AGE AND GROWTH OF SPANISH MACKEREL, *SCOMBEROMORUS MACULATUS*, FROM FLORIDA AND THE GULF OF MEXICO

WILLIAM A. FABLE, JR., ALLYN G. JOHNSON, AND LYMAN E. BARGER[1]

ABSTRACT

Otoliths from 1,787 Spanish mackerel, *Scomberomorus maculatus*, were used to estimate age and growth rates of this species from Florida and the Gulf of Mexico. There was a wide range of lengths within an age group: the oldest male was 7 years old, while the oldest female was 9 years old. Length at age was significantly different for sexes, sampling areas, and collection gear. The von Bertalanffy growth equations were as follows: males (all areas combined) $l_t = 794\ (1 - e^{-0.24(t + 0.94)})$; females (all areas combined) $l_t = 739\ (1 - e^{-0.33(t + 0.99)})$; males (Florida only) $l_t = 776\ (1 - e^{-0.27(t + 0.73)})$; females (Florida only) $l_t = 731\ (1 - e^{-0.38(t + 0.73)})$, where l = fork length (mm) and t = years.

Spanish mackerel, *Scomberomorus maculatus*, are found in the western Atlantic Ocean from the Gulf of Maine to the Yucatan Peninsula (Collette et al. 1978), and have their center of abundance off Florida (Trent and Anthony 1978). They support extensive commercial and recreational fisheries in the U.S. south Atlantic and Gulf of Mexico. In 1985, U.S. commercial landings totaled 5.8 million pounds (2,631 t) (U.S. Department of Commerce 1986a) while recreational landings were estimated to be 2.1 million pounds (953 t) (U.S. Department of Commerce 1986b). Information on Spanish mackerel published prior to 1978 actually concerned two species, *S. maculatus* and *S. brasiliensis* (Collette et al. 1978). Collette et al. (1978) determined that Spanish mackerel south of the Yucatan Peninsula (on the Central and South American Atlantic coasts) are *S. brasiliensis*, and those along U.S. coasts are *S. maculatus*.

There is disagreement in the literature on the interpretation of annuli on otoliths of Spanish mackerel. The first information on age and growth of *S. maculatus* was from fish collected in southeast Florida (Klima 1959). Later, Mendoza (1968) gave some limited age and growth information on *S. maculatus* from Veracruz, Mexico, and Powell (1975) provided the most recent information on Spanish mackerel age, growth, and reproduction in Florida. Powell interpreted annuli on Spanish mackerel otoliths differently than did Klima, and the different age determinations yielded different growth estimates. Mendoza (1968) did not estimate growth except by presenting his data in tabular form.

We undertook this investigation to resolve these uncertainties in the literature and to derive more current age and growth parameters. This information will provide a better basis for rational management of this species.

STUDY AREA AND METHODS

We collected 1,929 Spanish mackerel from 1977 through 1981 from the south Atlantic and Gulf of Mexico coasts of the United States. Most (1,422) of the fish came from northwest Florida and only 10 came from north of south Florida on the Atlantic coast (Table 1). Fork length (FL) of each

TABLE 1.—Numbers of Spanish mackerel collected for age and growth study.

Area	Year 1977	1978	1979	1980	1981	Total
Texas	—	48	—	—	—	48
Mississippi/ Louisiana	41	79	—	23	—	143
Northwest Florida	59	377	31	955	—	1,422
South Florida	—	87	31	59	129	306
Georgia	—	10	—	—	—	10
Total	100	601	62	1,037	129	1,929

[1]Southeast Fisheries Center Panama City Laboratory, National Marine Fisheries Service, NOAA, 3500 Delwood Beach Road, Panama City, FL 32407-7499.

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mackerel was measured to the nearest millimeter. Sagittal otoliths were removed, washed, and stored dry. The clearest, most legible otolith from each fish (based on visual observation) was examined to estimate age and growth.

Whole otoliths were placed in a black-bottomed watch glass containing 100% glycerin and examined with a binocular microscope at 28× using reflected light. Otolith radius (OR) was measured in ocular micrometer units (1 unit = 0.0363 mm) on the posterior surface from the focus to the distal margin along the axis of the sulcus acousticus (Powell 1975). Growth marks were counted and measured from the focus along the radius to their distal edge. The marks were opaque (light) under reflected light, while the interspaces were hyaline or translucent (dark).

