% during 1976-77 (Matlock and Weaver 1979) and 80-87% during 1975-1979 (Green et al. 1985). Matlock (1984) estimated the total annual mortality rate to be 80% for all Texas bays during 1977-1981.

Apparent total annual mortality rates in Florida for red drum ages 2-6 are high, especially for a species that may live about 25-35 years. Theoretically, fish with such longevity (assuming constant mortality rate) would have a natural mortality rate of only about 12-18%; this rate allows for survival to the observed maximum ages (Royce 1972, Hoenig 1983). Our much greater estimates of total annual mortality for fish ages 2-6 may reflect one or more of the following: (1) a higher rate of natural mortality for younger fish (i.e., natural mortality is not constant), (2) high fishing-mortality rates within estuaries, and/or (3) emigration from estuaries (sampling area) before age 4 on the Gulf coast or age 6 on the Atlantic coast. In the first two cases, estimates of total mortality are unbiased, although component parts (fishing and natural mortality) are not the same. In the third case, total annual mortality would be overestimated because older fish that left the sampling area would be underrepresented in the catch.

While data for evaluating whether natural mortality changes with age are not available, tag-recapture data suggest that fishing mortality is high and that emigration does occur. Annual tag-return rates of

Table 6

Weight-length regressions of red drum sampled from the Gulf and Atlantic coasts of Florida. W = weight (g); FL = fork length (mm).

Area	N	FL (mm)	a (1 SE)	b (1 SE)	r ²
Gulf	491	242-1000	6.1673 × 10 ⁻⁶ (0.4301 × 10 ⁻⁶)	3.0984 (0.0114)	0.993
Atlantic	484	257-1110	9.3993 × 10 ⁻⁶ (0.6616 × 10 ⁻⁶)	3.0275 (0.0115)	0.993

70-80% occurred in southwest Florida during the 1961-65 Schlitz Tagging Programs, and the average tag-return rate throughout the state was 46% (Beaumariage 1969). More recent annual tag-return rates in Florida were 11-25% (Murphy and Taylor 1985) and 12% (Rago and Goodyear 1985), but if these are adjusted to account for a probable low tag-reporting rate, e.g., 36% in Texas (Green et al. 1983), then actual annual recapture rates in Florida could still be high: 31-69%. Limited data on the emigration of red drum suggest a little exchange from estuarine to nearshore waters. Subadult red drum tagging studies within Tampa Bay have shown that about 2-6% of recaptured red drum came from outside the Bay (Murphy and Taylor 1985); similar results (1.4%) were reported for the Texas coast (Osburn et al. 1982). Fishing effort and "catchability" of red drum are probably lower in nearshore waters than within the estuary, which could cause the rates of emigration to be underestimated.

Weight-length and length-length relations

Weight-length regressions (Table 6) were not significantly different ($p > 0.05$) between sexes on each coast,

Atlantic		
slope	df = 1, 480	F = 0.21
elevation	df = 1, 481	F = 0.34
Gulf		
slope	df = 1, 487	F = 1.60
elevation	df = 1, 488	F = 1.32,

although the slopes and elevations were different between coasts with sexes combined,

slope	df = 1, 971	F = 18.96
elevation	df = 1, 972	F = 27.5.

Predicted weights for subadult red drum were similar; e.g., the predicted weight of a 500-mm fish is about 1.4 kg on both coasts. However, adult red drum on the Gulf

Table 7

Length-length regressions of red drum in Florida. TL = total length (mm); FL = fork length (mm); SL = standard length (mm). Sample fork length range for all regressions was 225-1110 mm.

Y = a + bX					
Y	X	N	a (1 SE)	b (1 SE)	r ²
FL	TL	1074	23.9383 (0.6704)	0.9162 (0.0011)	0.999
TL	FL	1074	-25.2080 (0.7600)	1.0898 (0.0013)	0.999
TL	SL	1075	10.3832 (0.8970)	1.1829 (0.0017)	0.998
SL	TL	1075	-7.6225 (0.7689)	0.8343 (0.0012)	0.998
FL	SL	1075	32.8951 (0.6934)	1.0850 (0.0013)	0.998
SL	FL	1075	-29.4619 (0.6738)	0.9202 (0.0011)	0.998

coast were heavier at a given length than they were on the Atlantic coast; e.g., a 900-mm fish weighs 8.8 kg on the Gulf coast and 8.3 kg on the Atlantic coast.

