Age, growth, maturity, and spawning of Spanish mackerel, *Scomberomorus maculates* (Mitchill), from the Atlantic Coast of the southeastern United States

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Abstract.—Sectioned sagittae of 1,039 Spanish mackerel, *Scomberomorus maculatus* (Mitchill), from the Atlantic coast of the southeastern United States (North Carolina to Florida) were examined. The oldest male was age 6 and the oldest female age 11. Marginal increment analysis indicated that annulus formation peaks in May–June. The von Bertalanffy growth equation parameters (L_∞, k, and t_0, respectively) were: 538 mm fork length (FL), 0.31, and –2.31 for males; 723 mm FL, 0.24, and –1.80 for females; and, 760 mm FL, 0.18, and –2.44 for sexes combined. Gonads from 1,742 specimens were examined histologically to assess reproductive state. Mature gonads were present in 89% of age-0 males and 100% of older ages, whereas 5% of females were mature at age 0, 95% at age 1, and 100% at older ages. Females matured at 288–450 mm FL and males matured at 209–336 mm FL. Estimates of length at 50% maturity (L_{50}) were 35.8 cm FL for females and 23.9 cm FL for males. Females were in spawning condition from May to August; ripe males were captured April–November. Resting specimens were included in the assessment of maturity and the disadvantages of their inclusion are discussed.

Age, growth, maturity, and spawning of Spanish mackerel, *Scomberomorus maculatus* (Mitchill), from the Atlantic Coast of the southeastern United States*

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The Spanish mackerel, *Scomberomorus maculatus* (Mitchill), is a migratory scombrid of importance to commercial and recreational fisheries in the Gulf of Mexico and along the Atlantic coast of the southeastern United States (Trent and Anthony, 1978). Concerns about overfishing have prompted the establishment of size and bag limits, as well as recreational and commercial landings quotas, with regulations based on the hypothesis that there is an Atlantic migratory group and one or more Gulf of Mexico groups (SAFMC, 1988). Previous studies of the age and growth of Spanish mackerel have been based on specimens from the Gulf of Mexico, or from southeastern Florida where migratory groups are thought to overlap (Klima, 1959; Powell, 1975; Fable et al., 1987; Helser and Malvestuto, 1987). Whole sagittae were examined in these studies, but Collins et al. (1989) found that ages from sectioned otoliths were more accurate than those from whole otoliths for the congeneric king mackerel (*S. cavalla*). Thus, age and growth of Atlantic group Spanish mackerel have not been rigorously examined.

The annual reproductive cycle of Spanish mackerel has been described (Klima, 1959; Beaumariage, 1970; Powell, 1975; Finucane and Collins, 1986), but it has not been clearly established histologically for the Atlantic group. Klima (1959) and Powell (1975) collected specimens from southern Florida, an area where migratory groups may overlap. Of the four studies cited, only Powell (1975) used a histological technique. In previous studies of size and age at maturity, specimens were not clearly from the Atlantic group and age at maturity was not quantified (see Klima, 1959; Powell, 1975), and few small females were examined (see Klima, 1959; Finucane and Collins, 1986). The present study describes the age, growth, size and age at maturity, and reproductive cycle of Spanish mackerel from the Atlantic coast of the southeastern United States.

Methods

Specimens were collected with hook-and-line, trawls, gill nets, and block (stop) nets. Spanish mackerel abundance varies seasonally through most

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of their range owing to their migratory nature, so specimens were also acquired from recreational anglers, commercial gill netters, and seafood dealers throughout the southeastern United States. In addition, Spanish mackerel otoliths collected by the National Marine Fisheries Service (NMFS) Panama City (Florida) Laboratory were made available for this study. All specimens used in the present study were collected between Beaufort, North Carolina and Riviera Beach, Florida. All length measurements refer to fork length (FL). Except for those provided by NMFS, which were measured to the nearest cm, all fish were measured to the nearest mm.

