Contemporary versus historical estimates of king mackerel (*Scomberomorus cavalla*) age and growth in the U.S. Atlantic Ocean and Gulf of Mexico

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CONTEMPORARY VERSUS HISTORICAL ESTIMATES OF KING MACKEREL (*SCOMBEROMORUS CAVALLA*) AGE AND GROWTH IN THE U.S. ATLANTIC OCEAN AND GULF OF MEXICO

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ABSTRACT

King mackerel, *Scomberomorus cavalla* (Cuvier, 1829), is an economically important coastal pelagic fish in United States waters of the Atlantic Ocean (Atlantic) and Gulf of Mexico (GOM). In this study, von Bertalanffy growth functions (VBGFs) were fitted to size-at-age data collected from eastern GOM (n = 1447) and Atlantic (n = 869) populations in the summers of 2006 and 2007 from fishery-dependent and fishery-independent sources (GOM females: L_∞ = 124.5 cm, k = 0.256, t_0 = −0.173 yr; GOM males: L_∞ = 92.2 cm, k = 0.353, t_0 = −0.166 yr; Atlantic female: L_∞ = 111.6 cm, k = 0.464, t_0 = 0.506 yr; Atlantic males: L_∞ = 98.9 cm, k = 0.510, t_0 = 0.502 yr). Results from likelihood ratio tests indicated contemporary VBGFs were significantly different between sexes and populations. Differences in growth between contemporary and historic samples were tested in two ways. First, results from likelihood ratio tests indicated a significant time effect among VBGFs fit to fishery-dependent samples from three time periods (1977–79, 1986–92, and 2006–07). Second, results from analysis of variance indicated sex-specific differences existed in size-at-age for ages 2–10 between contemporary and historic data. The GOM population, which has experienced an estimated 2.5 fold increase in spawning stock biomass (SSB) since the early 1990s, displayed a decline in size-at-age for ages 2–7, while the Atlantic population, which has experienced an approximately 45% decline in estimated spawning stock biomass (SSB) over the same time period, displayed an increase in size-at-age for ages 4–10. These trends are most likely due to density-dependent responses to changes in population size.

King mackerel, *Scomberomorus cavalla* (Cuvier, 1829), is a large, economically important coastal pelagic species with a range extending from Massachusetts to Brazil in the Atlantic Ocean (Atlantic) and throughout the Gulf of Mexico (GOM) and Caribbean Sea (Collette and Nauen, 1983). Tagging efforts in the 1970s and 1980s indicated there are three migratory groups of king mackerel exploited in United States' waters: a western GOM population, an eastern GOM population, and an Atlantic population (Johnson et al., 1994). The fisheries management-defined boundary between the eastern and western GOM populations is assumed to be the mouth of the Mississippi River, while the management-defined boundary between the eastern GOM and Atlantic populations in Florida is the Volusia-Flagler County line from November to March and the Monroe-Collier County line from April to October. Prior estimates of individual growth were significantly different among the three groups, thus supporting the existence of three distinct populations (DeVries and Grimes, 1997). However, genetic analyses indicated no difference between the eastern and western GOM groups, but a significant difference between GOM and Atlantic fish (Gold et al., 1997, 2002). Since 1985, the Gulf of Mexico and South Atlantic Fisheries Management Councils (GMFMC and SAFMC) have jointly assessed and managed the U.S. GOM and Atlantic populations as separate populations with overlapping winter ranges (GMFMC and SAFMC, 1985). The most recent stock assessments estimated the GOM population was subject to overfishing from the 1970s until 1996, while the Atlantic population had never undergone overfishing (SEDAR16, 2009).

Historic king mackerel age and growth estimates from fishery-dependent data indicated differences existed between sexes and populations (DeVries and Grimes, 1997; Johnson et al., 1983). Estimated von Bertlanffy growth functions (VBGFs) from 1977–79 and 1986–92 samples indicated females grew larger than males in both the GOM and Atlantic, and that Eastern GOM fish grew larger than Atlantic fish, with western GOM individuals reaching intermediate sizes (DeVries and Grimes, 1997). Differences in growth rates between sexes and populations were consistent between the two time periods, indicating these patterns were temporally stable. Higher growth rates in the GOM have been attributed to high productivity in the nutrient rich waters surrounding the Mississippi River's delta (DeVries and Grimes, 1997; Grimes, 2001).

