REPRODUCTIVE BIOLOGY OF KING MACKEREL, *SCOMBEROMORUS CAVALLA*, FROM THE SOUTHEASTERN UNITED STATES

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ABSTRACT

The reproductive biology of king mackerel, *Scomberomorus cavalla*, was studied from specimens collected off Texas, Louisiana, and northwest Florida in the Gulf of Mexico and off North and South Carolina in the Atlantic Ocean. Gonads were examined from 1,163 females and 595 males obtained in 1977-78. Spawning was prolonged. Most king mackerel were reproductively active from May through September. A few fish were in spawning condition as early as April and as late as October. All females were mature at 850-899 mm fork length (FL). Estimates of fecundity ranged from about 69,000 to 12,207,000 eggs for fish from 446 to 1,489 mm FL, 618 to 25,610 g total weight (TW), and 1 to 13 years of age. Fecundity (F) was usually significantly correlated with FL, TW, and age in each area but TW was the best predictor of fecundity in all areas combined ($F = 1.854 \times 10^1 (TW)^{1.361}$) with $r^2 = 0.856$.

King mackerel, *Scomberomorus cavalla*, is one of the most valuable commercial and recreational fish in the Gulf of Mexico and south Atlantic. It is an epipelagic, neritic species that occurs in the western Atlantic Ocean from Massachusetts to Rio de Janeiro, Brazil (Collette and Russo 1979, 1984). Most of the king mackerel caught off the southeastern United States are landed in Florida (Manooch 1979) where it is an important component of charter boat catches (Moe 1963; Brusher et al. 1978). Commercial landings in Florida during 1983 totaled 2,017 t and the estimated recreational catch from the Gulf of Mexico was 1,090,000 fish in 1984 (U.S. Department of Commerce 1985a, b).

Although much has been written on king mackerel, little is known of its reproductive biology (Manooch et al. 1978). Ovarian histology and size-at-maturity has been described by Alves and Tome (1967) for fish from Brazil and by Beaumariage (1973) for fish from Florida. Maturation based on blood hormone levels from fish off northwest Florida was reported by MacGregor et al. (1981). Spawning times and areas have been inferred from ichthyoplankton collections of king mackerel larvae (Dwinell and Futch 1973; Finucane and Collins 1977; Houde et al. 1978[2]; McEachran et al. 1980). The only fecundity estimates in the literature were made by Ivo (1974) for fish from Brazil.

The purpose of our study was to provide additional information on king mackerel reproductive biology by determining spawning season, length-at-maturity, and fecundity from four areas off the southeastern coast of the United States. This information will be useful in the management of king mackerel since the measure of reproductive potential is a basic element of productivity and stock dynamics (Baglin 1982).

METHODS

King mackerel were sampled from commercial and recreational catches in four separate areas along the coast of the southeastern United States during 1977 and 1978 (Fig. 1). These areas were I, the northwestern Gulf of Mexico off the central and south coasts of Texas; II, the northcentral Gulf off Louisiana and Mississippi; III, the northeastern Gulf off northwest Florida; and IV, the western Atlantic Ocean off South and North Carolina.

Procedures for processing gonads, weighing, and measuring fish followed the methods of Finucane and Collins (1984). If no total weight had been recorded for a fish, we estimated TW by using the formula $TW = 1.4959 \times 10^{-5} (FL)^{2.89284}$ (TW = total weight in grams; FL = fork length in millimeters). This formula (Ricker 1975) was derived

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[2]Houde, E. D., J. C. Leak, C. E. Dowd, S. A. Berkely, and W. J. Richards. 1979. Ichthyoplankton abundance and diversity in the eastern Gulf of Mexico. Part I: Executive summary, abstract, text reference. Unpubl. manuscr., 119 p. Draft Final Report to Bureau of Land Management, Contract AA550-CT7-28. Rosenstiel School of Marine and Atmospheric Science, University of Miami, Miami, FL 33149.