One sagittal otolith from each fish was embedded in paraffin and sectioned (ca. 0.3 mm thick) with a Buehler Isomet saw equipped with a diamond blade. Sections were placed in cedar wood oil and examined under a dissecting microscope with both transmitted and reflected light. Most specimens provided by NMFS were processed similarly, but some consisted of otolith sections mounted on glass slides and were not immersed in cedar wood oil. Ages were assigned by two independent readers without reference to fish lengths or dates of capture. Otoliths considered aberrant by either reader or for which the readers disagreed on ages were deleted from the analyses. Distances from the focus to the margin (otolith radius) and to the distal edge of the opaque portion of each annulus were measured along the dorsal side of the sulcus acousticus with an ocular micrometer at 50× magnification.

Back-calculated lengths at age were computed for males, females, and sexes combined by the Fraser-Lee method (Poole, 1961; Carlander, 1982). The SYSTAT NONLIN module using the quasi-newton method (Wilkinson, 1987) was used to fit von Bertalanffy equations to individual back-calculated lengths at age.

For all specimens except those from NMFS (n=1,742), the posterior portion of the gonads was fixed in 10% seawater-formalin for 1–2 weeks and transferred to 50% isopropanol for 1–2 weeks; samples from NMFS (n=177) consisted only of otolith sections with associated length and macroscopically determined sex (male vs. female) data. Gonad samples were processed with an Auto-Technicon 2A Tissue Processor, vacuum infiltrated, and blocked in paraffin. Three transverse sections (6–8 μm thick) were cut from each sample with a rotary microtome, mounted on glass slides, stained with Harris hematoxylin, and counterstained with eosin-y.

Sex and reproductive state were assessed by one primary reader using histological criteria (Table 1). Sections from 50 randomly selected specimens were examined by a second reader early in the study to verify the assessments of the primary reader. Because only nine ripe female Spanish mackerel were captured, the occurrences of developing and spent females were also used to define the spawning period. Specimens with developing, ripe, spent, or resting gonads were considered sexually mature. For females, this definition of sexual maturity included specimens with oocyte development at or beyond the yolk vesicle stage and specimens with beta, gamma, or delta stages of atresia. The SYSTAT NONLIN module (Wilkinson, 1987) was used to fit a logistic model (% mature=100%/ $1 + e^{-g(L-L_{50})}$) to maturity data in 10 mm length intervals to estimate length at 50% maturity (L_{50}).

Because we were not able to obtain an adequate number of female specimens near the beginning of the spawning season to permit assessment of size/age at maturity, we used specimens collected throughout the year. To use all resting specimens in this assessment, we developed a criterion to distinguish the small percentage (<10%) of resting females with no atresia from immature (had never spawned) females. The criterion was based on the size of chromatin nucleolar (CN; as defined by Wallace and Selman 1981) oocytes, or oogo-

Table 1

Histological criteria used to determine reproductive state in Spanish mackerel, *Scomberomorus maculatus*. CN = chromatin nucleolar. References: Wallace and Selman (1981); Hunter and Macewicz (1985); Wenner et al (1986); West (1990).

Reproductive state	Female	Male
Immature	No atresia; predominance of CN oocytes and oogonia, most <70 μm.	Little or no spermatocyte development; empty lobules not present.
Developing	Primarily yolk vesicle and vitellogenic oocytes.	Spermatocyte development through lobules filled with spermatozoa.
Ripe	Mature oocytes (yolk droplets coalesce and peripheral migration of nucleus); hydrated oocytes.	Predominance of spermatozoa; little spermatogenesis.
Spent	Alpha atresia in >50% of vitellogenic and mature oocytes; beta atresia.	No spermatogenesis; residual spermatozoa in lobules and efferent duct.
Resting	Primarily CN (most >70 μm) and perinucleolar oocytes; beta, gamma, and delta atresia.	Some mitotic regeneration of spermatogonia and interstitial tissues; lobules and efferent duct empty.

nia if CN oocytes were not present. Perinucleolar oocytes were not included because this stage was not present in all immature females.