Estimating growth functions based on samples from size-selective fishery landings can lead to biased results (Goodyear, 1995). The use of only fishery-dependent samples may have biased estimates of historic king mackerel growth by excluding the smallest size classes, which had not fully recruited to the fishery. Historic estimates of the von Bertalanffy parameter t_0 (hypothetical age when length = 0) ranged from −6.78 to −1.63 yrs (DeVries and Grimes, 1997). These relatively large, negative values for t_0 were driven by the lack of age-0 fish in the data, a typical problem encountered with growth estimates based exclusively on fishery-dependent samples (Potts and Manooch, 2002; Taylor et al., 2005). Poorly estimated values of t_0 also may have resulted in unconstrained estimates of L_∞ and the growth coefficient, k, due to the correlation among von Bertalanffy parameters (e.g., Pilling et al., 2002). The problem of excluding small, young fish was exacerbated for king mackerel growth functions by the institution of a 30.5 cm fork length (FL) minimum size limit in 1990. The minimum size limits were increased to 50.8 cm FL for both populations in late 1992, and the GOM limit was increased again to 61.0 cm FL in 1998.

Size-selective fishing mortality also has the potential to act as an artificial selection pressure in exploited fish populations. Conover and Munch (2002) demonstrated in a laboratory study of Atlantic silverside, *Menidia menidia* (Linnaeus, 1766), that removal of the largest 10% of individuals from a population resulted in a decline in mean size-at-age within a few generations, which they inferred indicated a population genetics effect of overfishing. Hilborn and Minte-Vera (2008) demonstrated that such severe selectivity is rare in fisheries. However, declines in mean size-at-age have been reported for overexploited populations of red porgy, *Pagrus pagrus* (Linnaeus, 1758), and vermilion snapper, *Rhomboplites aurorubens* (Cuvier in Cuvier and Valenciennes, 1829), in the GOM and South Atlantic Bight (Harris and McGovern, 1997; Zhao et al., 1997; Hood and Johnson, 1999, 2000). A comparison of long-term trends in growth within the chronically overexploited GOM king mackerel populations vs the Atlantic population, which has never been classified as overfished, may indicate possible adaptive consequences of high fishing pressure.

The object of this study was to estimate contemporary sex- and population-specific VBGFs for eastern GOM and Atlantic king mackerel. We included fishery-independent as well as fishery-dependent samples in an effort to improve estimates of VBGF parameters. We also compared contemporary and historic age and growth data to look for evidence of long term changes in size-at-age.

Methods

King mackerel were sampled between May and November of 2006 and 2007 from fishery-dependent and fishery-independent sources with additional GOM juvenile samples collected in 2008. Fishery-dependent samples were collected from recreational and tournament landings between Panama City, Florida, and Dauphin Island, Alabama, for the GOM population and in Jacksonville, Florida, and Beaufort, North Carolina, for the Atlantic population. Fishery-independent GOM samples were collected on Southeast Area Monitoring and Assessment Program (SEAMAP) trawling cruises between Alabama and Brownsville, Texas. Additional fishery-independent samples were collected with hook-and-line gear off in the northeastern GOM and with a cast-net off southeastern Florida in the Atlantic. Each fish was sexed macroscopically, FL was measured to the nearest centimeter, and both saggital otoliths were removed. Juveniles were arbitrarily defined as individuals that were both below the minimum size limit (GOM: 61.0 cm; Atlantic: 50.8 cm FL) and could not be sexed macroscopically; these fish were included in growth models for both sexes.

