Spatial and temporal variation in age and growth of king mackerel, *Scomberomorus cavalla,* 1977–1992

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Abstract.–A total of 12,180 king mackerel, *Scomberomorus cavalla*, collected from 1986 to 1992 from North Carolina to Yucatan, Mexico, and 2,033 collected in 1977 and 1978 from North Carolina to Texas were aged with whole or sectioned sagittal otoliths. Data were analyzed by region—Atlantic Ocean, eastern Gulf of Mexico, and western Gulf—reflecting the currently recognized stocks. Maximum sizes of females aged were 152, 158, and 147 cm FL in the Atlantic, eastern Gulf, and western Gulf, whereas the largest males were 121, 127, and 117 cm FL in those same regions. Maximum ages from the 1986–92 fish were 26, 21, and 24 yr for females and 24, 22, and 23 yr for males in the Atlantic, eastern Gulf, and western Gulf, respectively. Females grew faster and larger than males at every age in each region. A very consistent pattern of greatest growth in the eastern Gulf, intermediate in the western Gulf, and least in the Atlantic was present each year during 1986–92, most noticeably among females. During 1977–78, Atlantic females also had distinctly lower growth than Gulf fish. These consistent regional differences support the current hypothesis that there are three stocks as suggested by previous analyses of other types of data. Within a region and sex, growth was lower in 1977–78 than in 1986–92 in both the Atlantic and eastern Gulf, but higher for western Gulf females.

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King mackerel, *Scomberomorus cavalla,* are economically valuable and highly sought after by U.S. recreational and commercial fishermen from North Carolina to Texas (Manooch, 1979). They also support a substantial commercial fishery in Mexico (Gulf of Mexico and South Atlantic Fishery Management Councils[1]) Some populations have been overfished and since 1983 the species has been managed by a joint fishery management plan of the Gulf of Mexico and South Atlantic Fishery Management Councils.[2] The species is managed as two stocks, an Atlantic migratory group and a Gulf migratory group, although the Councils recognize that there are actually two groups in the Gulf—an east and a west (Grimes et al., 1987; Johnson et al., 1994; Gulf of Mexico and South Atlantic Fishery Management Councils[3]). However, the paucity of data from the large Mexican fishery, which has a major impact on the western Gulf stock, precludes managing the two Gulf groups separately. Because tag return data (Sutter et al., 1991) collected during 1975–78 indicated considerable seasonal movement between the Gulf of Mexico and Atlantic Ocean, the boundary between the Gulf and Atlantic stocks was defined as the Volusia-Flagler County line off northeast Florida during November–March and the Monroe-Collier County line off southwest Florida during April–October. The Gulf stock has been heavily overfished throughout much of its management history, unlike the Atlantic stock, which has never been considered overfished (Mackerel Stock Assessment Panel[4]).

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[1] Gulf of Mexico and South Atlantic Fishery Management Councils. 1992. Amendment 6 to the fishery management plan for coastal migratory pelagics in the Gulf of Mexico and South Atlantic. Gulf of Mexico Fishery Management Council, The Commons at Rivergate, 3018 U.S. Highway 301 North, Suite 1000, Tampa, FL 33619-2266; and South Atlantic Fishery Management Council, Southpark Building, Suite 306, 1 Southpark Circle, Charleston, SC 29407-4699, 35 p.

[2] Gulf of Mexico and South Atlantic Fishery Management Councils. 1982. Fishery management plan, final environmental impact statement, regulatory impact review, final regulations for coastal migratory pelagic resources (mackerels) in the Gulf of Mexico and South Atlantic region. Gulf of Mexico Fishery Management Council, Tampa, FL; and South Atlantic Fishery Management Council, Charleston, SC, var. pagination.

[3] Gulf of Mexico and South Atlantic Fishery Management Councils. 1990. Amendment Number 5 to the fishery management plan for the coastal migratory pelagic resources (mackerels), 33 p. Gulf of Mexico Fishery Management Council, Tampa, FL; and South Atlantic Fishery Management Council, Charleston, SC, 33 p.

[4] Mackerel Stock Assessment Panel. 1994. 1994 report of the mackerel stock assessment panel. Miami Laboratory, Natl. Mar. Fish. Serv., NOAA, 75 Virginia Beach Dr., Miami, FL 33149-1003. Contrib. Rep. MIA-93/94-42.

Several studies have examined spatial, temporal, and gear-related variation in life history and fishery parameters of king mackerel. The parameters have included mean back-calculated sizes, (Beaumariage, 1973; Manooch et al., 1987), von Bertalanffy growth rates (Johnson et al., 1983; Manooch et al., 1987), and size, age, and sex composition of the catch (Beaumariage, 1973; Johnson et al., 1983; Trent et al., 1983; Trent et al., 1987). The usefulness of this information for current stock assessments is limited for several reasons. Much of the previous work was based on data collected 15 to 25 years ago when exploitation was much lower, the species unmanaged, and population size, at least in the eastern Gulf of Mexico, higher. In addition, all age estimates were based on examination of whole otoliths, which results in considerable under-ageing of older, larger fish (Collins et al., 1989). In addition, some studies were geographically limited (Beaumariage, 1973; Trent et al., 1987), and because stock boundaries were unknown when the data were collected, none of the data were partitioned according to stock boundaries.

The primary objective of this study was to examine variation in age and growth in relation to space, time, and sex of king mackerel collected during 1977–78 and 1986–92.

Methods

Most king mackerel used in this study were collected during 1986–92 as part of a continuing cooperative program between the states from North Carolina to Texas and the National Marine Fisheries Service that was designed to provide age and length-frequency data needed to conduct annual stock assessments. Samples from 1977 and 1978 were collected by Johnson et al. (1983) for their age and growth study. All fish were measured to the nearest centimeter fork length (FL) and are reported in our study in those units.

Three regions, which reflect stock boundaries according to current hypotheses (Grimes et al., 1987; Johnson et al., 1994; Gulf of Mexico and South Atlantic Fishery Management Councils[3]), were sampled during 1986–92. The regions were 1) Atlantic: North Carolina to about Miami, FL; 2) eastern Gulf: Florida Keys through Mississippi, and, during April–October, Louisiana; and 3) western Gulf: Mexico, Texas, and, during November–March, Louisiana. All Louisiana samples were collected during April–October; therefore they were classified as eastern Gulf. We did not adjust the Atlantic–eastern Gulf boundary seasonally, as the current fishery management plan does, because only 378 of the 5,490 Atlantic fish aged were collected in the area of mixing off eastern Florida during November–March. These 378 fish were used in the analyses.

For the 1986–92 samples, taken from North Carolina to Yucatan, Mexico, we used stratified sampling (Ketchen, 1950), attempting to collect sagittal otoliths from 20 fish from each unique year, region, sex, and 10-cm size-interval combination. That quota was often exceeded for abundant size intervals and not reached for rarer size intervals.

The fish from Johnson et al.'s (1983) study were collected from recreational hook-and-line catches from North Carolina to Texas. Johnson et al. also used stratified sampling, with each sex and 10-cm size-interval combination comprising a stratum. For the analysis, regional classifications were the same as those used for the 1986–92 samples.

In most cases, heads were shipped to our laboratory where otoliths were removed and stored dry. The majority (>90%) of otoliths collected in the United States were taken from recreational hook-and-line catches, and the remainder from various commercial fisheries. All Mexican samples were collected from commercial fisheries.