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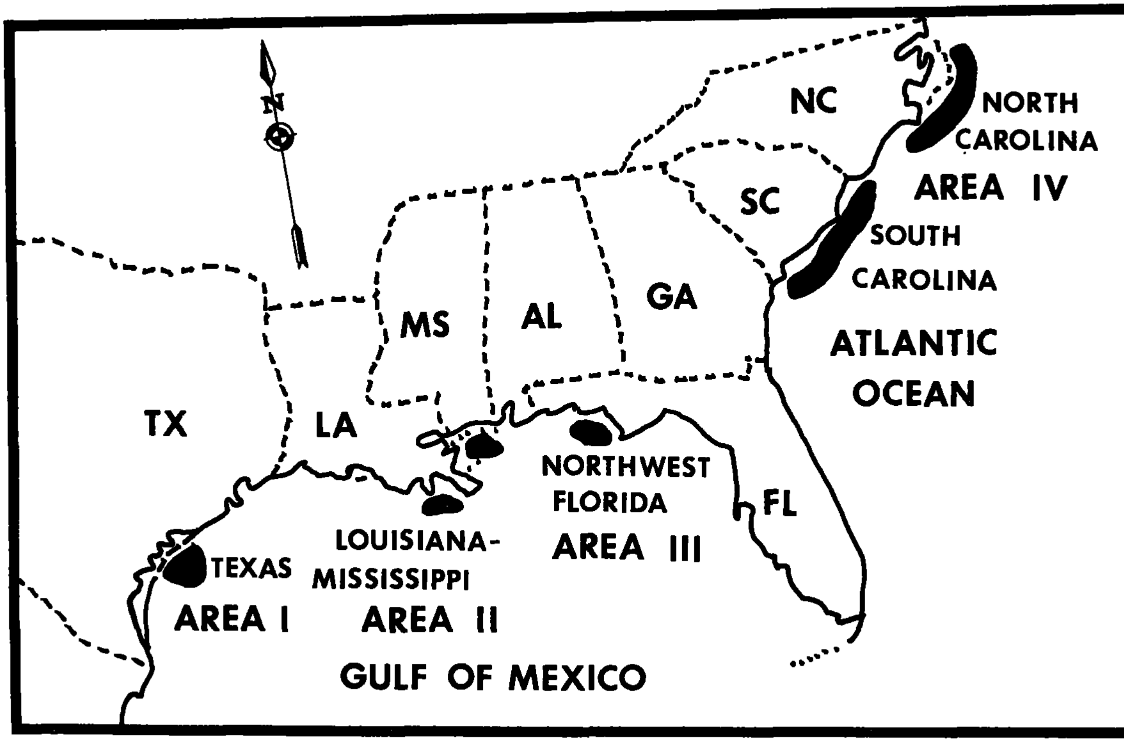

FIGURE 1.—Sampling areas for king mackerel, *Scomberomorus cavalla*, in the Gulf of Mexico and Atlantic Ocean during 1977-78.

from a length-weight regression (r = 0.996; n = 186) of king mackerel data from all areas.

Egg size distributions within the ovary were statistically compared to ensure that subsamples taken for studies of maturation and fecundity were representative (Yuen 1955; Otsu and Uchida 1959). Both ovarian lobes were divided into three sections (anterior, middle, and posterior) of about equal length. At a selected point along each of these sections, a 2-4 mm thick cross section was cut and removed. A wedged-shaped portion was then taken from each of the three cross sections and divided into three zones: inner, middle, and outer. A sample of 150 yolked eggs from each of the zones was examined with a microscope and all eggs were measured to the nearest 0.02 mm at 500× on whatever axis the egg happened to be located in respect to an ocular micrometer scale (Clark 1934). A chi-square test of independence (Steel and Torrie 1960) was used to test for significant differences in mean egg diameters (EDs) among the sections, zones, and zones within a section in each lobe.

Each wedge-shaped sample of eggs was placed in a dish with 10% Formalin[8] and the eggs were then teased apart. Samples containing only unyolked eggs (≤0.20 mm ED) were considered to be from immature fish and only 100 eggs from these samples were measured. Samples with yolked eggs (≥0.20 mm ED) were considered to be from mature fish and 300 eggs were measured.

Seasonal maturation was determined by plotting monthly mean EDs of the most advanced eggs found in each ovary and by gonadosomatic indices (GSI = the percentage of TW represented by gonad weight). The range and 95% confidence interval of the monthly mean GSIs were also plotted. To compare the variation of GSIs, we calculated the coefficient of variation for each month. We estimated the length at which the fish first matured by computing mean GSIs for fish in each 50 mm interval and used the length at which the greatest increase in mean GSIs between consecutive FL intervals occurred. For this analysis we only used data that were collected during the fish's most sexually active months as indicated by the highest values of mean EDs and GSIs. An additional estimate was made for females by assigning immature or mature status to each fish according to egg stage and then calculating the percentage of mature fish by FL intervals.

[8]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Fecundity estimates were based on the number of yolked eggs ⩾0.20 mm in diameter in the most mature ovaries. Similar methods were discussed by Hunter and Goldberg (1980) and used by Morse (1980). A diameter of 0.20 mm was used to separate immature and mature eggs, because it was at this size that yolk first appeared. A gravimetric method was used for fecundity and followed the procedures of Finucane and Collins (1984). Ages of fish were determined from otoliths (Johnson et al. 1983). Analysis of covariance was used to test for differences in fecundity by year and area. Regression and correlation were used to examine the linear and curvilinear relationships between fecundity and fork length, total weight, and age.