Otolith opaque zones (annuli) were counted to determine age (Johnson et al., 1983; DeVries and Grimes, 1997). Analysis of the marginal distances and the frequency of marginal opaque zones by month were consistent with earlier reports that opaque zones form annually between February and May (Manooch et al., 1987; DeVries and Grimes, 1997). Otoliths from males > 800 mm FL and females > 900 mm FL were sectioned for aging. Otoliths to be sectioned were embedded in epoxy and three thin (~0.5 mm) transverse sections were made through the nucleus using a low speed saw. The sections were fixed to a microscope slide with mounting medium and their annuli counted under a dissection microscope at 10× magnification with transmitted light. Otoliths from males < 800 mm FL and females < 900 mm FL were immersed in water in an opaque, black dish and aged whole under a dissection microscope at 7× magnification with reflected light. For both whole and sectioned otoliths, the number of opaque zones was recorded and the margin (area between the last opaque zone and the edge of the otolith) was classified as nonexistent, small, average, or large relative to the previous increment (distance between the penultimate and final opaque zone). The margin was classified as nonexistent if the last opaque zone was on the edge of the otolith. A small margin was < 1/3 the width of the previous increment. An average margin was 1/3–2/3 the width of the previous increment, and a large margin was > 2/3 the width of the previous increment. The number of opaque zones, or annuli count, was converted to adjusted age based on a margin classification with an algorithm established by the NOAA Fisheries Panama City Laboratory for aging king mackerel. For fish collected from January 1 to May 31, age was equivalent to annuli count if the margin was nonexistent or small. If the margin was average or large, age was advanced 1 yr. For fish collected from June 1 to July 20, age was advanced 1 yr if the margin was large or if the margin was average and there were more than two annuli. For fish collected from July 21 to December 31, age was always equivalent to the annuli count. Integer adjusted ages were converted to fractional ages for analysis by adding 0.25 yrs to fish collected during April–June, 0.50 yrs to fish collected during July–September, and 0.75 yrs to fish collected during October-December (DeVries and Grimes, 1997).

Ten percent of otolith samples were read a second time by an experienced technician at the NOAA Fisheries Panama City Laboratory. The average percent error (APE) was calculated between the two sets of age estimates (Beamish and Fournier, 1981). The calculated APE served as a measure of between-reader agreement and aging precision. Reader bias was evaluated with a linear regression of reader one vs reader two ages.

Fractional age and length at capture were used to fit population- and sex-specific von Bertalanffy growth functions (VBGFs) to (i) contemporary combined-source (fishery-dependent and -independent samples) and (ii) fishery-dependent samples only using a maximum likelihood estimation. The VBGF model assumes a normal left-truncated error distribution to account for the minimum size censoring (GOM: 61.0 cm; Atlantic: 50.8 cm FL) in fishery-dependent samples (Ortiz and Palmer, 2008). The minimum size for fishery-independent samples was set to 0 cm FL. The VBGF model also assumed a constant coefficient of variation (CV) to account for non-homogeneous variance of size across ages.

Differences in growth function parameters were tested between combined-source and fishery-dependent models with likelihood ratio tests (Cerrato, 1990). Growth functions fitted to fishery-dependent data were also tested for differences between sexes and populations. The likelihood ratio (χ^2) statistic was calculated as:

$$\chi^2 = -N \times \ln\left(\frac{SS_\Omega}{SS_\omega}\right) \tag{1}$$

where N = combined sample size for the two data sets being tested, SS_Ω = sum of squared residuals when fitting the two VBGFs separately, and SS_ω = sum of squared residuals when fitting a single VBGF to the two data sets combined (Kimura, 1980). Assuming a normal left-truncated error distribution and a constant CV meant that the functions were not fit by simply minimizing the sum of squares. Thus, it was possible to obtain a lower sum of squares when the two test groups were fit together than when they were fit separately producing a negative χ^2 value. Where this situation occurred, the VBGF fit clearly was not improved by modeling the two groups separately and was interpreted as a non-significant difference requiring no further testing. Tests were conducted for differences in each of the three VBGF parameters as well as the model as a whole between sexes, and populations. An arbitrarily conservative significance level ($\alpha = 0.01$) was chosen for the likelihood ratio tests to account for inflation of the probability of Type I error due to the number of tests conducted.