To develop the criterion, histological sections of ovaries from randomly-selected resting (n=21; 319–449 mm) and immature (n=32; 252–410 mm) females were examined and the area of one lobe was measured with an image analysis system. Five specimens were selected, if available, per 25-mm size interval for each of the two reproductive states. Atresia, which is evidence of previous oocyte development, was present in each resting female, but it was not present in each immature female. The oocytes and/or gonad area in resting females were noticeably larger than those in immature females; additionally, body length (<ca. 290 mm) indicated that some specimens were immature. For each specimen, a histological section and one of two axis orientations on the section were also randomly selected. The minimum and maximum dimensions of each of the five largest CN oocytes along the selected axis were measured and an average diameter was calculated for each oocyte. The largest CN oocytes were selected because previous studies have shown that the size of the largest oocyte can be used to assess ovarian development (see MacGregor, 1957; Greeley et al., 1987). We measured five oocytes instead of one oocyte to more accurately assess the size of the largest oocytes.

The accuracy of the criterion was assessed by comparing the length-frequency distributions of resting females and females with evidence of certain maturity (e.g., developing, ripe, or spent state). Because oocyte diameter and gonad area data were not normally distributed, the Mann-Whitney test was used in statistical analyses.

Results

Otoliths from 1,039 Spanish mackerel were examined, of which 132 were unreadable (i.e., considered aberrant by one or both readers). Readers agreed on ages for 96.5% of readable otoliths. Except for the small, secondary peak caused by the November sample of only seven individuals, the distribution of monthly percentages of otoliths with opaque margins was unimodal. Annual ring formation peaking in May–July is indicated (Fig. 1). Linear regressions of FL on otolith radius (OR) were male FL = 113.8 + 8.3 OR, n=228, r^2=0.55; female FL = 36.2 + 11.6 OR, n=502, r^2=0.71; combined FL = 40.1 + 11.2 OR, n=748, r^2=0.66. Females grew more rapidly and lived longer than males (Table 2). The oldest males were age 6 (n=3) and the oldest females, age 11 (n=2). The von Bertalanffy growth equation parameters (L_∞, k, and t_0, respectively)

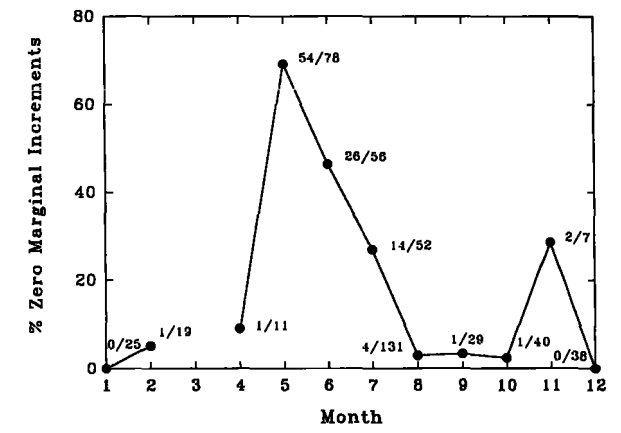

Figure 1
Monthly percentages of Spanish mackerel with marginal increments of zero (= opaque margins), with number of zero marginal increments over number in sample for each month.

were 538 mm, 0.31, and –2.31 for males; 723 mm, 0.24, and –1.80 for females; and, 760 mm, 0.18, and –2.44 for sexes combined. The von Bertalanffy estimates of L_∞ were reasonable compared with maximum observed lengths. One male (600 mm) and two females (760 and 730 mm) exceeded the asymptotic lengths.

All female specimens were used in the assessment of maturity because resting and immature females could be distinguished based on the size of the largest CN oocytes or oogonia if atresia was not present. The largest CN oocytes or oogonia in resting ovaries (with atresia) were significantly larger than those in immature ovaries (Fig. 2; U=633, P<0.001, df=1). The average diameter of these oocytes was usually >70 µm in resting ovaries. It was not necessary to use the CN oocyte/oogonium criterion often because >90% of the resting ovaries had beta or delta stage, and with less frequency gamma stage, atretic follicles. Gonad area was also larger in resting ovaries compared to immature ovaries (U=43, P<0.001, df=1; immature= 3.78+ 3.24 mm^2 per lobe; resting=9.93+3.33 mm^2 per lobe); however, oocyte characteristics should be used to assess reproductive state.