For the 1986–92 samples, otoliths from males <80 cm and females <90 cm were read whole. The whole otoliths were placed in a black-bottomed dish containing glycerin and examined with a dissecting microscope at 12–25× with reflected light. For larger fish (males ≥80 cm and females ≥90 cm), three transverse sections about 0.7 mm thick were made about the focus with a Beuhler Isomet low-speed saw. Sections were mounted on glass slides with FLO-TEXX, a clear polymer mounting medium. Sections were examined under transmitted, polarized light at 50 or 125× with a compound microscope. Annuli of whole otoliths were identified according to the criteria of Johnson et al. (1983), and sections according to the criteria of Waltz.[5] The dorsal half of the section was usually read because it was clearer than the ventral. Otoliths collected during 1986–88 were read independently by two readers, and if there was disagreement, a second reading was made. If the second reading disagreed with the first, the otolith was excluded from analysis. After 1988, otoliths were read by the senior author alone.

Ageing methods for the 1977 and 1978 collections were basically the same, except that we sectioned males ≥75 cm and females ≥80 cm FL and used whole ages from Johnson et al. (1983) for fish below these sizes.

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[5] Waltz, W. 1986. Data report on preliminary attempts to assess and monitor size, age, and reproductive status of king mackerel in the south Atlantic Bight. South Carolina Wildl. Mar. Res. Dep. MARMAP rep. for contract 6-35147.

Ages, to the nearest whole year, were assigned solely on the basis of number of visible annuli for fish collected from mid-July through December. Fish collected 1 January through mid-July had one year added to their age if the marginal increment was estimated to be >80% of the previous annual increment. Ages from samples collected by Johnson et al. (1983) were adjusted similarly with their marginal increment data. This adjustment was necessary because an annulus typically forms during the spring (Beaumariage, 1973; Johnson et al., 1983) but is often difficult to distinguish until later in the summer.

Von Bertalanffy growth equations were fitted to quarterly observed lengths-at-age by using Marquardt's nonlinear regression procedure (SAS Institute, Inc., 1988). Annual ages were converted to quarterly ages by adding 0.25 to the age if the fish was collected during April–June, 0.50 if collected during July–September, and 0.75 if collected during October–December. Quarterly ages were used to minimize the variance about the sizes-at-age because observed annual sizes-at-age, especially for young (1–2 yr old) fish that are growing faster than older fish, can vary considerably depending on month of capture.

For the 1986–92 data, we tested for differences in von Bertalanffy equations between sexes within regions and among regions within a sex, i.e. we compared fitted growth curves, using an F-statistic derived from the multivariate Hotelling's T^2 (Bernard, 1981; Vaughan and Helser, 1990). Estimates of the parameters L_∞, K, and t_0 are often correlated, making univariate statistical tests inappropriate for comparing differences between like parameters from two groups of fish (Bernard, 1981). To analyze the 1977–78 growth data, we simply examined plots of the von Bertalanffy curves and their 95% confidence limits. We did not use Hotelling's T^2 to test the 1986–92 data for interannual differences, the 1977–78 data for any growth differences, or to compare the 1977–78 and 1986–92 data, primarily because size and age distributions of the samples varied considerably among regions (and to some extent between sexes) and secondarily because the sample size was sometimes quite small. Von Bertalanffy parameter estimates, which are used as data for the Hotelling's T^2 test, would certainly be influenced by sample size and age distributions; if the two groups being tested had dissimilar distributions, then a significant difference might not be biologically meaningful.

Bernard (1981) noted that one of the assumptions for Hotelling's T^2 is that the two sets of estimates being compared have a common variance structure. However, citing Ito and Schull (1964), "if the variance-covariance matrices are unequal, the probability of a Type I error and correspondingly the power of the T^2 deviate from tabulated values with the same degrees of freedom. However, when both N_1 and N_2 are equal, different variance-covariance matrices do not effect the error level or the power of the test." To run each test with equal sample sizes so we could avoid the problems just mentioned, we randomly sampled from the larger group a number of observations equal to the sample size of the smaller group, then used parameter estimates derived from that sample in the test. However, all growth curves shown in the figures in the present study were based on the full number of available observations.

Results

We aged 14,213 king mackerel—12,180 collected during 1986–92, 2,033 from 1977–78. The numbers of females and males aged from 1986–92 were 3,407 and 2,083 from the Atlantic, 2,753 and 1,285 from the eastern Gulf, and 1,662 and 990 from the western Gulf. From the 1977–78 collections, the numbers of females and males aged were 323 and 128 from the Atlantic, 1,011 and 343 from the eastern Gulf, and 188 and 40 from the western Gulf (Table 1). The geographical distribution of the 1986–92 samples varied annually, and although fish were collected off every coastal state from Virginia to Texas and in Veracruz, Campeche, and in Yucatan, Mexico, the greatest proportion were collected in North Carolina in the Atlantic region, northwest Florida in the eastern Gulf, and south Texas in the western Gulf (Table 1). Most fish collected in 1977–78 came from North Carolina, northwest Florida, and Louisiana (Table 1).

Size and age distributions

Size distributions of aged fish were similar among regions during 1986–92, although females tended to predominate at larger sizes (Fig. 1). In contrast, in 1977–78, size distributions differed markedly, among both regions and sexes (Fig. 1). Males do not grow as large as females, and this difference was reflected in their narrower size distributions (Fig. 1; Table 2). Annual size distributions of aged fish, 1986–92, showed similar ranges each year but some variation in modal sizes (Table 2). The maximum sizes of females aged from 1986–92 were 152 (age 18 [yr]), 158 (age 18), and 147 (age 11) cm for the Atlantic, eastern Gulf, and western Gulf; sizes of males ranged to 121 (age 20), 127 (age 16), and 117 (age 13) cm for those same regions. Maximum sizes of 1977–78 samples were slightly smaller than those from 1986–92 in 5 out of 6 region and sex combinations, most likely because the older data had much smaller

Table 1

Geographical distribution of aged king mackerel for 1977–78, 1986–92, and each year from 1986 to 1992. N.E. Florida = Nassau-Flagler County. E. Florida = Volusia-Palm Beach County. S.E. Florida = Broward-Dade County. S. Florida = Monroe County. S.W. Florida = Sarasota-Collier County. W. Florida = Citrus-Manatee County. N.W. Florida = Escambia-Levy County. N. Texas = Jefferson-Calhoun County. S. Texas = Aransas-Cameron County.