Differences in growth also were tested between contemporary and historic fishery-dependent samples collected during 1977–1979 and 1986–1992 (DeVries and Grimes, 1997). Growth functions computed from samples collected during the two earlier time periods were compared with functions computed from fishery-dependent data sampled during the current study. A minimum size limit of 30.5 cm FL was first enacted on August 20, 1990; thus, historic growth functions were fit with the same methods used with the contemporary data, assuming a constant CV and a minimum size of 0 cm FL before the size limit was introduced and 30.5 cm FL for samples collected after that date. The migratory routes of the GOM and Atlantic populations overlap around south Florida during the winter months making it impossible to assign individual samples collected from this region to a given population (DeVries et al., 2002; Clardy et al., 2008; Shepard et al., 2010). For this reason, samples collected in south Florida between 1986 and 1992 were excluded from analysis. No samples were collected in that region from 1977 to 1979. Also, only historic samples collected between May and November were used to fit historic growth functions in order to maintain a sampling season consistent with the contemporary data. Likelihood ratio tests were performed for each sex/population combination to test for differences in the fitted growth functions among the three time periods (1977–79, 1986–92, and 2006–07). As above, $\alpha = 0.01$ was used to control for Type I error.

Lastly, differences in mean size-at-age were tested among time periods with an analysis of variance (ANOVA). The test was conducted with a three factor (age, population, and time period), fully-crossed model with a Scheffe adjusted multiple comparisons procedure sliced by age and population to determine which age/population combinations displayed significant time period effects. Data from males and females were analyzed separately. Analysis of mean size-at-age was conducted on the fishery-dependent adjusted age data rather than from model predictions.

Results

King mackerel (n = 2316) were sampled for age and growth analysis between May and November in 2006 and 2007, with additional juveniles (n = 62) collected in 2008, from the northern GOM and the Atlantic off the southeastern United States (Table 1). GOM females ranged from 41.0 to 167.2 cm FL and GOM males from 38.0 to 125.4 cm FL with GOM juveniles analyzed with both sexes ranging from 7.5 to 49.9 cm FL; Atlantic females ranged from 48.6 to 138.0 cm FL and Atlantic males from 44.0 to 122.0 cm FL with Atlantic juveniles ranging from 9.0 to 13.3 cm FL (Table 2). Maximum age was 19, 20, 19, and 23 yrs for GOM females, GOM males, Atlantic females, and Atlantic males, respectively (Table 2). The APE computed between age estimates for the 237 individuals read by two readers was 3.39%. The fitted slope of the linear regression between reader age estimates was not significantly different from one (t = 0.849, P = 0.397) and the intercept was not significantly different from zero (t = 0.447, P = 0.653), thus indicating no systematic bias existed between readers.

Contemporary combined-source and fishery-dependent VBGFs were significantly different for each sex/population combination (Figs. 1, 2; Table 2). All parameters, as well as overall functions, were significantly different in each of the four comparisons (likelihood ratio test; $P < 0.001$). The models fit to combined-source data displayed lower estimates of L_∞, higher estimates of k, and more negative estimates of t_0 than models fit to fishery-dependent data alone.

For the combined-source VBGFs, fishery-dependent residuals exhibited a distinctly different pattern from those of the fishery-independent samples (Fig. 3). Fishery-dependent residuals tended to be positive for the youngest and oldest individuals and neutral for intermediate ages. The net-sampled, fishery-independent age-0 and age-1 individuals displayed neutral residuals in both populations. Residuals about the

Table 1. The number of female, male, and juvenile king mackerel, *Scomberomorus cavalla*, sampled from the northern Gulf of Mexico (GOM) and Atlantic Ocean each year for age and growth analysis from Southeast Area Monitoring and Assessment Program (SEAMAP) trawls, fishery-independent hook-and-line and cast net sampling, and fishery-dependent hook-and-line commercial, recreational, and tournament landings.