Length-length regressions show that total length and standard length increase more rapidly than fork length as fish get larger (Table 7). Total length is about 1% greater at 300 mm FL and 6% greater at 1000 mm FL. Standard length is 18% less than fork length at 300 mm FL but only 12% less at 1000 mm FL.

Summary

The following are significant features of the life history of red drum in Florida: rapid growth through age 4 or 5, relatively early sexual maturation (total maturity by age 3-6), a discrete peak in spawning activity during September-October, a life span of up to about 35 years, and spawning grounds located in nearshore waters, in passes and inlets, and inside large estuaries. These characteristics and the apparently high rate of annual mortality for red drum ages 2-6 suggest that only a small portion of the population survives to reach maturity. However, this annual rate of mortality (disappearance) has a component of emigration that warrants investigation. Recent management measures enacted by the Gulf of Mexico Fishery Management Council and the Florida Marine Fisheries Commission have limited fishing on the spawning stocks and have reduced fishing pressure on the immature fish.

Acknowledgments

We wish to thank all fishermen who enthusiastically contributed to this study, especially Walter Bell, Cecil Goodrich, and James Burch. Special thanks go to Robert McMichael, Lewis Bullock, and Mark Godcharles for assistance with field work. This paper benefited from reviews by Roy Williams, Glenn Parsons, Behzad Mahmoudi, and Judith Leiby. Age validation work was supported by a MARFIN grant, NA86-WC-H-06136, from the National Oceanic and Atmospheric Administration through the National Marine Fisheries Service. Marjorie Myers skillfully typed all drafts of this manuscript.