Otoliths were classified into age groups based on the number of opaque nonmarginal marks (Powell 1975). A mark was considered complete when a hyaline (dark) interspace or margin was visible from successive growth. Three readers independently examined each of 520 otoliths to test the precision of our ageing technique. This information was analyzed using the method of Beamish and Fournier (1981). All other otoliths were independently examined by two readers; if their results did not agree, the data were not used.

To compare age estimates based on surface (whole) and internal (sectional) examination, we sectioned 70 otoliths which had been previously examined on the surface (2-10 otoliths from different fish from each age 0+ through 8+), following the methods of Johnson et al. (1983).

We determined time of annulus formation and validated our ageing technique by comparing monthly percentage frequencies of otoliths with opaque margins. A high percentage frequency (>45%) indicated recent annulus formation. We used a chi-square test to compare the monthly frequencies.

The relationship between otolith radius and fork length was determined and used to back calculate fork lengths at earlier ages (Tesch 1971; Ricker 1975; Everhart et al. 1975). We used analysis of covariance (ANCOVA) with age as the covariate to test for differences in growth rates (lengths at age) of fish collected in different locations, by different gears, and of different sexes. Mean back-calculated lengths were used to calculate von Bertalanffy (1938) growth parameters, employing a computer program developed by Abramson (1971).

RESULTS AND DISCUSSION

Validation

Age validation has often been overlooked in the age and growth literature (Beamish and McFarlane 1983). Although there are numerous methods available to establish the annual nature of otolith growth rings, we applied marginal increment analysis, because it was the only practical method to use on this migratory, pelagic species.

Annulus formation occurred in March, April, or May (Fig. 1). A chi-square test ($\chi^2 = 338.47$, df = 1, $P < 0.001$) showed a highly significant difference between the occurrence of otoliths with opaque margins in these months versus the other nine months of the year. Our findings are in agreement with Powell (1975) in that the main period of opaque mark formation was in the spring or early summer. He reported mark formation in May, June, and July by examination of marginal increments. Previously Klima (1959) described both summer and winter growth rings and evaluated the marginal condition to decide that marks were deposited annually. Our observations on the appearance of annuli in Spanish mackerel otoliths agreed with Powell (1975), in that we also were unable to discern the "first winter mark" that Klima (1959) described.

Age

To estimate the precision of our ageing, we compared sections to whole otoliths and evaluations by different readers. Examination of 70 sectioned otoliths provided a 97.4% agreement with previous surface examination of the same otoliths. Surface age determinations of three readers on 520 otoliths had a 97.7% agreement. Using the technique of Beamish and Fournier (1981), the index of average percent error was 0.3273, which we think is excellent.

Of 1,929 Spanish mackerel examined, 1,787 (92.6%), ranging from 148 to 802 mm FL, were aged. The oldest female was 9 years old, while the oldest male was 7 years old. Powell's (1975) oldest fish, a female, was 8 years old, while Klima's (1959) oldest males and females were both 6 years old. These data and the data presented in Tables 2 and 3 indicate that females live longer than males.

We found a wide range of lengths within an age group for both sexes (Tables 2, 3), as did Powell, with some Spanish mackerel of age 0 through 5 in