		Number aged																	
	State or	Females									Males								
Region	area	77–78	86–92	86	87	88	89	90	91	92	77–78	86–92	86	87	88	89	90	91	92
Atlantic	Virginia		20	—	—	—	16	1	—	3	—	3	—	—	—	1	1	—	1
Ocean	N. Carolina	234	1,982	64	134	68	313	454	402	547	71	1,239	59	101	37	255	274	230	
	S. Carolina	88	568	55	99	113	70	55	78	98	56	255	31	25	50	38	38	31	42
	Georgia	—	292	24	5	45	98	63	13	44	—	144	5	9	15	41	35	2	37
	N.E. Florida	—	52	21	31	—	—	—	—	—	—	6	5	1	—	—	—	—	—
	E. Florida	—	459	30	56	22	5	21	171	154	—	379	63	77	74	6	14	12	133
	S.E. Florida	—	34	6	15	10	3	—	—	—	—	57	14	20	23	—	—	—	—
Eastern	S. Florida	6	215	5	1	2	29	36	75	67	12	132	6	2	3	27	31	24	39
Gulf	S.W. Florida	—	—	—	—	—	—	—	—	—	—	—	—	5	—	—	—	—	—
	W. Florida	—	110	2	—	—	—	—	—	108	—	14	2	2	—	—	—	—	10
	N.W. Florida	532	1,209	51	94	96	227	128	321	292	283	643	7	49	22	125	79	215	146
	Alabama	—	303	50	172	54	7	9	3	8	—	122	22	60	29	—	9	1	1
	Mississippi	7	290	31	55	51	6	69	47	31	—	104	7	8	31	4	26	12	16
	Louisiana	466	628	23	61	56	46	39	195	208	48	265	22	14	12	12	2	108	95
Western	Louisiana	147	1	—	—	—	—	—	—	1	2	—	—	—	—	—	—	—	—
Gulf	N. Texas	41	281	—	45	90	54	14	47	31	38	181	4	27	56	30	14	23	27
	S. Texas	—	1,026	48	158	130	184	134	206	166	—	553	44	103	39	79	74	102	112
	Veracruz	—	225	—	—	6	47	75	50	47	—	183	—	—	9	44	31	53	46
	Campeche	—	21	—	—	—	13	8	—	—	—	16	—	—	—	7	9	—	—
	Yucatan	—	106	—	—	62	—	1	37	6	—	57	—	—	19	—	—	24	14

samples sizes and the sampling was more limited geographically and temporally.

During 1986–92, the overall age distributions of samples were quite similar among regions and between sexes within regions, but during 1977–78 they varied noticeably (Fig. 2). Maximum ages of king mackerel from 1986–92 in the Atlantic, eastern Gulf, and western Gulf were 26 (137 cm), 21 (127–150 cm), and 24 (144 cm) for females and 24 (117 cm), 22 (110 cm), and 23 (101 cm) for males. Maximum ages from 1977–78 samples from the same respective regions were 20, 19, and 18 for females and 18, 19, and 19 for males. Fish older than age 20 were very rare in the 1986–92 samples—only 22 of 7,822 females (0.15%) and 13 of 4,358 males (0.18%).

Growth

Growth was significantly different between sexes ($P<0.01$ in 1986–92) in each region during 1986–92 and 1977–78, and females grew faster and larger than males at every age (Fig. 3; Table 3). Although we did not test the 1977–78 data with Hotelling's T^2, it is obvious that the confidence limits do not overlap (Fig. 3). During 1986–92, the predicted sizes at age of females were at least 20 cm larger than males by age 13, 9, and 11 in the Atlantic, eastern Gulf, and western Gulf, respectively.

Age-at-size was highly variable in all regions for both sexes, especially after fish reached 70 cm FL (Tables 4 and 5). For example, Atlantic females 100.1 to 110.0 cm FL ranged from age 4 to 20, whereas males from that same region and size ranged from age 6 to 22.

The pooled 1986–92 data showed that growth was highest in the eastern Gulf, intermediate in the western Gulf, and lowest in the Atlantic for both sexes, and the differences, which were greatest among females, were statistically significant ($P<0.01$) (Fig. 3; Table 3). Asymptotic length (L_∞) was the parameter most often (7 of 9 instances) responsible for the significant differences between growth curves (Table 3), although twice it was t_0. Estimates of L_∞ were 126.7, 134.1, and 137.8 cm for Atlantic, western Gulf, and eastern Gulf females, and 96.4, 102.8, and 102.6 cm for males (Table 6). Above age 7 years, the predicted size at age of eastern Gulf

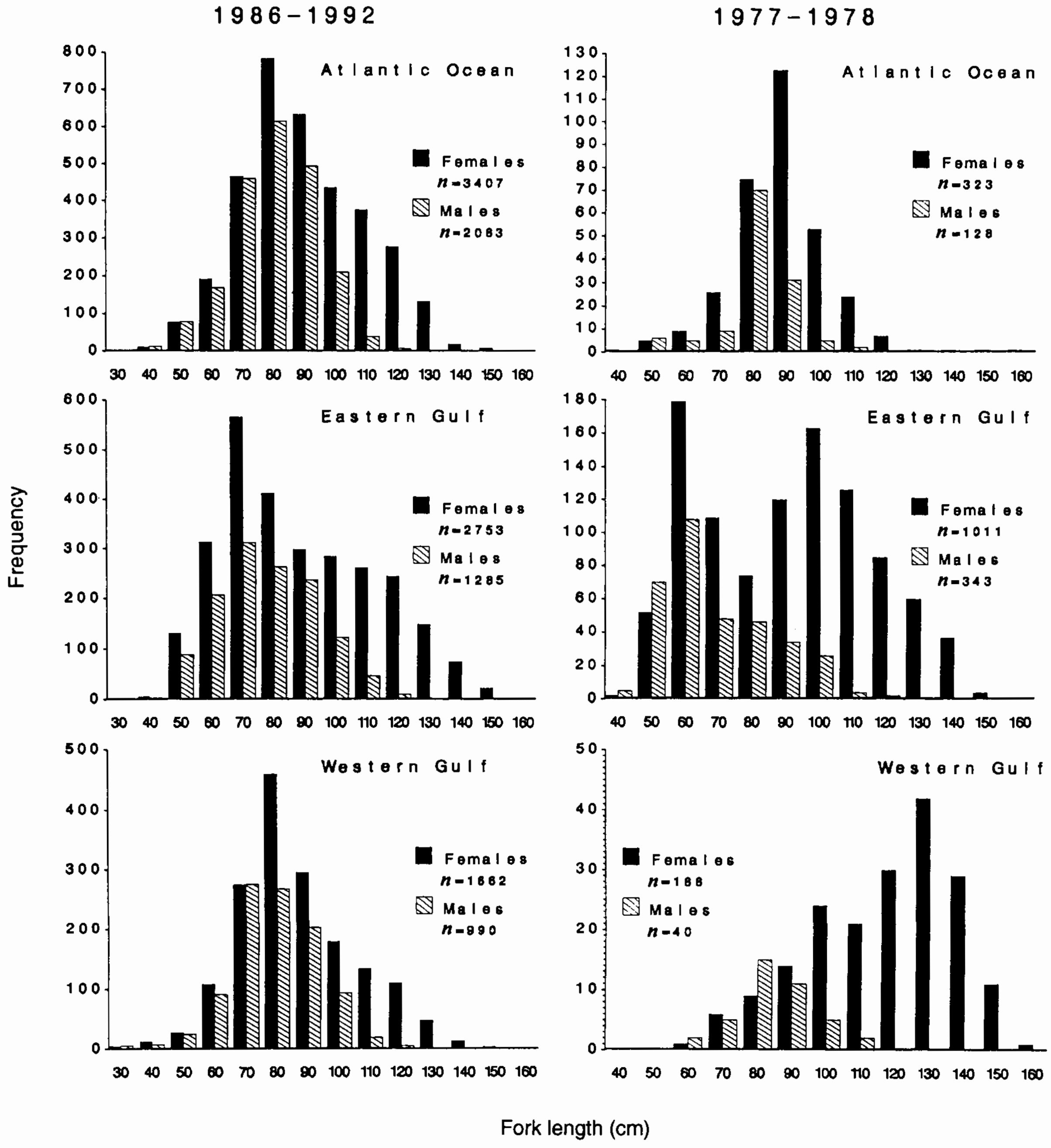

Figure 1

Length-frequency distribution by sex and region of king mackerel included in the analysis and collected during 1977–78 and 1986–92.

females averaged 12.2 cm (SD=0.4) larger than Atlantic females, whereas eastern Gulf males averaged 6.9 cm (SD=0.4) larger than Atlantic males.