RESULTS

Gonads from 1,165 female and 593 male king mackerel were examined. Fish ranged in FL from 351 to 1,554 mm, in TW from 658 to 31,780 g, and in age from 1 to 13 yr. Temporal coverage varied from 3 mo in area I to 12 mo in area II. Number and percentage composition of fish by area were area I, 85 and 4.8%; area II, 646 and 36.7%; area III, 768 and 43.7%; and area IV, 259 and 14.7%.

Analysis of the egg size distribution indicated that there were significant differences (α = 0.05) in ED between the inner, middle, and outer zones within ovarian sections; there were no differences between sections. Therefore, we took a wedge-shaped sample (representing the three cross-sectional zones) from the middle of the right or left ovary as representative of the entire ovary for ED analysis. King mackerel ovaries were grouped into five reproductive stages based on ED. Stage I (immature ovaries) contained eggs ⩽0.06 mm. Eggs in stage II (resting ovaries) ranged from 0.07 to 0.20 mm. Stage III (maturing) and stage IV (mature) ovaries contained eggs 0.21-0.50 mm and 0.51-0.71 mm, respectively. Stage V eggs measured 0.71-1.20 mm and indicated ripe ovaries.

The seasonal progression of mean GSIs and EDs indicated that king mackerel have a prolonged spawning season that varied between areas (Figs. 2-5). Peak spawning months occurred from May through September as observed in 14 ripe females from areas I, II, and IV. A few fish were in spawning condition as early as April and as late as October. In area I, GSIs and EDs peaked in July and August for both sexes. Area II fish had the highest GSIs and EDs for both sexes during May. In area III, GSIs for both sexes were greatest during June

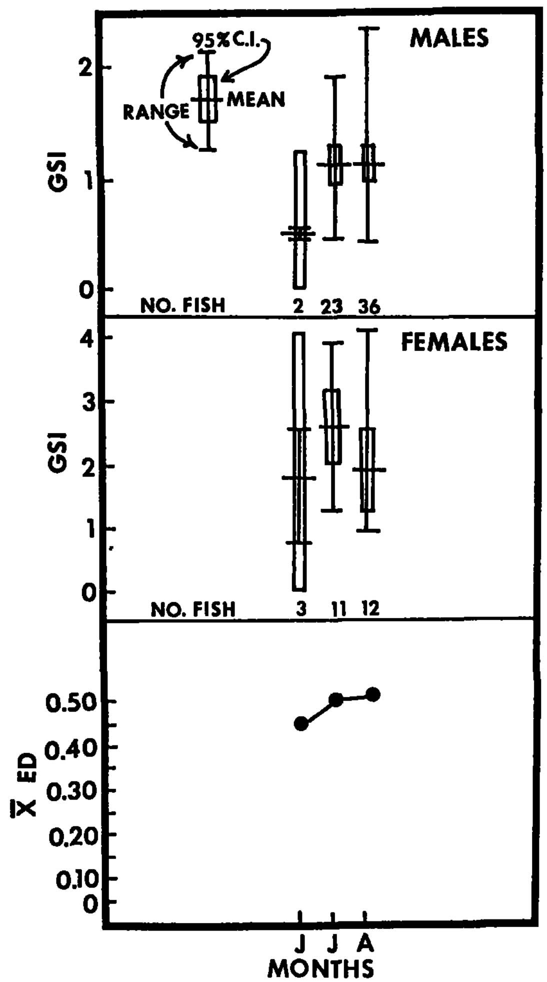

FIGURE 2.—Seasonal maturation cycle of male and female king mackerel from area I (Texas) shown by monthly gonadosomatic index (GSI) and mean egg diameters (EDs) in mm.

while EDs peaked in August. Area IV fish had the highest female GSIs and EDs during July.

Serial spawning was suggested by several lines of evidence. Distribution of EDs was multimodal during spawning months. The highest coefficient of variation for GSIs occurred during the spawning months, suggesting that eggs were maturing and released serially throughout the spawning season (Table 1).

The size at maturation of king mackerel also varied between areas. Maturity was based on the number and percentage of fish with stage III-stage V ova for each 50 mm FL interval. Length intervals in which at least 50% of the females were mature for areas I-IV, respectively, were 450-499 mm, 600-649 mm, 600-649 mm, and 650-699 mm