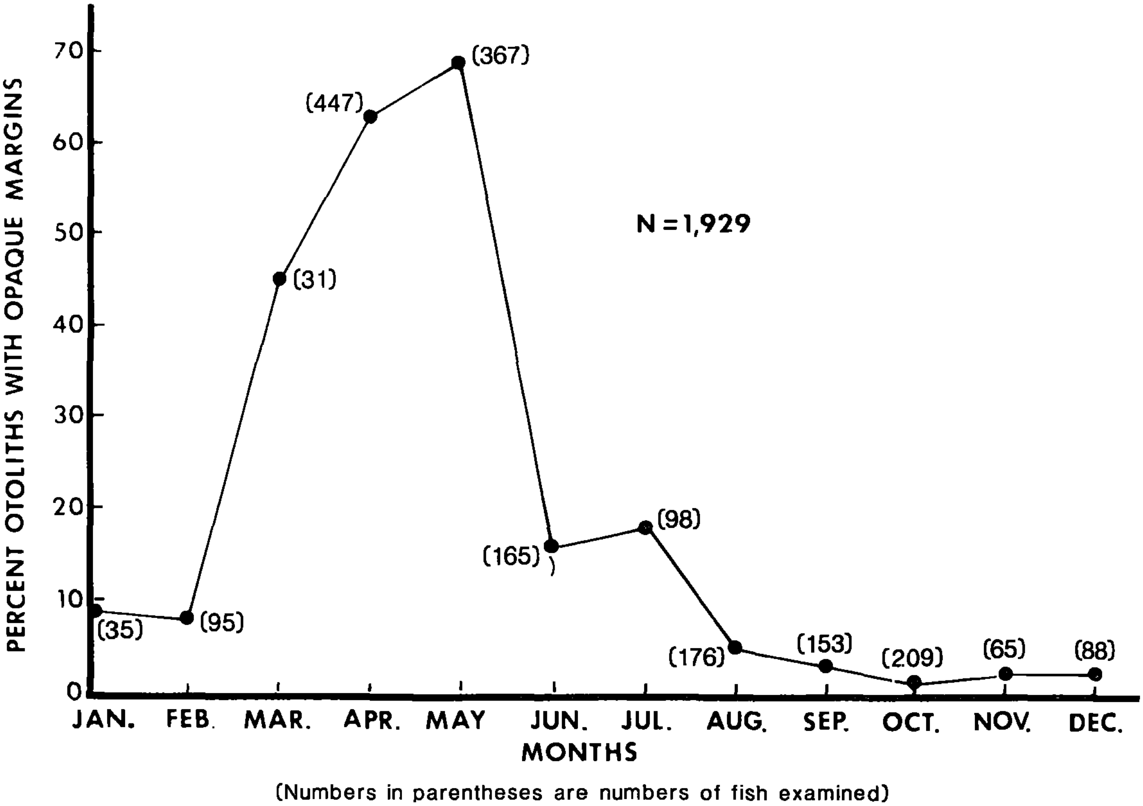

FIGURE 1.—Monthly percentage frequencies of Spanish mackerel otoliths with opaque margins.

the same size interval. In the closely related king mackerel, *S. cavalla*, Johnson et al. (1983) reported a similar situation. Our results substantiate wide variation in growth rates of individual Spanish mackerel.

Growth

Otolith radius (OR) was closely correlated with fish length (FL). The curvilinear relation $FL = 1.5091\ OR^{1.2639}$ ($r = 0.944$) had a slightly better fit than the linear equation $FL = -102.8061 + 6.1295\ OR$ ($r = 0.936$). We used the former equation to back calculate lengths at former ages for 949 fish that had at least one annulus (838 fish had no annuli and were classified as age 0). Neither Klima nor Powell reported any equations for an OR versus FL relationship.

The mean back-calculated annual increments of fork lengths for male and female Spanish mackerel from all areas and years combined (Tables 4, 5) indicate that growth rates were rapid until age 5 in females and to age 6 in males (the age 6 increment in males was based on one fish). After these ages, growth rates slowed appreciably. Early growth was more rapid in females than males (first annual increment 123.6 as compared to 98.7). However, males maintained a higher growth rate through age 6, except for age 5, when the female annual increment was 55.3 mm versus 47.9 mm in males.

Our back-calculations for Spanish mackerel showed variation in mean fork lengths at age between sexes, areas, and years (Table 6). Females from south Florida grew faster than any other group and males from there grew faster than any other males. For Spanish mackerel from northwest Florida, where the largest number of fish were collected, analysis of covariance (ANCOVA) indicated significant differences in growth (length-at-age) between sexes and collecting gears (Table 7).

ANCOVA was also used to test the significance of growth differences among geographic areas

TABLE 2.—Fork length (mm) composition, in percent, of male Spanish mackerel by age group (locations combined).

Length group	Age in years 0	1	2	3	4	5	7	Total number of fish
175-199	100.0							1
200-224	100.0							1
225-249	100.0							5
250-274	100.0							2
275-299	68.3	31.7						41
300-324	76.5	23.5						102
325-349	51.0	47.1	1.9					155
350-374	47.7	47.7	4.5					88
375-399	20.7	59.8	17.1	1.2				82
400-424	5.5	78.2	14.5					55
425-449	22.2	33.3	22.2	22.2				9
450-474	9.1	54.5	18.2		9.1	9.1		11
475-499		50.0			50.0			2
500-524		16.7	33.3	33.3	16.7			6
525-549		40.0	40.0	20.0				5
550-574			50.0			50.0		2
575-599				33.3	66.6			3
600-624								0
625-649						100.0		3
650-674								0
675-699							100.0	1
700-724						100.0		1
Total								575

TABLE 3.—Fork length (mm) composition, in percent, of female Spanish mackerel by age group (locations combined).