The pattern of highest growth in the eastern Gulf, intermediate growth in the western Gulf, and lowest growth in the Atlantic seen in the pooled 1986–92 data was very consistent and present each year during that period. These consistent regional differences were especially noticeable among females (Fig. 4). Among males, the eastern Gulf growth curve was clearly higher than that for the Atlantic each year, whereas the growth curve for the western Gulf was intermediate in younger fish but converged with the eastern curve at about age 12–14 (Fig. 5).

In 1977 and 1978, as during 1986–92, growth of females was lowest for Atlantic fish; however, unlike

Table 2

Annual length frequency distributions of aged king mackerel, 1986–1992, by region and sex. See Figure 1 for overall 1977–78 and 1986–92 size distributions.

		Number aged													
		Females							Males						
Region	Size interval FL (cm)	86	87	88	89	90	91	92	86	87	88	89	90	91	92
Atlantic Ocean	20–39.9	—	—	—	—	1	—	—	1	—	—	3	—	—	—
	40–59.9	23	72	7	14	14	16	17	36	50	12	5	27	20	13
	60–79.9	94	83	86	129	135	193	248	102	86	91	122	115	117	239
	80–99.9	57	83	91	205	230	289	315	35	88	87	195	186	107	217
	100–119.9	21	58	53	127	150	116	196	3	9	9	16	34	31	26
	120–139.9	5	42	21	30	57	50	67	—	—	—	—	—	—	1
	140–159.9	—	2	—	—	7	—	3	—	—	—	—	—	—	—
	Total	200	340	258	505	594	664	846	177	233	199	341	362	275	496
Eastern Gulf	20–39.9	—	—	—	—	—	—	—	—	—	—	—	—	—	—
	40–59.9	30	26	9	93	20	58	49	7	14	1	45	22	83	23
	60–79.9	50	135	94	79	99	242	267	20	69	37	58	60	128	170
	80–99.9	34	60	58	65	55	124	206	31	46	53	43	53	129	96
	100–119.9	30	73	55	39	66	153	133	8	11	5	22	11	20	17
	120–139.9	11	72	35	35	33	56	58	—	—	1	—	1	—	1
	140–159.9	7	17	8	4	6	8	1	—	—	—	—	—	—	—
	Total	162	383	259	315	279	641	714	66	140	97	168	147	360	307
Western Gulf	20–39.9	—	—	—	6	—	4	—	—	—	—	7	—	2	—
	40–59.9	—	3	11	12	14	8	29	—	3	8	9	11	6	35
	60–79.9	14	54	76	68	107	171	83	20	47	43	62	58	130	103
	80–99.9	19	88	101	124	70	108	104	27	69	65	64	53	56	57
	100–119.9	9	42	64	51	32	42	33	1	11	7	18	6	8	4
	120–139.9	6	15	36	32	10	7	2	—	—	—	—	—	—	—
	140–159.9	—	1	—	5	1	—	—	—	—	—	—	—	—	—
	Total	48	203	288	298	234	340	251	48	130	123	160	128	202	199

during 1986–92, western Gulf females grew faster and larger than eastern Gulf females according to the growth curves (Fig. 3). Among males, growth also appeared to be lowest in the Atlantic, although the differences were slight (Fig. 3).

There was interannual variation in growth within a region and sex during 1986–92; however, it probably reflected sample differences as much as any actual differences (Tables 1 and 2); therefore we did not test these growth curves statistically.

Plots of the von Bertalanffy curves (Fig. 6) suggested that growth was slightly less in 1977–78 than in 1986–92 in the Atlantic and eastern Gulf for both sexes, whereas western Gulf females grew faster in 1977–78 than in 1986–92. The average differences (and standard errors) in predicted size at age between 1986–92 and 1977–78 for all ages above age 7 were 1) eastern Gulf females: +2.0 ± 0.1 cm; 2) eastern Gulf males: +2.9 ± 0.1 cm; 3) Atlantic females: +5.8 ± 0.1 cm; 4) Atlantic males: +1.7 ± 0.1 cm; and 5) western Gulf females: –9.6 ± 0.6 cm.

Discussion

Our findings were based on data collected as part of a long-term, stratified, nonrandom sampling program (following the suggestions of Ketchen [1950]) designed to provide age-length keys for annual stock assessments. Most fish sampled were caught by hook and line and gill nets, both of which are size-selective gears. Goodyear (1995), using computer simulations, demonstrated that samples equally stratified by length and those from size-selective fisheries often yield biased estimates of mean size-at-age; for this reason he recommended that only simple random sampling be used to generate models of fish growth. He found that most often mean lengths-at-age were overestimated by 5–15% for all but the youngest age classes, which were sometimes underestimated. Goodyear explained that at the youngest ages, the smaller individuals of an age class are often sampled disproportionately to their true abundance, whereas for older ages, the same happens for the larger (faster growing) fish in a given age class.

Given Goodyear's (1995) findings and our nonrandom sampling design, it may be that our growth models overestimated length-at-age to some degree for all but the youngest age classes, but probably not as much as Goodyear found in his study. Although we had sampling quotas for each year, region, sex, and 10-cm size interval combination, for many different reasons we invariably exceeded those quotas for all but the rarest size classes, often greatly for the most common length intervals; Table 2 and Figure 1 provide clear evidence of this. Because of this oversampling, our actual design fell somewhere between simple random sampling and length-stratified sampling, and thus should have reduced the bias to some extent. Given this rather small potential bias and the fact that our sample sizes and spatial and temporal coverages greatly exceeded all previous