Citations

- Bearden, C.M.**
1967 Salt-water impoundments for game fish in South Carolina. *Prog. Fish-Cult.* 29(3):123-128.
- Beaumariage, D.S.**
1969 Returns from the 1965 Schlitz tagging program, including a cumulative analysis of previous results. Fla. Dep. Nat. Resour. Mar. Res. Lab. Tech. Ser. 59, 38 p.
- Carr, W.E.S., and T. Chaney**
1976 Harness for attachment of an ultrasonic transmitter to the red drum, *Sciaenops ocellata*. *Fish. Bull.*, U.S. 74: 998-1000.
- Carr, W.E.S., and J.R. Smith**
1977 A study of the spawning movements and a tentative spawning site of the red drum, *Sciaenops ocellata*. Unpubl. final rep. to Florida Sea Grant Coll. Prog., Univ. Florida, Gainesville, 31 p.
- Chapman, D.G., and D.S. Robson**
1960 The analysis of a catch curve. *Biometrics* 16(3):354-368.
- Christmas, J.Y., and R.S. Waller**
1973 Estuarine vertebrates, Mississippi. In Christmas, J.Y. (ed.), Cooperative Gulf of Mexico estuarine inventory and study, Mississippi, p. 320-343. Gulf Coast Res. Lab., Ocean Springs, MS.
- Daniel, L.B. III**
1988 Aspects of the biology of juvenile red drum, *Sciaenops ocellatus*, and spotted seatrout, *Cynoscion nebulosus* (Pisces: Sciaenidae), in South Carolina. M.S. thesis, College of Charleston, Charleston, SC, 58 p.
- 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.*, U.S. 79:547-555.
- Doerzbacher, J.F., A.W. Green, H.R. Osburn, and G.C. Matlock**
1988 A temperature compensated von Bertalanffy growth model for tagged red drum and black drum in Texas bays. *Fish. Res. (Amst.)* 6:135-152.
- Foucher, R.P., and R.J. Beamish**
1980 Production of nonviable oocytes by Pacific hake (*Merluccius productus*). *Can. J. Fish. Aquat. Sci.* 37:41-48.
- Goodyear, C.P.**
1987 Status of the red drum stocks in the Gulf of Mexico. Contrib. CRD 86/87-34, Southeast Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Miami, FL 33149, 49 p.
- Green, A.W., G.C. Matlock, and J.E. Weaver**
1983 A method for directly estimating the tag-reporting rate of anglers. *Trans. Am. Fish. Soc.* 112:412-415.
- Green, A.W., H.R. Osburn, G.C. Matlock, and H.E. Hegen**
1985 Estimated survival rates for immature red drum in north-west Gulf of Mexico bays. *Fish. Res. (Amst.)* 3:263-277.
- Grier, H.J.**
1981 Cellular organization of the testis and spermatogenesis in fishes. *Am. Zool.* 21:345-357.
- Grier, H.J., R.G. Taylor, and R.O. Reese**
1987 The mechanism of tubule elongation during testicular recrudescence in the redfish, *Sciaenops ocellatus* (Perciformes). In Kullander, S.O., and B. Fernholm (eds.), Proc. V Congr. Eur. Ichthyol., Stockholm, 1985, p. 285-291. Swedish Mus. Nat. Hist., Stockholm.
- Gunter, G.**
1950 Correlation between temperature of water and size of marine fishes on the Atlantic and Gulf coasts of the United States. *Copeia* 1950:298-303.
- Heffernan, T.L.**
1977 Survey of adult drum (*Sciaenops ocellata*), 1973. Proj. Rep. 1973, Tex. Parks Wildl. Dep. Coastal Fish., Austin, p. 37-66.
- Hoening, J.M.**
1983 Empirical use of longevity data to estimate mortality rates. *Fish. Bull.*, U.S. 82:898-902.
- Holt, G.J., S.A. Holt, and C.R. Arnold**
1985 Diel periodicity of spawning in sciaenids. *Mar. Ecol. Prog. Ser.* 27:1-7.
- Howell, W.H.**
1983 Seasonal changes in the ovaries of adult yellowtail flounder, *Limanda ferruginea*. *Fish. Bull.*, U.S. 81:341-355.
- Humason, G.L.**
1972 Animal tissue techniques. W.H. Freeman, San Francisco, 641 p.
- Hunter, J.R., and B.J. Macewicz**
1985 Measurement of spawning frequency in multiple spawning fishes. In Lasker, R (ed.), An egg production method for estimating spawning biomass of pelagic fishes: application to the northern anchovy, *Engraulis mordax*, p. 79-94. NOAA Tech. Rep. NMFS 36.
- Hysmith, B.T., R.L. Colura, and G.C. Matlock**
1983 Effects of stocking rate and food type on growth and survival of fingerling red drum. In Stickney, R.R., and S.P. Meyers (eds.), Proc., Warmwater Fish Culture Workshop, March 1-4, 1982, p. 133-144. World Maricult. Soc.
- Jannke, T.E.**
1971 Abundance of young sciaenid fishes in Everglades National Park, Florida in relation to season and other variables. Univ. Miami Sea Grant Prog. Sea Grant Tech. Bull. 11, 128 p.
- Johnson, D.R., and N.A. Funicelli**
In press Spawning of red drum in Mosquito Lagoon, east-central Florida. *Estuaries*.
- Kilby, J.D.**
1955 The fishes of two coastal marsh areas of Florida. *Tulane Stud. Zool.* 2(8):176-247.
- Lux, F.E., and J.V. Mahoney**
1969 First record of the channel bass, *Sciaenops ocellata* (Linnaeus), in the Gulf of Maine. *Copeia* 1969:632-633.
- Mansueti, R.J.**
1960 Restriction of very young red drum *Sciaenops ocellata*, to shallow estuarine waters of Chesapeake Bay during late autumn. *Chesapeake Sci.* 1(3-4):207-210.