Length group	Age in years 0	1	2	3	4	5	6	7	8	9	Total number of fish
175-199	100.0										1
200-224	100.0										2
225-249	80.0	20.0									5
250-274	100.0										3
275-299	96.7	3.3									30
300-324	84.8	13.6	1.5								66
325-349	77.0	23.0									152
350-374	52.4	46.4	1.2								166
375-399	46.7	51.1	2.2								137
400-424	41.1	52.5	5.7	0.7							141
425-449	22.8	62.4	12.9	2.0							101
450-474	25.3	49.3	20.0	2.7	1.3		1.3				75
475-499	8.1	48.4	40.3	3.2							62
500-524	5.3	52.6	31.6	8.8		1.8					57
525-549	1.9	39.6	32.1	17.0	9.4						53
550-574		25.0	22.5	37.5	15.0						40
575-599		5.0	30.0	40.0	2.5						40
600-624		5.9	23.5	41.2	23.5	5.9					17
625-649			13.6	45.5	22.7	13.6	4.5				22
650-674			6.3	25.0	25.0	25.0	6.3	6.3	6.3		16
675-699				16.7	33.3	25.0	8.3	16.7			12
700-724						42.9	14.3		42.9		7
725-749				16.7		33.3		16.7	16.7	16.7	6
750-774											0
775-799							100.0				1
Total											1,212

TABLE 4.—Mean back-calculated fork lengths (mm) at age for male Spanish mackerel from all areas, 1977-81.

Age group	$\bar{X}$ FL at capture	N	Average back-calculated FL at age 1	2	3	4	5	6	7	
I	363.9	237	296.9							
II	413.7	33	306.4	382.2						
III	488.1	7	318.2	415.4	458.2					
IV	536.8	4	353.8	423.5	483.9	529.8				
V	605.0	5	374.9	448.2	522.4	567.1	596.3			
VI	—	0	—	—	—	—	—	—		
VII	679.0	1	342.0	521.8	570.9	606.5	642.5	657.1	671.7	
		287	300.8	399.5	489.8	556.1	604.0	657.1	671.7	Weighted mean
				98.7	90.3	66.3	47.9	53.1	14.3	Annual increment

TABLE 5.—Mean back-calculated fork lengths (mm) at age for female Spanish mackerel from all areas, 1977-81.

Age group	$\bar{X}$ FL at capture	N	Average back-calculated FL at age 1	2	3	4	5	6	7	8	9	
I	420.1	437	344.6									
II	503.6	113	340.8	463.1								
III	580.9	62	349.2	480.2	550.8							
IV	596.7	30	356.9	471.1	529.2	580.0						
V	682.0	11	359.9	471.0	565.1	625.4	666.6					
VI	683.0	3	405.1	472.9	546.5	602.5	643.7	673.7				
VII	654.7	3	324.1	431.8	485.4	529.2	572.3	617.3	645.7			
VIII	696.0	2	329.7	458.9	521.0	557.6	615.2	649.6	670.5	688.0		
IX	737.0	1	399.0	470.0	529.0	596.7	653.4	685.3	704.6	717.5	730.5	
		662	345.4	469.0	543.8	587.9	643.2	650.8	663.8	697.8	730.5	Weighted mean
				123.6	74.8	44.1	55.3	7.6	13.0	34.0	32.7	Annual increment

TABLE 6.—Weighted means of back-calculated fork lengths (mm) for male and female Spanish mackerel from all areas and years having appreciable numbers (over 100) of mackerels sampled.