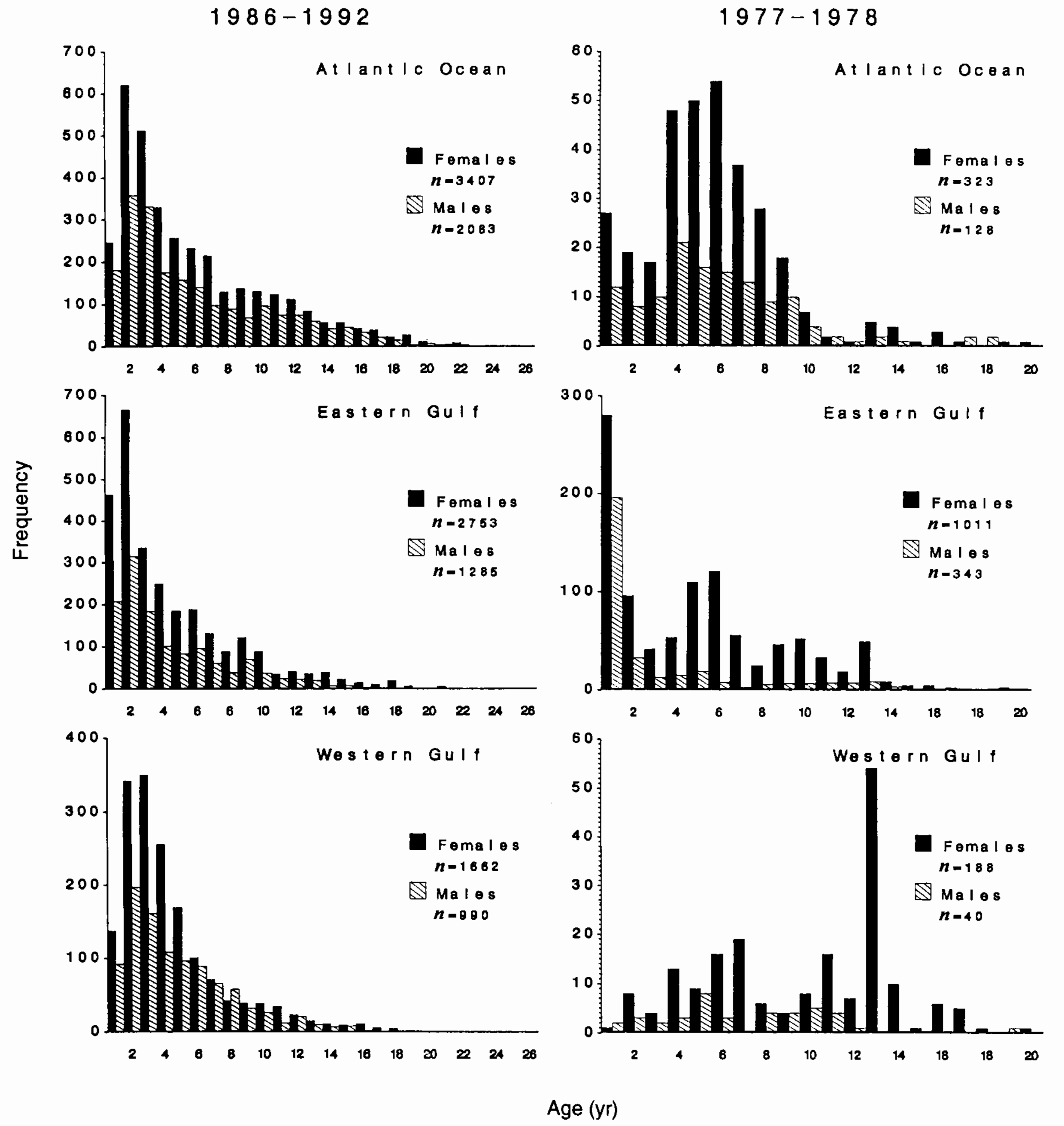

Figure 2

Age distributions by sex and region of king mackerel included in the analysis and collected during 1977–78 and 1986–92.

king mackerel studies (all of which sampled size-selective fisheries and only one (Beaumariage, 1973) of which clearly used simple random sampling), we feel our growth estimates are the best available. Most important, there is no obvious reason to suspect that the bias would be greatly different among regions or among years; thus our conclusions about the temporal and regional differences in growth should be valid.

Our finding of similar maximum longevity for both sexes differs from all previous studies (except

Figure 3

Von Bertalanffy growth curves and 95% confidence limits by region and sex for king mackerel collected during 1977–78 and 1986–92. Growth curves were calculated by using individual quarterly observed sizes-at-age. The upper three curves in each panel represent females; the lower three represent males.

Table 3

Results of Hotelling's T^2 tests comparing 1986–92 von Bertalanffy growth curves for king mackerel. The larger group in each comparison was randomly subsampled so that it's sample size equaled that of the smaller group. Underlined *F*'s in right three columns indicate parameters that did not significantly affect growth differences. Values in bold = parameter which most affected growth differences. NS = not significant. *n* = sample size for each group in the comparison. AOF = Atlantic Ocean females; EGF = eastern Gulf females; WGF = western Gulf females; AOM = Atlantic Ocean males; EGM = eastern Gulf males; WGM = western gulf males.

Groups compared	Calculated F[1]	*n*	Denom. df[2]	Critical value of *F* needed for 95% Roy-Bose simultaneous confidence limits to bracket zero		
				L_∞	K	t_0
AOF–EGF	363.8[2]	2,753	5,502	**28.4**	2.6	17.7
AOF–WGF	51.2	1,662	3,320	**3.2**	0.1	1.2
EGF–WGF	37.6	1,662	3,320	0.5	2.8	**8.2**
AOM–EGM	46.3	1,285	2,566	**16.5**	0.6	0.1
AOM–WGM	10.1	990	1,976	**9.8**	7.9	5.7
EGM–WGM	10.7	990	1,976	0.0	2.3	**4.0**
AOF–AOM	369.6	2,083	4,162	**211.8**	53.2	11.4
EGF–EGM	259.5	1,285	2,566	**133.3**	13.1	0.1
WGF–WGM	103.1	990	1,976	**46.2**	5.0	0.0

[1] Critical F = 3.12 (α = 0.05, 2-tailed test) for all tests.
[2] Numerator df = 3 for all comparisons (3 parameters).

Beaumariage, 1973) that reported that females lived longer than males. The 26-year-old female and 24-year-old male we found are the oldest king mackerel reported. Collins et al. (1989), in the only other study that used sectioned otoliths, found a 21-year-old female as well as 16-year-old males. The oldest fish reported in all other studies that used whole otoliths, was age 14 for females and age 12 for males (Beaumariage, 1973; Johnson et al., 1983; Manooch et al., 1987; Sturm and Salter; 1990). Our findings support those of Collins et al. (1989), i.e. that sectioned sagittae provide higher age estimates than whole otoliths for king mackerel, especially for fish >85 cm FL. Among females ages 8–12 from the Johnson et al. (1983) study (the 1977–78 collections in our study), our age estimates based on sagittal

Table 4

Total age distributions by 10-cm length class, by region, for all female king mackerel collected during 1986–92.