- Matlock, G.C.**
1984 A basis for the development of a management plan for red drum in Texas. Ph.D. diss., Texas A&M Univ., College Station, 291 p.
1985 Red drum sex ratio and size at sexual maturity. Manage. Data Ser. 85, Tex. Parks Wildl. Dep., Coastal Fish. Branch, Austin, 7 p.
- Matlock, G.C., and J.E. Weaver**
1979 Fish tagging in Texas bays during November 1975–September 1976. Manage. Data Ser. 1, Tex. Parks Wildl. Dep., Coastal Fish. Branch, Austin, 136 p.
- Matlock, G.C., R.L. Colura, A.F. Maciorowski, and L.W. McEachron**
1987 Use of on-going tagging programs to validate scale readings. In Summerfelt, R.C., and G.E. Hall (eds.), Age and growth of fish, p. 279–286. Iowa State Univ. Press, Ames.
- McKee, D.A.**
1980 A comparison of the growth rate, standard length-weight relationship and condition factor of red drum *Sciaenops ocellatus* (Linnaeus), from an electric generating station cooling lake and the natural environment. M.S. thesis, Corpus Christi State Univ., Corpus Christi, TX, 53 p.
- Mercer, L.P.**
1984 A biological and fisheries profile of red drum, *Sciaenops ocellatus*. Spec. Sci. Rep. 41, NC Dep. Nat. Resour. Community Dev. Div. Mar. Fish., Raleigh, 89 p.
- Miles, D.W.**
1950 The life histories of the spotted seatrout, *Cynoscion nebulosus*, and the redfish, *Sciaenops ocellatus*. Annu. Rep. (1949–1950), Tex. Game, Fish and Oyster Comm. Mar. Lab., p. 66–103. Tex. Parks Wildl. Dep., Austin.
1951 The life histories of the spotted seatrout, *Cynoscion nebulosus*, and the redfish, *Sciaenops ocellatus*; sexual development. Annu. Rep. (1950–1951), Tex. Game, Fish and Oyster Comm. Mar. Lab. 11 p. Tex. Parks Wildl. Dep., Austin.
- Moe, M.A. Jr.**
1969 Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Fla. Dep. Nat. Resour. Mar. Res. Lab. Prof. Pap. Ser. 10, 95 p.
- Murphy, M.D., and R.G. Tylor**
1985 A tag/recovery study of red drum, *Sciaenops ocellatus*, on the Gulf coast of Florida—Spring 1984. Unpubl. manuscr., Fla. Mar. Res. Inst., Dep. Nat. Resour., St. Petersburg, 19 p.
- Music, J.F., and J.M. Pafford**
1984 Population dynamics and life history aspects of major marine sportfishes in Georgia's coastal waters. Ga. Dep. Nat. Resour. Coastal Resour. Div. Cont. Ser. 38, Atlanta, 382 p.
- Osburn, H.R., G.C. Matlock, and A.W. Green**
1982 Red drum (*Sciaenops ocellatus*) movements in Texas bays. Contrib. Mar. Sci. 25:85–97.
- Overstreet, R.M.**
1983 Aspects of the biology of the red drum, *Sciaenops ocellatus*, in Mississippi. Gulf Res. Rep. (Suppl. 1), p. 45–68.
- Pearson, J.C.**
1929 Natural history and conservation of the redfish and other commercially important 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(2):92–107.
- Rago, P.J., and C.P. Goodyear**
1985 Estimation of mortality rates and population size from tagging studies in Everglades National park, 1984–85. U.S. Fish Wildl. Serv., Gainesville, FL, 32 p.
- Ricker, W.E.**
1975 Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382 p.
- Robson, D.S., and D.G. Chapman**
1961 Catch curves and mortality rates. Trans. Am. Fish. Soc. 90:181–189.
- Roessler, M.**
1967 Observations on the seasonal occurrence and life histories of fishes in Buttonwood Canal, Everglades National Park, Florida. Ph.D. thesis, Univ. Miami, Coral Gables, FL, 155 p.