Age group	All locations 1978	All locations 1980	All locations 1981	Northwest Florida 1978	Northwest Florida 1980	Northwest Florida All years	Louisiana All years	South Florida 1981	South Florida All years	All Florida All years
Males										
I	285	303	356	281	300	293	321	384	332	299
II	356	403	465	347	392	380	384	483	438	399
III	[1]448	474	531	[1]470	[1]460	[1]463	[1]440	558	508	494
IV		538	584		[1]529	[1]529	[1]479	607	566	561
V		[1]561	652		[1]561	[1]561	[1]454	[1]652	[1]654	[1]631
VI			[1]657					[1]657	[1]657	[1]657
VII			[1]672					[1]672	[1]672	[1]672
Females										
I	325	347	371	326	346	342	334	366	364	348
II	428	465	507	434	466	454	436	509	500	475
III	492	526	573	486	536	517	500	574	573	557
IV	[1]564	518	614	[1]555	[1]542	[1]548	518	615	614	607
V		[1]485	655				[1]536	655	654	654
VI		[1]540	665				[1]540	665	665	665
VII		[1]572	682				[1]572	682	682	682
VIII			[1]698					[1]698	[1]698	[1]693
IX			[1]730					[1]730	[1]730	[1]730

[1]Lengths based on less than 5 fish.

TABLE 7.—Results of analysis of covariance for growth differences observed in Spanish mackerel collected in northwest Florida, and fish collected in all areas by recreational hook and line, and gill net.

Source	Sum of squares	df	Mean square	P	Tail probability
Gill net					
Gear	2,499.15	2	1,249.57	13.04	0.00
Sex	5,275.31	1	5,275.31	55.03	0.00
Gear × sex	136.80	2	68.40	0.71	0.49
Age	41,384.91	1	41,384.91	431.73	0.00
Error	75,440.13	787	95.86		
n = 794					
NW Florida					
Area	3,792.09	2	1,896.05	22.83	0.00
Sex	476.13	1	476.13	5.73	0.02
Area × sex	689.00	2	344.50	4.15	0.02
Age	42,623.18	1	42,623.18	513.16	0.00
Error	38,955.39	469	83.06		
n = 476					
Recreational hook and line					
Area	1,132.44	2	566.22	5.42	0.00
Sex	2,673.83	1	2,673.83	25.59	0.00
Area × sex	183.17	2	91.58	0.88	0.42
Age	124,338.42	1	124,338.42	1,190.00	0.00
Error	78,886.76	755	104.49		
n = 762					

(sex, area × sex, and age were also included in the covariance model) for recreational hook and line samples and gill net samples. Area differences were highly significant for both gear types, and sex differences were highly significant for gill net-caught fish, but somewhat less so for hook and line samples (Table 7). The area × sex interaction was significant for hook and line, but not gill net samples.

These ANCOVA results demonstrate that females grew significantly faster than males. The significant differences between sampling gears are no doubt due to gear selectivity, i.e., hook and line selecting for larger fish of a given age and gill nets selecting for a specific size fish. Significant differences between sampling areas (consistent for both sampling gears) substantiate faster growth in south Florida (fish were larger at a given age) than in northwest Florida or Louisiana.

We compared back-calculated lengths-at-age of Spanish mackerel (from all areas and from Florida alone) with those of Powell (1975); lengths at ages 1 and 2 for both sexes were shorter, while those for ages 3-5 were increasingly longer (Table 8). There was a greater discrepancy between our data and Powell's for males than for females. Florida males from our study were 38 mm shorter than Powell's at age 1, but by age 5 they were 120 mm longer. Florida females from our study were

TABLE 8.—Mean back-calculated fork lengths (mm) at age by sex for Spanish mackerel from Powell (1975) and this study. Powell's data were transformed from standard length by his formula FL = 1.0728 SL + 2.4267.

			Fable et al.			
Age	Powell		Florida		All areas	
group	Males	Females	Males	Females	Males	Females
I	337	373	299	348	301	345
II	421	481	399	475	400	469
III	459	542	494	557	490	544
IV	489	580	561	607	556	588
V	511	621	631	654	604	643
VI			657	665	657	651
VII			672	682	672	664
VIII				698		698
IX				730		731

25 mm shorter than Powell's at age 1, but by age 5 they were 33 mm longer. Some of this discrepancy can be explained by the fact that Powell used the direct proportion method for his back-calculations, whereas the program by Abramson (1971) employs the regression method. Carlander (1981) pointed out potential problems with this method, but they primarily concern the fact that when using the scales for ageing, not all scales on a fish are the same size. This problem is of lesser importance when ageing is done from otoliths.