Use of the CN oocyte/oogonium criterion to assess maturity was not free of error, as the CN oocyte/oogonium size distributions for resting and immature females overlapped at 60–80 µm (Fig. 2). This error was negligible because the length-frequency distributions of resting females and females with evidence of certain maturity (e.g., developing, ripe, or spent state) overlapped, and the smallest individuals of both groups were in the same size interval (Fig. 3).

Female spanish mackerel become sexually mature later and at a larger size than males. Mature gonads

Table 2

Mean observed lengths at capture (mm FL) and mean back-calculated lengths at age for Spanish mackerel, by sex and for sexes combined.

Age	No. of specimens	Mean observed length at capture	Mean back-calculated lengths at successive annuli										
			1	2	3	4	5	6	7	8	9	10	11
Males													
1	58	372	332										
2	45	409	344	396									
3	37	430	345	393	423								
4	34	454	346	397	426	449							
5	22	504	364	416	448	475	499						
6	3	469	329	383	411	430	449	466					
	Total number		199	141	96	59	25	3					
	Weighted mean		343	399	429	458	493	466					
Females													
1	129	402	343										
2	124	465	362	444									
3	93	520	371	453	508								
4	49	560	366	446	501	546							
5	32	595	364	441	495	537	581						
6	7	636	363	448	500	548	594	630					
7	4	685	390	468	528	570	610	646	679				
8	3	690	328	419	482	529	569	609	642	675			
9	0	—	—	—	—	—	—	—	—	—	—		
10	0	—	—	—	—	—	—	—	—	—	—	—	
11	2	745	364	446	503	541	573	606	632	665	686	718	740
	Total number		443	314	190	97	48	16	9	5	2	2	2
	Weighted mean		359	447	503	544	584	627	657	671	686	718	740
Sexes combined													
1	190	393	337										
2	171	450	353	430									
3	134	494	358	433	482								
4	83	517	349	421	468	506							
5	54	558	354	424	472	510	548						
6	10	586	345	424	470	510	550	581					
7	4	685	392	469	529	571	610	646	679				
8	4	687	337	426	514	538	577	615	646	677			
9	0	—	—	—	—	—	—	—	—	—	—		
10	0	—	—	—	—	—	—	—	—	—	—	—	
11	2	745	366	441	504	542	574	606	632	665	686	718	740
	Total number		652	462	291	157	74	20	10	6	2	2	2
	Weighted mean		349	429	477	511	553	603	657	673	686	719	740

were present in 5% of the females at age 0, 95% at age 1, and 100% at age ≥2 (Table 3). Eighty-nine percent of the males were mature at age 0 and 100% at age ≥1 (Table 4). Estimates of L_{50} were 35.8 + 0.2 cm (SE) for females and 23.9 + 0.3 cm (SE) for males. The smallest mature female was 288 mm, and the largest immature female was 450 mm (Table 3). The smallest mature male was 209 mm, and the largest immature male was 336 mm (Table 4).

The combined percentage total of developing, ripe, and spent females by month indicated that May through August was the spawning period (Fig. 4). Ripe females were collected in inner continental shelf waters with a depth of ca. 9 m. They were collected in August in Onslow Bay (North Carolina) and off Cumberland Island (Georgia), and in May off Charleston (South Carolina). Males were present in ripe condition for a longer period (April–November) than were females (Fig. 4).