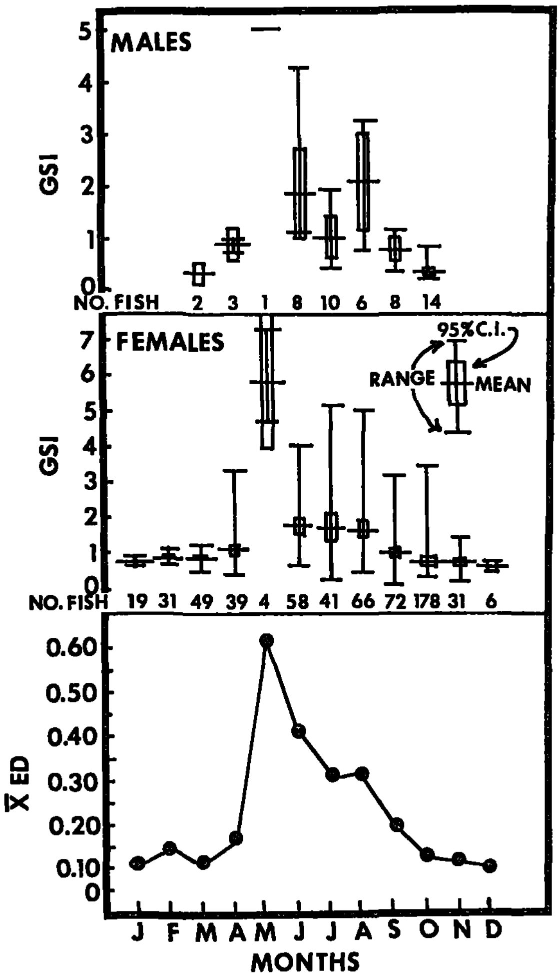

FIGURE 3.—Seasonal maturation cycle of male and female king mackerel from area II (Louisiana and Mississippi) shown by monthly gonadosomatic index (GSI) and mean egg diameters (EDs) in mm.

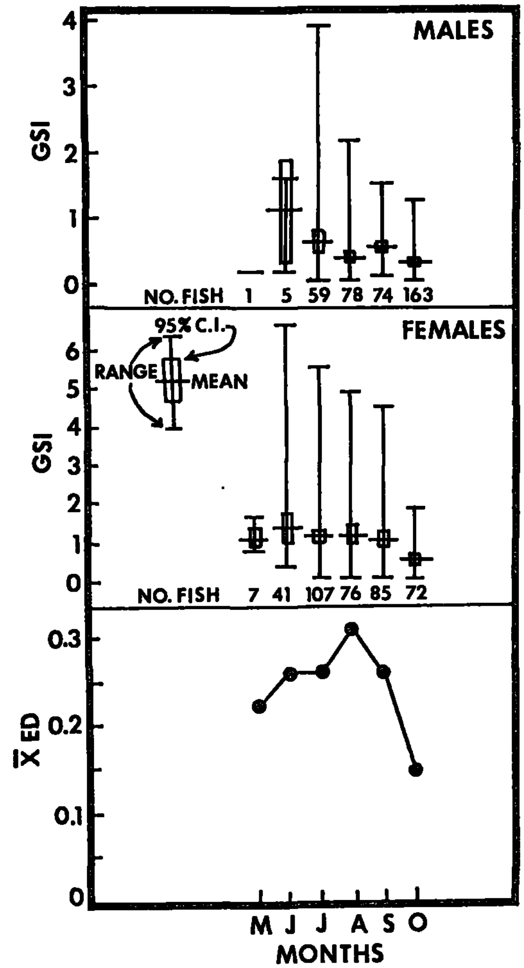

FIGURE 4.—Seasonal maturation cycle of male and female king mackerel from area III (northwest Florida) shown by monthly gonadosomatic index (GSI) and mean egg diameters (EDs) in mm.

TABLE 1.—Coefficient of variation for monthly GSIs of female (F) and male (M) king mackerel in each area.

	Area I		Area II		Area III		Area IV	
Month	F	M	F	M	F	M	F	M
January	—	—	12.7	—	—	—	—	—
February	—	—	12.5	—	—	—	—	—
March	—	—	18.0	7.1	—	—	—	—
April	—	—	43.6	15.3	—	—	—	—
May	—	—	20.4	[1]	28.2	—	56.3	52.9
June	51.7	16.0	55.0	57.1	96.9	56.4	39.1	—
July	33.6	35.4	77.3	58.2	95.5	104.8	36.2	[1]
August	54.2	38.9	66.2	43.4	95.5	75.7	44.4	2.5
September	—	—	56.7	38.7	85.9	51.9	64.9	61.5
October	—	—	36.8	48.4	62.7	51.6	41.7	54.5
November	—	—	32.8	—	—	—	—	—
December	—	—	20.0	—	—	—	—	—