Our estimates of the von Bertalanffy growth coefficient (k) are smaller, and our asymptotic lengths (L_∞) are larger (especially for males) than those derived by Powell (1975) and Nomura (1967) (Table 9). Nomura used Klima's (1959) data to compute growth curves for Florida fish. Our L_∞ estimates are much closer to the maximum observed lengths in our samples (802 mm FL female and 723 mm FL male) than were the estimates from other authors. The differences between our estimates and Powell's (1975) are easily explained because we included the oldest fish in our back-calculations, whereas Powell only included fish up to 5 years old, forcing his growth coefficient (k) to be higher. Therefore, we believe our growth parameters are a more accurate reflection of population growth and more appropriate to use in assessment of the status of the stock.

TABLE 9.—Von Bertalanffy growth parameters for Spanish mackerel.

	Males			Females		
Author	K	L_∞ (FL mm)	t_0 (years)	K	L_∞ (FL mm)	t_0 (years)
Fable et al. all areas combined	0.24	794	−0.94	0.33	739	−0.99
Fable et al. Florida	0.27	776	−0.73	0.38	731	−0.73
Powell (1975)	0.48	555	−1.12	0.45	694	−0.78
Nomura (1967) using Klima's (1959) data	0.40	607	+0.15	0.40	720	+0.28

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LITERATURE CITED

ABRAMSON, N. J.
1971. Computer programs for fish stock assessment. FAO Fish. Tech. Pap. 101. Rome, Italy.

BEAMISH, R. J., AND D. A. FOURNIER.
1981. A method for comparing the precision of a set of age determinations. Can. J. Fish. Aquat. Sci. 38:982-983.

BEAMISH, R. J., AND G. A. MCFARLANE.
1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Soc. 112:735-743.

CARLANDER, K. D.
1981. Caution on the use of the regression method of back-calculating lengths from scale measurements. Fisheries 6(1):2-4.

COLLETTE, B. B., J. L. RUSSO, AND L. A. ZAVALA-CAMIN.
1978. *Scomberomorus brasiliensis*, a new species of Spanish mackerel from the western Atlantic. Fish. Bull., U.S. 76:273-280.

EVERHART, W. H., A. W. EIPPER, AND W. D. YOUNGS.
1975. Principles of fishery science. Cornell Univ. Press, Ithaca, N.Y., 288 p.

JOHNSON, A. G., W. A. FABLE, JR., M. L. WILLIAMS, AND L. E. BARGER.
1983. Age, growth and mortality of king mackerel, *Scomberomorus cavalla*, from the southeastern United States. Fish. Bull., U.S. 81:97-106.

KLIMA, E. F.
1959. Aspects of the biology and the fishery for Spanish mackerel, *Scomberomorus maculatus* (Mitchill), of southern Florida. Fla. Board Conserv. Mar. Res. Lab. Tech. Ser. No. 27, 30 p.

MENDOZA, A.
1968. Aspects of the biology and the fishery of the Spanish mackerel, *Scomberomorus maculatus* (Mitchill), in the state of Veracruz. Bios 1(2), 22 p.

NOMURA, H.
1967. Dados biologicos sombre a serra, *Scomberomorus maculatus* (Mitchill), das aguas cearenses. Arq. Estac. Biol. Mar. Univ. Fed. Ceara 7(1):29-39.

POWELL, D.
1975. Age, growth, and reproduction in Florida stocks of Spanish mackerel, *Scomberomorus maculatus*. FDNR, Fla. Mar. Res. Publ. No. 5, 21 p.

RICKER, W. E.
1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191, 382 p.

TESCH, R. W.
1971. Age and growth. *In* W. E. Ricker (editor), Methods of assessment of fish production in fresh waters, p. 98-130. Blackwell Scientific Publ., Oxf.

TRENT, L., AND E. A. ANTHONY.
1978. Commercial and recreational fisheries for Spanish mackerel, *Scomberomorus maculatus*. *In* E. L. Nakamura and H. R. Bullis, Jr. (editors), Proceedings of the Mackerel Colloquium, p. 17-32. Gulf States Mar. Fish. Comm. No. 4.

U.S. DEPARTMENT OF COMMERCE.
1986a. Fisheries of the United States, 1985. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Curr. Fish. Stat. 8380, 121 p.
1986b. Marine recreational fishery statistics survey, Atlantic and Gulf coasts, 1985. U.S. Dep. Commer., Natl. Mar. Fish. Serv., Curr. Fish. Stat. 8327, 130 p.

VON BERTALANFFY, L.
1938. A quantitative theory of organic growth (inquiries on growth laws. II). Hum. Biol. 19(2):181-213.