Size (cm)	Age (yr)																								
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	24	*n*
Atlantic Ocean																									
35	25.0	50.0	25.0																						4
45	9.8	84.3	5.9																						51
55		65.1	34.9																						126
65		26.6	69.3	3.8	0.3																				290
75		5.0	41.0	40.7	11.2	1.8	0.4																		735
85		0.7	8.7	22.9	27.0	20.8	11.5	5.7	1.4	0.8	0.3	0.1	0.1												722
95			1.6	7.4	8.8	13.7	18.4	18.0	9.0	7.4	6.3	4.7	2.5	1.4	0.6	0.2									511
105					1.6	5.1	11.0	15.0	10.5	11.3	10.5	10.5	8.6	5.1	3.2	2.9	1.6	1.9	0.5	0.5	0.3				373
115						1.2	2.7	5.9	9.2	11.2	12.1	10.9	12.7	8.9	5.6	6.2	5.3	3.0	1.8	1.8	0.9		0.6		338
125							0.9	2.3	1.8	6.0	7.8	10.6	9.6	11.5	9.2	8.3	7.8	8.7	4.1	5.5	3.2	1.4	1.4		218
135								2.9		2.9	2.9		2.9	8.8	8.8	8.8	8.8	11.8	8.8	17.6	2.9		5.9	2.9[1]	34
145																42.9			14.3	14.3		14.3	14.3		7
155													25.0						50.0				25.0		4
Eastern Gulf																									
35	100.0																								4
45	12.5	87.5																							72
55		91.6	8.4																						249
65		34.1	58.8	6.6	0.4																				454
75		3.1	62.7	25.2	8.4	0.6																			512
85		0.3	16.7	43.4	24.4	7.7	3.9	2.6		0.3	0.3	0.3													311
95			1.8	13.7	31.7	23.2	16.9	4.6	1.8	3.5	1.4	0.7	0.4		0.4										284
105				0.7	11.3	22.5	24.5	13.9	8.9	9.9	5.0	0.3	0.7	1.0		0.3									302
115					1.7	8.4	16.0	22.3	13.0	16.0	11.3	4.6	1.3	1.7	0.8	1.3	1.3	0.4							238
125						2.2	8.6	8.1	11.8	15.1	17.2	6.5	10.8	6.5	5.9	2.7	0.5	0.5	2.2	0.5	0.5	0.5			186
135								0.9	2.8	13.2	7.5	3.8	14.2	11.3	12.3	9.4	4.7	6.6	9.4	1.9		1.9			106
145										2.3	2.3	9.1	2.3	11.4	22.7	9.1	11.4	4.5	9.1	6.8	2.3	6.8			44
155																25.0			50.0	25.0					4
Western Gulf																									
35		100.0																							10
45		91.7	8.3																						12
55	2.5	70.0	27.5																						80
65		35.1	51.0	9.9	4.0																				151
75		1.6	41.4	41.6	12.9	2.3	0.2																		442
85			15.2	33.0	29.6	15.7	4.7	0.8	0.8	0.3															382
95			0.5	11.2	27.1	28.5	16.8	9.3	2.8	1.4	0.9	0.9	0.5												214
105				0.6	12.2	15.4	21.8	19.2	10.9	7.1	6.4	3.8	0.6		0.6				0.6	0.6					156
115					1.7	10.3	8.5	12.0	10.3	12.8	13.7	11.1	9.4	4.3	0.9	0.9	1.7	0.9	1.7						117
125						2.9	2.9	4.3	4.3	12.9	7.1	12.9	12.9	10.0	8.6	8.6	7.1	2.9	1.4	1.4					70
135								4.2	4.2		16.7	16.7	4.2	12.5	12.5	8.3	16.7	4.2							24
145											16.7	16.7						33.3	16.7					16.7	6

[1] This size class also contained one fish (2.9%) at age 26.

sections exceeded their original estimates based on whole otoliths 67–100% of the time.

The slightly higher maximum ages in the Atlantic than in the eastern or western Gulf during 1986–92 may reflect lower fishing mortality rates for the Atlantic than for the Gulf where age structure was truncated by fishing pressure[4]; alternatively, this finding may be a sampling artifact. A much higher proportion of Atlantic samples were collected at fishing tournaments, which target larger and older fish, and Atlantic sample sizes exceeded eastern and western Gulf sample sizes by 36% and 107%; therefore the chances of obtaining an older fish were greater.

That females grew faster and attained larger maximum sizes than males agrees with previous studies (Beaumariage, 1973; Johnson et al., 1983; Manooch et al., 1987; Collins et al., 1989; Sturm and Salter 1990). The large variation in ages within size intervals that we found was also noted by Johnson et al. (1983).

Significant differences in growth among the three regions for both sexes during 1986–92 and the persistence of that pattern in each of the seven years support the hypothesis that there are three stocks as suggested by allozyme, mark-recapture, catch and fishing effort, and juvenile birth-date distribution data (Grimes et al., 1987; Johnson et al., 1994; Gulf of Mexico and South Atlantic Fishery Management Councils[3]). That similar differences between Atlantic and eastern Gulf growth were present in 1977–78 is further evidence that these growth differences

Table 5

Total age distributions by 10-cm length class, by region, for all male king mackerel collected during 1986–92.

Size (cm)	Age (yr)																								*n*
	0	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	
Atlantic Ocean																									
35		100.0																							4
45		100.0																							58
55		61.6	37.6	0.8																					125
65		13.7	71.1	14.8	0.4																				263
75		0.8	19.3	43.0	21.8	10.0	2.7	1.1	0.6		0.3	0.2	0.2												632
85			0.4	3.5	6.3	16.8	20.7	12.4	10.9	7.6	7.6	5.4	5.0	0.9	0.9	1.1	0.2	0.2			0.2	0.2			542
95					0.3	0.9	2.3	5.8	6.4	7.3	13.1	11.3	11.0	13.1	8.1	7.8	5.8	2.9	2.6		0.3	0.6	0.3		344
105							3.1	3.1	4.1	2.0	7.1	5.1	7.1	11.2	10.2	11.2	10.2	9.2	6.1	4.1	3.1	2.0	1.0		98
115											6.2	6.2	12.5			12.5	18.8	12.5			6.2		12.5	6.2[1]	16
125																					100.0				1
Eastern Gulf																									
35																									
45	8.8	91.2																							57
55		74.8	25.2																						155
65		13.9	73.0	13.1																					267
75		0.7	27.8	43.7	19.0	6.0	1.8	0.7	0.4																284
85			0.4	8.4	15.1	24.4	26.1	9.2	5.0	8.0	2.1	0.4	0.8												238
95				1.5	4.5	4.0	11.9	14.9	9.5	18.4	12.4	6.0	8.5	5.0	1.5	1.0	0.5	0.5							201
105				1.6	3.1		4.7	7.8	7.8	17.2	9.4	17.2	4.7	10.9	4.7	3.1	1.6	3.1	1.6				1.6		64
115							4.8	9.5	4.8	14.3		4.8	9.5	4.8	9.5	19.0	4.8			9.5	4.8				21
125											33.3						33.3		33.3						3
Western Gulf																									
35	9.1	90.9																							11
45		85.7	14.3																						7
55		70.3	28.4	1.4																					74
65		9.3	56.5	29.0	5.2																				193
75		2.1	22.5	33.9	24.3	11.4	4.6	0.7	0.4																280
85			1.3	3.9	11.3	22.9	23.4	16.9	10.8	4.8	3.5	0.4	0.9												231
95					2.7	7.5	14.4	15.1	17.1	13.0	10.3	6.2	7.5	2.7	2.1	0.7				0.7					146
105							2.5	7.5	15.0	5.0	5.0	2.5	15.0	12.5	7.5	12.5	5.0		5.0	2.5				2.5	40
115									11.1		11.1	11.1	22.2	11.1	11.1	22.2									9

[1] This size class also contained one fish (6.2%) at age 24.

are consistent features of king mackerel populations. Assuming that these differences persisted from 1977 to 1992, during which time exploitation rates varied considerably (Mackerel Stock Assessment Panel[4]), we suggest that these differences are not just temporary density-dependent responses to varying population sizes or exploitation rates.

Our findings of regional (stock) growth differences are also consistent with those of Gold et al. (in press), who compared mtDNA haplotypes and found weak genetic differences between Atlantic and Gulf king mackerel. Although our results are not indicative of genetic discontinuity, our data demonstrate that the three groups of fish experience sufficiently different environmental and fishery conditions to produce identifiable and consistent differences in growth.

Contrary to our finding of regional differences in growth within sexes, Beaumariage (1973) reported that growth rates did not differ for either sex between the Gulf and Atlantic coasts of Florida. His results may reflect that many of his Atlantic fish were collected off southeast Florida during winter and thus may have been Gulf-group fish. In addition, the use of whole otoliths for ageing undoubtedly introduced error in length-at-age estimates, possibly obscuring regional differences.