[1]$n = 1$

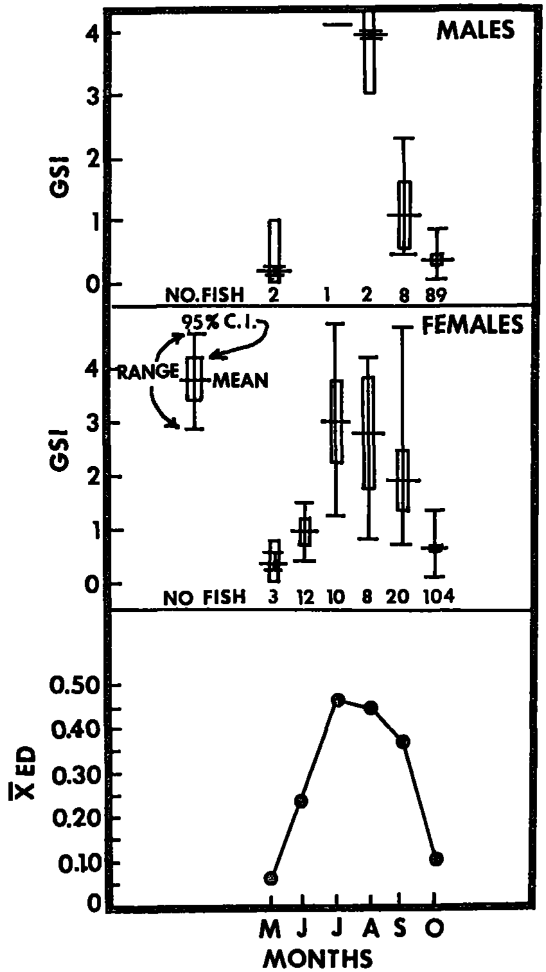

FIGURE 5.—Seasonal maturation cycle of male and female king mackerel from area IV (North and South Carolina) shown by monthly gonadosomatic index (GSI) and mean egg diameters (EDs) in mm.

(Table 2). All females were mature at 850-899 mm. Another maturation pattern was noted when the midpoints of fork length intervals were plotted against mean GSIs for each area (Fig. 6). The size interval where greatest increases in GSIs occurred were 650-699 mm (area I), 700-749 mm (area II), 450-499 mm (area III), and 650-699 (area IV).

Fecundity ranged from 69,000 to 12,207,000 eggs in 65 king mackerel from all areas. Fish ranged in FL from 446 to 1,489 mm, in TW from 681 to 25,610 g, and in age from 1 to 13 yr (Table 3). Analysis of covariance with TW as the covariate showed no significant differences (α = 0.05) in fecundity between years or among areas. The best predictor of fecundity based on regression and correlation analysis was TW for areas II, IV, and all areas combined and FL for areas I and III (Table 4). Log transformed linear models were better predictors of fecundity than nontransformed models in all areas but area IV.

DISCUSSION

Our results on the seasonal maturation and protracted spawning season of king mackerel agree closely with other studies. In waters off Florida, Beaumariage (1973) found late-maturing (stages III and IV) eggs in king mackerel from May through October. In the northeastern Gulf of Mexico (area III), Dwinell and Futch (1973) caught king mackerel larvae during the same time interval and MacGregor et al. (1981) reported early- or late-maturing ovaries from August through October. In the northwestern Gulf of Mexico off Texas (area I), Finucane and Collins (1977) and McEachran et al. (1980) noted catches of larvae from May through August, and April through October, respectively. In the area off Cape Fear, NC, to Cape Canaveral, FL, Powles[4] collected king mackerel larvae from May through September.

Length at maturation was difficult to determine because the sample size of small fish (<600 mm) was limited in all areas except area III (northwest Florida). Using only fish from this area, maturity first occurred about 450-499 mm and 50% of the fish were mature at about 550-599 mm. These estimates of maturity agreed with some of the other studies. Female king mackerel first reached sexual maturity at 630 mm and 4 yr of age (Gesteira and Mesquita 1976) or at 586 mm (Alves and Tome 1967) off Brazil. Another study on Brazilian fish, however, noted that females were first mature at 770 mm and 5-6 yr of age (Ivo 1972). In Florida waters, Beaumariage (1973) estimated that females 3 yr or younger were immature and probably had not spawned. He believed that the first major spawning by females and males occurred at 880 and 770 mm SL, respectively. Some of his 1-yr-old females contained stage IV eggs that had been aborted or reabsorbed since he did not find ripe (stage V) eggs until the fish were 4 yr old. His standard length for king mackerel from Florida at age 1 was 610 mm (651 mm FL), which was higher than our estimate of length at first maturity.

[4]Powles, H. W. Abundance and distribution of king mackerel, (*Scomberomorus cavalla*) and Spanish mackerel (*S. maculatus*) larvae of the southeast United States. Unpubl. manuscr. Gouvernement du Canada, Peches et Oceans, Division des Sciences halieutiques, C. P. 15500, Quebec, Canada G1K 7Y7.