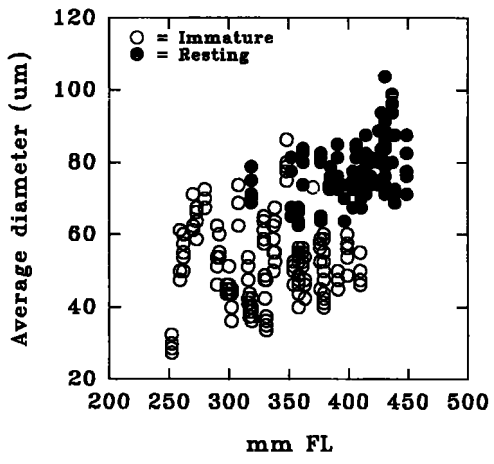

Figure 2

Individual average diameters (minimum + maximum dimensions/2) of the five largest chromatin nucleolar oocytes or oogonia along a randomly selected axis of a histological section from immature (n=32) and resting (n=21) Spanish mackerel, *Scomberomorus maculatus*.

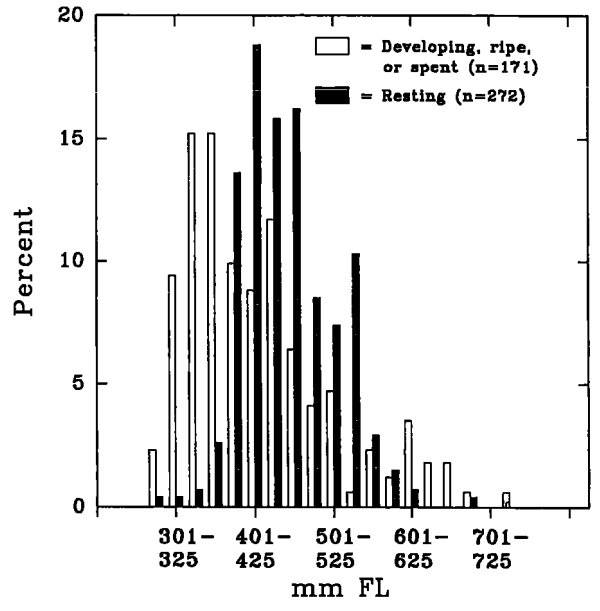

Figure 3

Length-frequency distributions for female Spanish mackerel, *Scomberomorus maculatus*, with evidence of certain maturity (e.g., developing, ripe, or spent state) and those in the resting state. All specimens examined histologically.

Table 3

Percentage of mature specimens by size class in 1136 female Spanish mackerel, *Scomberomorus maculatus*. Specimens in the developing, ripe, spent, or resting reproductive states were considered mature. All specimens were examined histologically. n = number of specimens.

mm FL	Age 0		Age 1		Age >1		No age	
	%	*n*	%	*n*	%	*n*	%	*n*
151–175							0	(2)
176–200							0	(10)
201–225							0	(72)
226–250							0	(117)
251–275	0	(1)					0	(125)
276–300	0	(16)	67	(3)			4	(84)
301–325	7	(55)	83	(6)			14	(56)
326–350	2	(48)	87	(15)			29	(56)
351–375	5	(20)	85	(13)	100	(1)	70	(33)
376–400	0	(11)	100	(19)	100	(16)	88	(25)
401–425	100	(1)	100	(26)	100	(21)	96	(24)
426–450	100	(1)	100	(20)	100	(28)	94	(18)
451–475			100	(15)	100	(30)	100	(12)
476–500			100	(5)	100	(23)	100	(7)
501–750			100	(1)	100	(68)	100	(32)
Totals	5	(153)	95	(123)	100	(187)		673

Table 4

Percentage of mature specimens by size class in 606 male Spanish mackerel, *Scomberomorus maculatus*. Specimens in the developing, ripe, spent, or resting reproductive states were considered mature. All specimens were examined histologically. n = number of specimens.

mm FL	Age 0		Age >0		No age	
	%	*n*	%	*n*	%	*n*
151–175					0	(1)
176–200					0	(12)
201–225					18	(50)
226–250					62	(68)
251–275	100	(1)			79	(93)
276–300	33	(3)	100	(1)	84	(57)
301–325	87	(23)	100	(3)	100	(21)
326–350	96	(23)	100	(13)	94	(18)
351–375	100	(2)	100	(18)	100	(23)
376–400			100	(28)	100	(27)
401–425			100	(35)	100	(9)
426–600			100	(54)	100	(23)
Totals	89	(52)	100	(152)		(402)