Johnson et al. (1983) reported that female king mackerel from Louisiana grew faster than females from other areas of the Gulf and from the Atlantic. However, their predicted sizes-at-age for Louisiana females ages 4–8, the ages with adequate sample sizes (n=16–78) that could be accurately aged with whole otoliths, were no more than 3.1 cm different from our eastern Gulf fish. For fish older than age 8, their estimates were increasingly larger than ours, most likely because the use of whole otoliths resulted in underageing these larger fish.

The growth differences between 1977–78 and 1986–92, i.e. lower growth during the former period seen in both sexes in the Atlantic and eastern Gulf (Fig. 6), could be a density-dependent response. Populations were much larger in the late 1970's and early 1980's than during 1986–92 (Mackerel Stock Assessment Panel[4]). The key point to remember is that within sexes, the growth differences among regions clearly present in 1986–92 apparently existed as far back as 1977–78.

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Table 6

Von Bertalanffy parameters and 95% asymptotic confidence intervals for male and female king mackerel by region for fish collected during 1986–92 and 1977–78, calculated using quarterly observed sizes-at-age.

			Females			Males		
Collection years		Parameter	n	Estimate	Asymptotic 95% confidence interval	n	Estimate	Asymptotic 95% confidence interval
1986–92	Atlantic	L_∞	3,407	126.7	125.0 to 128.5	2,083	96.4	95.7 to 97.1
	E. Gulf	L_∞	2,796	137.8	135.8 to 139.8	1,330	102.6	101.1 to 104.1
	W. Gulf	L_∞	1,662	134.1	130.6 to 137.7	995	102.8	100.5 to 105.2
	Atlantic	K	3,407	0.145	0.137 to 0.154	2,083	0.262	0.248 to 0.276
	E. Gulf	K	2,796	0.172	0.163 to 0.181	1,330	0.247	0.227 to 0.267
	W. Gulf	K	1,662	0.150	0.136 to 0.164	995	0.203	0.180 to 0.226
	Atlantic	t_0	3,407	–3.15	–3.41 to –2.90	2,083	–1.98	–2.19 to –1.78
	E. Gulf	t_0	2,796	–1.83	–1.98 to –1.67	1,330	–1.84	–2.09 to –1.59
	W. Gulf	t_0	1,662	–2.69	–3.02 to –2.37	995	–2.74	–3.16 to –2.32
1977–78	Atlantic	L_∞	323	122.7	115.5 to 129.9	128	95.9	92.3 to 99.6
	E. Gulf	L_∞	1,011	137.1	133.4 to 140.8	343	99.0	96.6 to 101.3
	W. Gulf	L_∞	188	151.5	138.2 to 164.8	40	116.0	93.1 to 138.9
	Atlantic	K	323	0.124	0.096 to 0.151	128	0.211	0.159 to 0.262
	E. Gulf	K	1,011	0.160	0.145 to 0.175	343	0.269	0.229 to 0.309
	W. Gulf	K	188	0.127	0.080 to 0.175	40	0.094	0.026 to 0.163
	Atlantic	t_0	323	–4.54	–5.59 to –3.49	128	–3.14	–4.26 to –2.02
	E. Gulf	t_0	1,011	–2.12	–2.39 to –1.85	343	–1.63	–2.04 to –1.22
	W. Gulf	t_0	188	–2.78	–4.52 to –1.03	40	–6.78	–11.1 to –2.45

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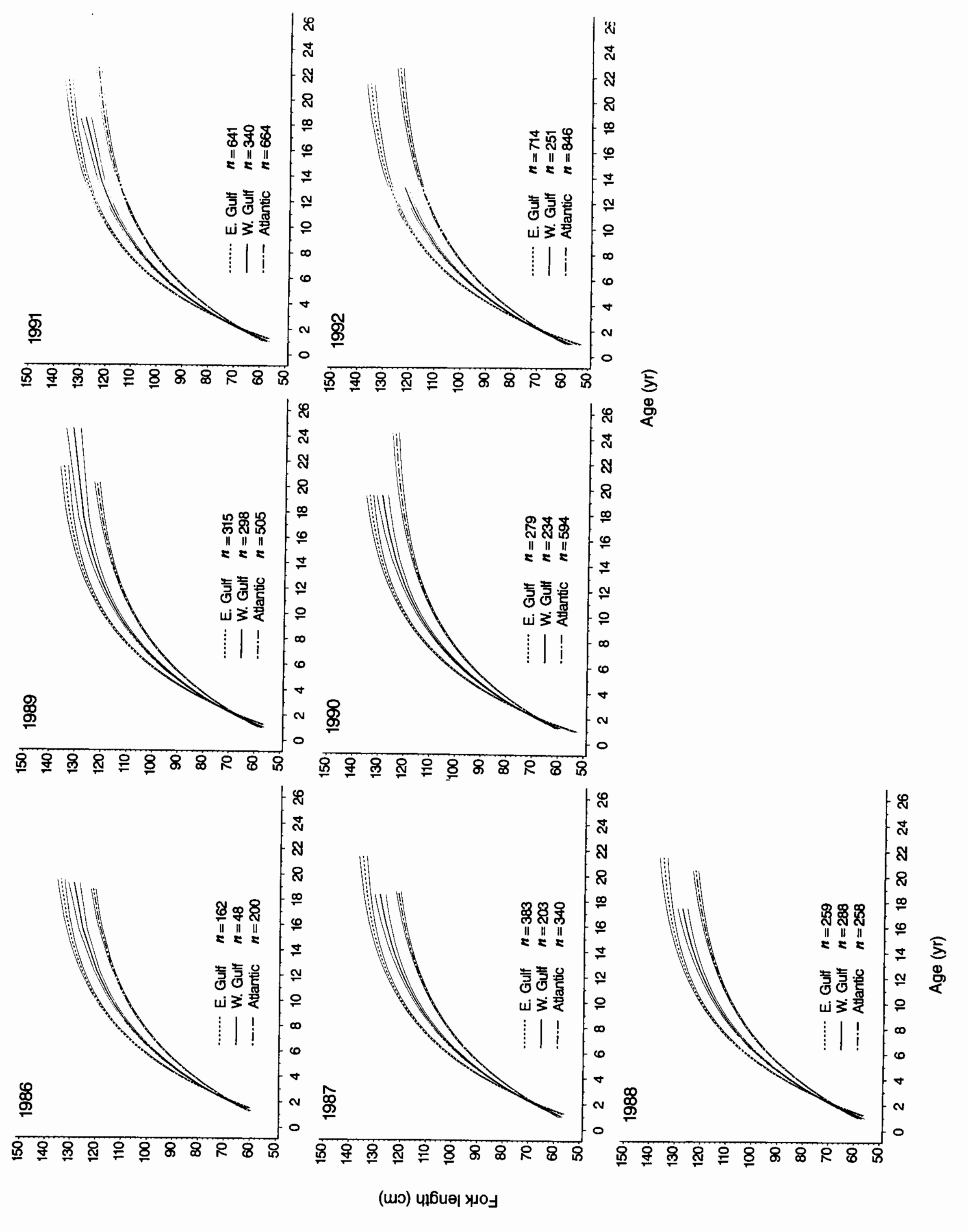

Figure 4

Annual von Bertalanffy growth curves and 95% confidence limits by region for female king mackerel collected 1986–92. Growth curves were calculated by using individual quarterly observed sizes-at-age.