TABLE 2.—Total sample number and percentage of mature (Stages III-V) king mackerel females collected during the peak maturation season in each area.[1]

	Area I (Texas)		Area II (Louisiana, Mississippi)		Area III (Northwest Florida)		Area IV (North and South Carolina)	
Fork length	No.	Mature (%)	No.	Mature (%)	No.	Mature (%)	No.	Mature (%)
300-349	0	—	0	—	0	—	0	—
350-399	1	0.0	0	—	1	0.0	0	—
400-449	0	—	0	—	2	0.0	0	—
450-499	1	100.0	0	—	3	33.3	0	—
500-549	0	—	0	—	16	6.3	0	—
550-599	0	—	0	—	28	46.4	0	—
600-649	2	100.0	2	100.0	31	71.0	1	0.0
650-699	0	—	0	—	31	71.0	4	75.0
700-749	4	100.0	1	100.0	35	80.0	2	100.0
750-799	8	100.0	0	—	29	62.1	5	100.0
800-849	6	100.0	0	—	41	75.6	4	100.0
850-899	2	100.0	5	100.0	29	100.0	11	100.0
900-949	2	100.0	6	100.0	21	100.0	8	100.0
950-999	0	—	22	100.0	19	100.0	7	100.0
1,000-1,049	0	—	19	100.0	13	100.0	3	100.0
1,050-1,099	0	—	18	100.0	4	100.0	3	100.0
1,100-1,149	0	—	18	100.0	6	100.0	1	100.0
1,150-1,199	0	—	13	100.0	4	100.0	1	100.0
1,200-1,249	0	—	18	100.0	2	100.0	0	—
1,250-1,299	0	—	14	100.0	1	100.0	0	—
1,300-1,349	0	—	17	100.0	0	—	0	—
1,350-1,399	0	—	11	100.0	0	—	0	—
1,400-1,449	0	—	3	100.0	0	—	0	—
1,450-1,499	0	—	2	100.0	0	—	0	—
Total	26		169		316		50	

[1]Area I, June-August; Area II, May-August; Area III, May-September; and Area IV, June-September.

Factors influencing the maturation cycle of king mackerel are not well known. Presumably, photoperiod and water temperature are important for spawning, egg, and larval development. Beaumariage (1973) indicated that seasonal changes in photoperiod influenced the spawning of king mackerel while McEachran et al. (1980) noted that larvae were more abundant at temperatures from 20.2° to 29.8°C and salinities from 28.2 to 34.4‰. A study by MacGregor et al. (1981) also showed that the levels of serum androgens and estrogens may be indicators of maturation in king mackerel.

Our inferences on spawning peaks and activity of king mackerel, as determined by largest mean EDs, usually coincided with those of other studies. Our largest mean ED of 0.61 mm agrees with the 0.60 mm reported by Alves and Tome (1967). In contrast, the largest mean ED of 0.33 mm shown by Beaumariage (1973) suggests that most of his fish were not ready to spawn. Our largest mean egg sizes from northwest Florida fish were similar to those reported by Beaumariage (1973) and probably indicates that spawning activity off the west coast of Florida is not extensive. Peak spawning months by area in this study were area I, August; area II, May; area III, August; and area IV, July. In the northwestern and northeastern gulf, (our areas I and III) the highest catches of larval king mackerel occurred during September (Dwinell and Futch 1973; McEachran et al. 1980). Houde et al. (fn. 2) stated that because of their rare catches of larvae, king mackerel does not appear to spawn frequently in the eastern gulf.

The reproductive cycle of king mackerel off the coast of Brazil is probably similar to that of this species from American waters. Ivo (1972) noted that spawning occurred throughout the year off the state of Ceara which is south of the Equator. Other studies indicate that they begin to spawn from October through December (Menezes 1969) with peaks in November and March (Gesteria and Mesquita 1976). Since the seasons are reversed in this area, they would correspond to our spring and late summer spawning peaks for king mackerel.

We were unable to determine the number of times individual king mackerel spawn during the year from the data. Beaumariage (1973) concluded that king mackerel were multiple spawners, based on their extended spawning season and presence of several modal groups of yolked eggs. Morse (1980) reported that individual Atlantic mackerel, *Scomber*