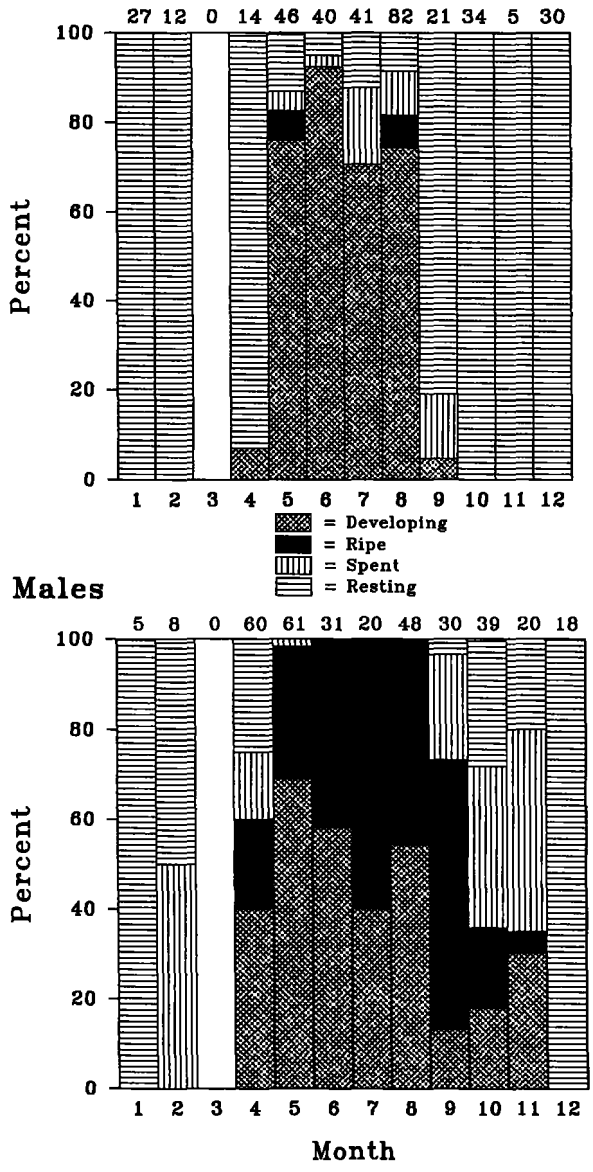

Figure 4

Percentage composition of reproductive states by month for 340 female and 352 male Spanish mackerel, *Scomberomorus maculatus*, based on histological criteria. Number of specimens examined is above the bar.

Discussion

While we lack direct evidence that growth rings on otoliths are deposited annually, indirect evidence supports that hypothesis. Otolith radius and FL are proportional as defined by the linear regression analysis, and the mean observed and back-calculated lengths at age agreed reasonably. In addition, the growth rings on otoliths apparently formed during a 2 to 3 month period. The relatively high (29%) percentage of otoliths with opaque margins in November was likely an artifact of the very small sample size (7) for that month.

The period of annulus formation that we observed agrees well with previous reports. Powell (1975) found that annuli formed during May–July in "Florida" (i.e. Gulf of Mexico and Atlantic) Spanish mackerel. Annulus formation may be slightly earlier (March–May) in fish from the northern Gulf of Mexico (Fable et al., 1987).