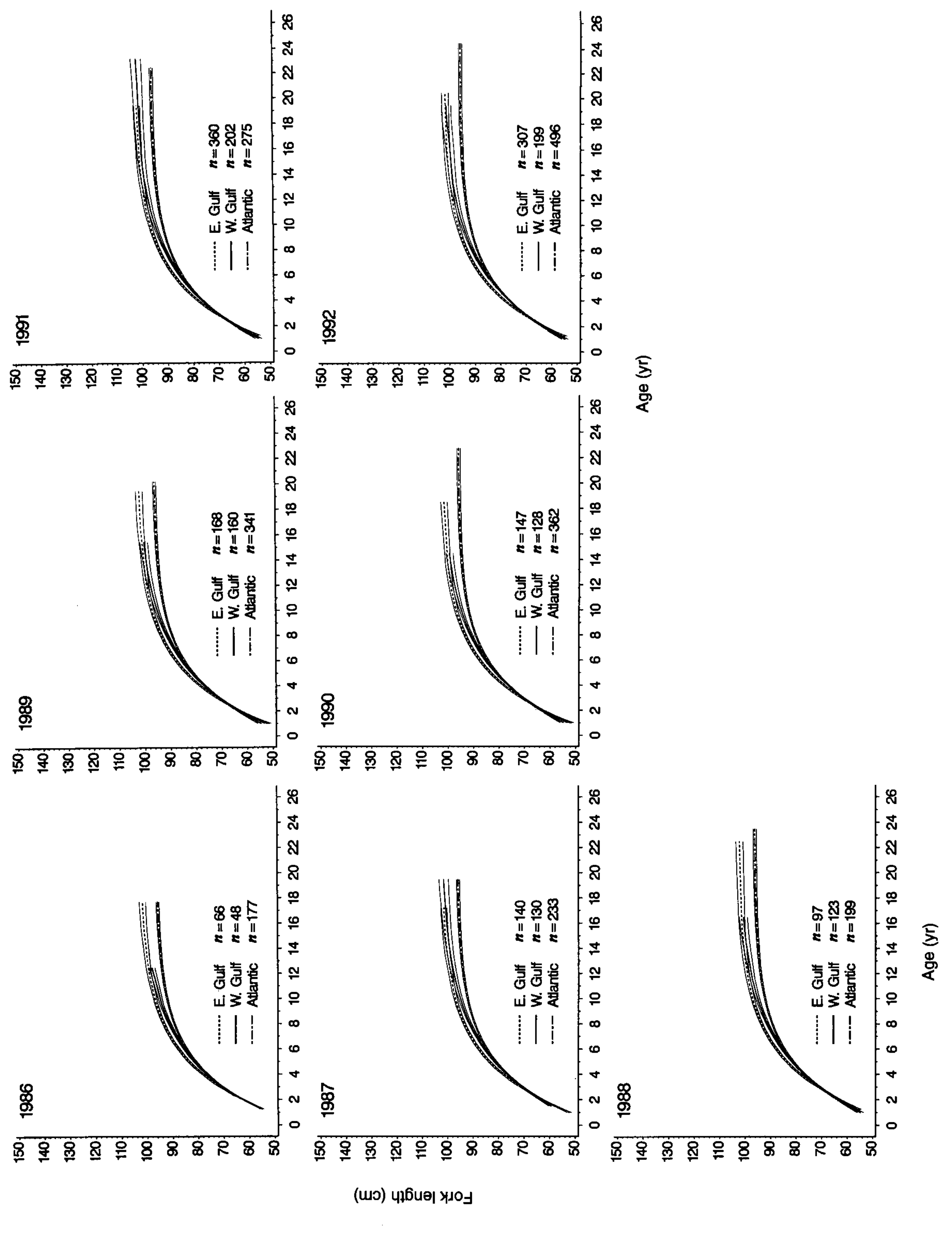

Figure 5

Annual von Bertalanffy growth curves and 95% confidence limits by region for male king mackerel collected 1986–92. Growth curves were calculated by using individual quarterly observed sizes-at-age.

with large numbers of processed otoliths. Doug Vaughan, NMFS, Beaufort Laboratory, provided programs and valuable statistical advice concerning comparisons of growth curves. Two anonymous reviewers provided valuable suggestions that helped improve the manuscript.

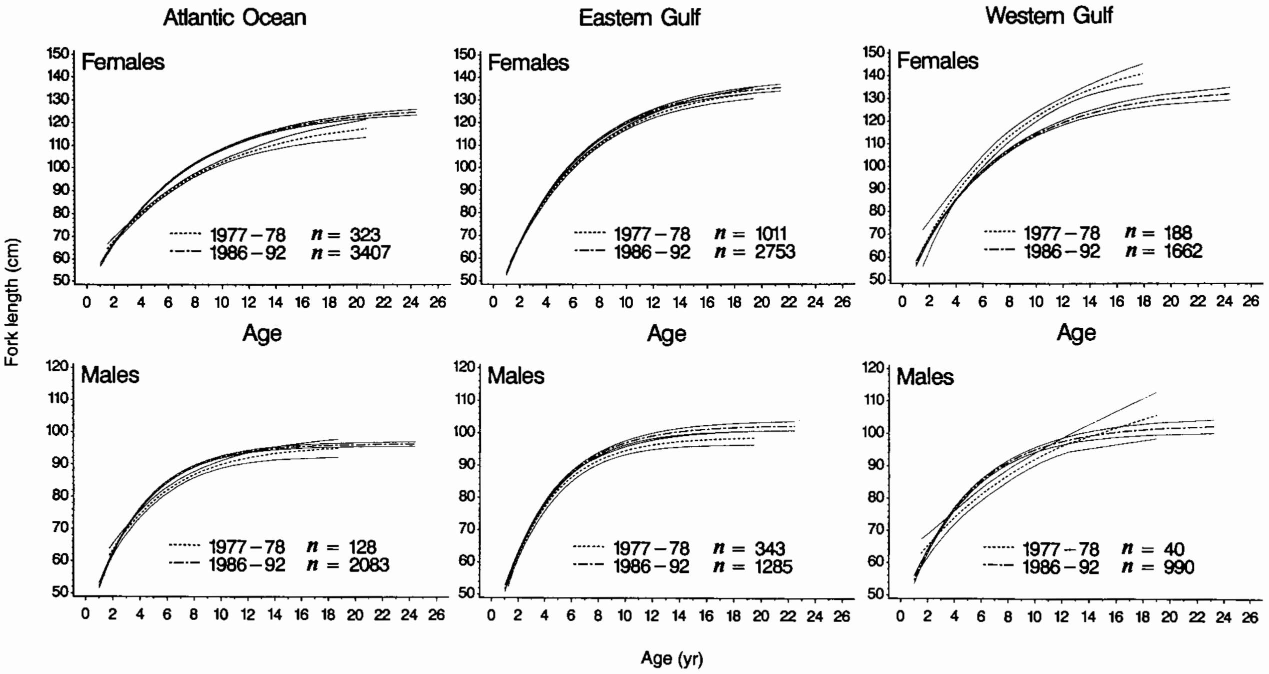

Figure 6

Overall von Bertalanffy growth curves and 95% confidence limits by region and sex for king mackerel, from 1977–78 and 1986–92. Curves were calculated by using quarterly observed size-at-age.

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