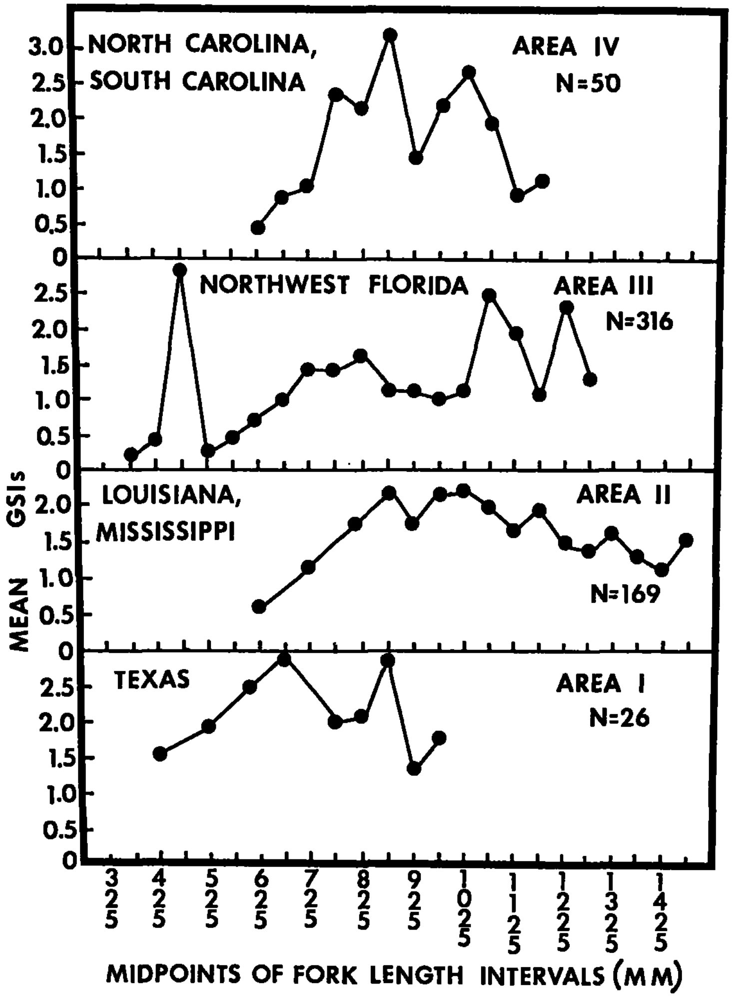

FIGURE 6.—Mean GSI plotted by midpoint of fork length interval for female king mackerel in each area.

scombrus, are capable of spawning six batches of eggs during the spawning season. Documentation of spawning frequency and numbers of eggs produced will require that king mackerel be held in captivity.

Major spawning areas for king mackerel could not be determined during this study because of the scarcity of ripe fish. Gonad maturation data suggest that spawning occurs throughout the sampling areas but the magnitude of spawning and extent of spawning areas are unknown. Ichthyoplankton surveys conducted by Wollam (1970), Houde et al. (fn. 2), and McEachran et al. (1980) have revealed general spawning locations of king mackerel by the occurrence of small larvae (<3 mm SL). These studies indicate that spawning probably occurs over the continental shelf of the northwestern and northeastern Gulf of Mexico. Most small larvae collected by McEachran et al. (1980) were captured over the middle and outer continental shelf in water depths of 35-130 m off the Texas coast.

No comparative fecundity data were available from the southeastern U.S.; however, Ivo (1974) determined fecundity for 39 fish from Brazilian waters. He found great variation in fecundity for fish with the same fork length.

The fact that disjunct spawning appears to occur off the Carolinas and in the northcentral and western Gulf of Mexico from spring through fall may suggest separate stocks of king mackerel in these areas.

TABLE 3.—Summary of data on king mackerel for which fecundity was estimated, 1977-78.