We found two 11-year-old fish, extending the reported longevity of Spanish mackerel slightly. Klima's (1959) oldest fish were 6 years old, Powell's (1975) was 8 years old, and Fable et al. (1987) reported one 9-year-old fish. Our mean back-calculated lengths at age tended to be slightly smaller than those of Powell (1975) after his standard lengths were converted to fork lengths (using his equations), and our values for von Bertalanffy asymptotic lengths (L_∞) were similar to his (555 mm for males, 694 mm for females). In comparison to the back-calculated lengths (Atlantic and Gulf of Mexico samples combined) of Fable et al. (1987), our back-calculated lengths were greater at age 1 and smaller at older ages. Their estimate of asymptotic length for females was similar to ours, but their estimate for males (794 mm) was much larger. Fable et al. (1987) reported greater asymptotic lengths for males than for females, while other studies found the reverse to be true (Powell, 1975; Helser and Malvestuto, 1987; present study). Powell (1975) excluded the oldest fish from all analyses owing to small sample sizes (19 fish age 6–8). Fable et al. (1987) used all age classes regardless of sample size and concluded that the resulting growth parameters were more realistic than those reported by Powell (1975). Whether the differences in growth parameter estimates between this and previous studies are due to methodological differences (e.g., sectioned vs. whole otoliths) or to differences in geographical coverage is not known.

Examination of 547 female Spanish mackerel <325 mm FL in the present study confirmed the lower limit of size at maturity reported by Finucane and Collins (1986), who based their estimate on nine specimens <325 mm FL from Georgia and the Carolinas (Table 5). Our estimate of size at maturity for females was higher than the estimate of Klima (1959). We found that males matured at smaller sizes than reported by Klima (1959) and Finucane and Collins (1986). These differences probably reflect the greater accuracy resulting from our histological versus their macroscopic methods.

Our age-at-maturity data generally concurred with the qualitative data in previous studies showing that female and male Spanish mackerel mature at ages 0–1 (Table 5). Using a histological method, Powell (1975)

Table 5
Summary of information available on size/age at maturity in Spanish mackerel, *Scomberomorus maculatus*.

Study and location	Size at maturity (mm FL)		Age at maturity (yr)	
	female	male	female	male
Present study; N. Carolina to SE Florida	288–450	209–336	0–1	0
Finucane and Collins (1986); Georgia and Carolinas	275–424	275–399	—	—
Powell (1975); South Florida, both coasts	—	—	1–?	—
Klima (1959); SE Florida	250–320	280–340	[1]1–2	[1]1–2

[1]Ages should be reduced by one year (see Powell [1975]).

found vitellogenic and/or mature oocytes in >50% of age-1 females sampled in Florida (Atlantic and Gulf coasts) during April through September. Klima (1959), using a macroscopic method, found that unreported percentages of ages 1–2 females and males were mature; however, Powell (1975) concluded that the ages in Klima (1959) should be reduced by one year. Thus, according to Powell (1975), the data reported by Klima (1959) showed that some age-0 specimens were mature. We found that more males than females (89% vs. 5%) were mature at age 0; most females matured at age 1.

Our data on the annual reproductive cycle agreed well with previous conclusions based on gonad condition (Beaumariage, 1970; Finucane and Collins, 1986) and on occurrence of larvae (Collins and Stender, 1987). Spawning occurs in Atlantic group females from mid-spring through summer. For males, we concurred with Finucane and Collins (1986) that developing or running ripe males are present from mid-spring through early fall.

Our method of assessing maturity was less efficient and perhaps less accurate than the method used by Hunter et al. (1992) for Dover sole, *Microstomus pacificus*. Hunter et al. (1992) collected specimens prior to the spawning period, when oocyte development was at the vitellogenic stage. Ovaries without yolked oocytes, postovulatory follicles, or atresia were considered immature. The primary advantages of their method are that specimens are collected over a shorter period of time and that it is not necessary to develop a criterion to distinguish resting and immature females. We were unable to acquire a sufficient number of specimens at the appropriate time to use their methodology.

Our conclusions concerning size and age at maturity were based on samples solely from the Atlantic migratory group, on ages from sectioned sagittae, and on histological examination of gonad tissue. Most female Spanish mackerel mature at age 1 and at lengths greater than 36cm FL (L_{50}). The minumum legal length for Spanish mackerel is currently set at 12 inches (30.5 cm) FL by the South Atlantic Fishery Management Council and most southeastern Atlantic states have adopted the same regulation. Thus, the harvest of age-0 immature females is permitted. Federal and state agencies responsible for the management of Atlantic group Spanish mackerel may wish to reexamine minimum length regulations in light of our results.

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