- Rohr, B.A.**
1964 Comparison of the growth rings in the scales, otoliths, dorsal rays, and second anal spine as related to growth of red drum, *Sciaenops ocellatus*. J. Miss. Acad. Sci. 10:208–212.
1980 Use of hard parts to age Gulf of Mexico red drum. In Williams, R.O., J.E. Weaver, and F.A. Kalber (eds.), Proc., Colloq. on biology and management of red drum and seatrout, Oct. 19–20, 1978, p. 15. Sponsored by Gulf States Mar. Fish. Comm., Ocean Springs, MS [abstract].
- Ross, J.L., J.S. Pavela, and M.E. Chittenden Jr.**
1983 Seasonal occurrence of black drum, *Pogonias cromis*, and red drum, *Sciaenops ocellatus*, off Texas. Northeast Gulf Sci. 6(1):67–70.
- Royce, W.F.**
1972 Introduction to fishery sciences. Academic Press, NY, 351 p.
- 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.
- Seber, G.A.F.**
1973 Estimation of animal abundance and related parameters. Griffin, London, 506 p.
- Simmons, E.G., and J.P. Breuer**
1962 A study of redfish, *Sciaenops ocellata* Linnaeus and black drum, *Pogonias cromis* Linnaeus. Publ. Inst. Mar. Sci. Univ. Tex. 8:184–211.
- Springer, V.G., and K.D. Woodburn**
1960 An ecological study of the fishes of the Tampa Bay area. Fla. Board Conserv. Mar. Lab. Prof. Pap. Ser. 1, 104 p.
- Swingle, W., T. Leary, C. Davis, V. Blomo, W. Tatum, M. Murphy, R. Taylor, G. Adkins, T. McIlwain, and G. Matlock**
1984 Fishery profile of red drum. Gulf of Mexico Fish. Manage. Council and Gulf States Mar. Fish. Comm., Tampa, FL, 164 p.
- Takita, T., T. Iwamoto, S. Kai, and I. Sogabe**
1983 Maturation and spawning of the dragonet, *Callionymus enneactis* in an aquarium. Jpn. J. Ichthyol. 30(3):221–226.
- Theiling, D.L., and H.A. Loyacano**
1976 Age and growth of red drum from a saltwater marsh impoundment in South Carolina. Trans. Am. Fish. Soc. 105: 41–44.
- Vaughan, D.S., and P. Kanciruk**
1982 An empirical comparison of estimation procedures for the von Bertalanffy growth equation. J. Cons. Int. Explor. Mer 40:211–219.
- von Bertalanffy, L.**
1957 Quantitative laws in metabolism and growth. Q. Rev. Biol. 32:217–231.
- Wakefield, C.A., and R.L. Colura**
1983 Age and growth of red drum in three Texas bay systems. Proc. Tex. Chapter Am. Fish. Soc. 5:77–87.
- Wallace, R.A., and K. Selman**
1981 Cellular and dynamic aspects of oocyte growth in teleosts. Am. Zool. 21:325–343.

Yamamoto, K.

1956 Studies on the formation of fish eggs, I. Annual cycle in the development of ovarian eggs in the flounder, *Liopsetta obscura*. J. Fac. Sci. Hokkaido Univ. Ser. VI Zool. 12:362-373.

Yamamoto, K., and H. Yoshioka

1964 Rhythm of development in the oocyte of the medaka *Oryzias latipes*. Bull. Fac. Fish. Hokkaido Univ. 15(1):5-20.

Yokel, B.J.

1966 A contribution to the biology and distribution of the red drum, *Sciaenops ocellata*. M.S. thesis, Univ. Miami, Coral Gables, FL, 160 p.

1980 A contribution to the biology and distribution of the red drum, *Sciaenops ocellata*. In Williams, R.O., J.E. Weaver, and F.A. Kalber (eds.), Proc., Colloq. on biology and management of red drum and sea trout, Oct. 19-20, 1978, p. 5. Sponsored by Gulf States Mar. Fish. Comm., Ocean Springs, MS [abstract].