	GOM			Atlantic		
	Female	Male	Juvenile	Female	Male	Juvenile
2006						
SEAMAP	1	0	36			
Independent	17	13	2	0	0	22
Recreational	137	64		279	118	
Tournament	166	28				
2007						
SEAMAP	0	0	85			
Independent	86	46	1			
Recreational	341	146		7	7	
Tournament	173	43		306	120	
Commercial				10	0	
2008						
SEAMAP			62			
Total	921	340	186	602	245	22

Table 2. Sample sizes size and age ranges, von Bertalanffy growth function parameters, and coefficients of variation (CV) estimated for female (F) and male (M) king mackerel, *Scomberomorus cavalla*, from the Gulf of Mexico (G) and Atlantic Ocean (A) populations during three time stanzas (2006–07, 1986–92, and 1977–79) with 2006–7 growth functions fit to fishery-dependent and -independent data (combined source) as well as fishery-dependent data alone (fishery-dependent).

	n	Size range (cm)	Age range (yrs)	L_∞	k	t_0	CV(%)
2006–07							
Combined source							
GF	1,088	7.5–167.2	0–19	124.5	0.256	–0.173	15.1
GM	516	7.5–125.4	0–20	92.2	0.353	–0.166	17.1
AF	622	9.0–138.0	0–19	111.6	0.464	0.506	10.3
AM	264	9.0–122.0	0–23	98.9	0.510	0.502	9.6
Fishery-dependent							
GF	802	41.0–167.2	1–19	171.9	0.082	–3.837	7.7
GM	274	38.0–125.4	1–20	118.5	0.094	–6.601	5.7
AF	600	48.6–138.0	1–19	128.6	0.181	–2.046	7.2
AM	242	44.0–122.0	1-23	111.3	0.173	–2.863	5.6
1986–92							
GF	2,492	35.0–158.0	0–21	133.6	0.194	–1.440	9.9
GM	1,112	43.0–127.0	0–19	100.1	0.298	–1.190	8.7
AF	3,534	33.8–152.0	0–26	116.1	0.244	–1.110	11.4
AM	2,195	35.0–121.0	1–24	93.6	0.370	–0.677	9.8
1977–79							
GF	1,005	35.4–154.0	1–19	135.2	0.170	–1.950	9.1
GM	331	42.8–116.5	1–19	97.7	0.292	–1.420	8.7
AF	323	52.7–127.8	1–20	120.2	0.134	–4.200	6.5
AM	128	52.0–107.0	1–18	92.8	0.274	–2.070	5.6

predicted VBGFs fit to fishery-dependent data alone appeared randomly distributed for all models (Fig. 4).

Contemporary fishery-dependent VBGFs displayed significant sex- and population-specific differences (Fig. 2; Tables 2, 3). The variation between sexes in both populations was driven entirely by L_∞, which was higher for females than males. Females in the GOM had a higher L_∞ and lower k and t_0 than females in the Atlantic. Finally, VBGFs fits for males were significantly different between the two populations, but none of the individual parameters were significant.

Contemporary fishery-dependent VBGFs were significantly different than historic growth functions in all comparisons (Fig. 5; Tables 2, 3). The likelihood ratio χ^2 values were higher for L_∞ than the other parameters in all comparisons, indicating that the higher contemporary L_∞ estimates were driving the overall model differences. Contemporary estimates of k were lower than estimates from both historic time periods in all comparisons, except with Atlantic females from 1977–79. Finally, contemporary estimates of t_0 were significantly lower than historic estimates in all comparisons, except with Atlantic females and males from 1977–79.

Results from the ANOVA computed on mean size-at-age indicate it has varied significantly over time and that the trends in size over time are not consistent across ages or between populations or sexes (Fig. 6). The model residuals were slightly non-normal (female: K-S = 0.039, P = 0.01; male: K-S = 0.049, P = 0.01), although this deviation from normality appeared to be driven by leptokurtosis rather than skew-