Date	Fork length (mm)	Gonad weight (g)	Total weight (g)	Gonad index (×100)	Age	Fecundity (estimated)
Area I (Texas)						
8/26/78	500	18.16	900	2.02	2	185,608
7/8/78	650	55.66	2,270	2,45	—	985,340
7/26/78	750	76.09	3,042	2.50	4	1,082,301
8/26/78	760	35.23	3,166	1.11	—	466,252
7/8/78	770	92.87	3,405	2.73	2	1,194,283
7/8/78	800	142.53	4,086	3.49	4	2,009,870
7/8/78	810	135.50	4,313	3.14	—	1,435,752
7/8/78	835	82.96	4,540	1.83	4	1,380,342
7/8/78	860	176.00	4,994	3.52	5	2,753,638
7/8/78	870	130.19	4,994	2.61	5	2,236,664
8/7/78	895	212.86	5,448	3.91	6	2,309,622
—	—	239.41	4,183	—	3	4,183,921
Area II (Louisiana)						
6/24/78	446	8.43	681	1.24	—	69,264
6/23/77	635	13.45	1,930	0.70	1	182,863
6/20/77	710	26.92	2,500	1.08	2	2,570,133
9/13/77	852	96.36	4,380	2.20	4	1,179,625
7/13/78	895	158.51	5,130	3.09	4	2,079,204
8/15/77	951	239.09	6,221	3.84	—	4,448,492
5/20/78	972	451.68	7,310	6.18	6	6,319,134
5/20/78	994	577.18	11,120	5.19	6	5,890,631
7/7/78	1,025	325.56	9,000	3.62	6	4,686,248
8/7/78	1,037	417.00	8,325	5.01	6	6,437,542
6/23/78	1,055	314.33	8,626	3.64	11	4,686,598
9/3/77	1,086	303.52	9,750	3.11	—	5,401,961
6/25/78	1,109	247.66	9,534	2.60	—	2,771,744
6/25/78	1,149	401.59	10,896	3.69	9	4,268,537
6/16/78	1,178	478.74	13,286	3.60	6	8,899,756
7/10/78	1,194	447.88	9,045	4.95	10	6,010,133
4/29/78	1,220	498.52	15,150	3.29	9	7,315,781
5/20/78	1,229	698.36	14,070	4.96	6	10,116,890
6/17/78	1,265	611.04	15,095	4.05	9	9,209,082
6/17/78	1,291	468.64	15,890	2.95	10	7,487,826
8/10/77	1,312	583.79	17,120	3.41	—	6,689,189
5/20/78	1,316	840.08	17,800	4.72	10	10,711,026
6/17/78	1,370	570.66	19,885	2.87	11	7,650,064
8/15/78	1,489	815.00	25,610	3.18	13	12,206,888
Area III (Northwest Florida)						
8/8/77	508	9.24	944	0.98	1	196,938
8/8/77	568	11.95	1,318	0.91	1	160,722
8/7/77	608	24.70	1,950	1.27	1	404,982
7/2/78	652	39.53	2,497	1.58	1	688,354
8/14/77	727	105.96	3,180	3.33	2	1,640,497
7/14/77	780	139.64	3,424	4.08	—	2,102,579
6/27/78	816	301.26	4,450	6.64	—	5,049,856
8/7/78	826	167.31	4,903	3.41	2	2,912,649
6/19/77	862	186.02	4,680	3.98	4	2,509,948
7/4/78	906	210.33	5,630	3.74	6	3,005,716
6/27/78	929	96.05	6,492	1.48	—	1,891,588
7/13/77	980	205.49	8,170	2.52	—	3,346,332
7/20/77	1,018	268.22	12,700	2.11	—	4,960,702
6/19/77	1,087	602.45	11,350	5.31	7	5,744,230
8/24/77	1,108	476.06	9,768	4.87	—	5,836,910
9/5/78	1,142	538.60	12,031	4.48	8	8,070,585
8/14/78	1,220	575.39	14,437	3.99	7	7,489,089
Area IV (North Carolina)						
7/13/77	617	171.17	5,765	2.97	—	2,625,338
9/9/78	780	131.11	3,632	3.61	3	1,667,418
7/28/78	841	207.22	5,766	3.59	4	2,330,248
9/21/78	844	100.07	4,722	2.12	4	969,206
7/26/78	865	150.50	4,631	3.25	—	1,639,189
7/15/78	869	227.67	4,767	4.78	—	2,795,451
9/9/78	880	119.88	4,858	2.47	5	1,236,055
7/1/78	900	170.57	6,628	2.57	4	3,321,377
8/27/78	972	214.00	7,173	2.98	6	3,204,055
8/27/78	996	282.01	7,718	3.65	6	2,652,453
9/9/78	1,000	267.35	6,992	3.82	8	2,797,301
8/30/78	1,050	416.04	9,988	4.17	8	6,102,347

TABLE 4.—Regressions of fecundity (F) on total weight (TW), fork length (FL), and age (A) of king mackerel by areas.

Area	Predictor	Equation	r^2
I	TW	$F = 8.554 \times 10^{1}(TW)^{1.465}$	0.745
(TX)	FL	$F = 8.816 \times 10^{-7}(FL)^{4.206}$	0.781
	A	$F = 2.487 \times 10^{5}(A)^{1.390}$	0.373
II	TW	$F = 1.475 \times 10^{1}(TW)^{1.381}$	0.847
(LA-MS)	FL	$F = 9.973 \times 10^{-7}(FL)^{4.175}$	0.840
	A	$F = 4.207 \times 10^{5}(A)^{1.313}$	0.721
III	TW	$F = 1.327 \times 10^{1}(TW)^{1.408}$	0.877
(NWF)	FL	$F = 1.918 \times 10^{-7}(FL)^{4.455}$	0.884
	A	$F = 4.684 \times 10^{5} + 9.494 \times 10^{5}(A)$	0.870
IV	TW	$F = 1.419 \times 10^{6} + (6.658 \times 10^{2})TW$	0.760
(NC-SC)	FL	$F = -2.554 \times 10^{6} + (5.840 \times 10^{3})FL$	0.257
	A	$F = -2.778 \times 10^{5} + (5.579 \times 10^{5})A$	0.436
I-IV	TW	$F = 1.854 \times 10^{1}(TW)^{1.361}$	0.856
(All areas)	FL	$F = 4.391 \times 10^{-6}(FL)^{3.974}$	0.820
	A	$F = 3.399 \times 10^{5}(A)^{1.356}$	0.730

Williams and Godcharles[5] have postulated on the basis of mark-recapture data that two migratory groups occur: one in the South Atlantic and the other in the Gulf of Mexico. Both of their ranges overlap in south Florida.

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