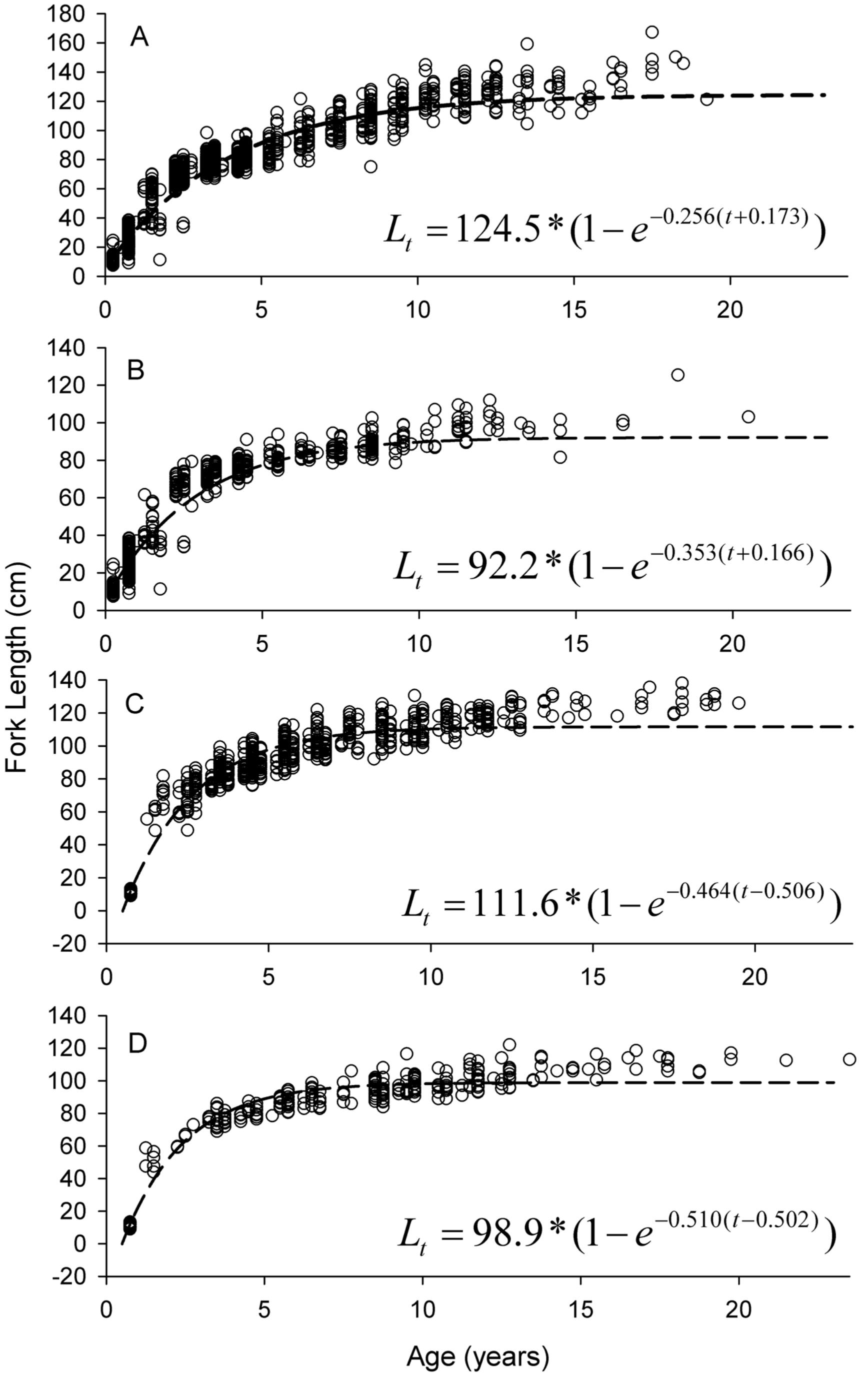

Figure 1. Fishery-dependent and -independent size-at-age data for king mackerel, *Scomberomorus cavalla,* sampled during summer 2006 and 2007 (supplemented with GOM juveniles collected in 2008). Dotted lines and equations are von Bertalanffy growth functions. (A) Gulf of Mexico females, (B) Gulf of Mexico males, (C) Atlantic Ocean females, (D) Atlantic Ocean males. Note that y-axis scale in (A) differs from others.

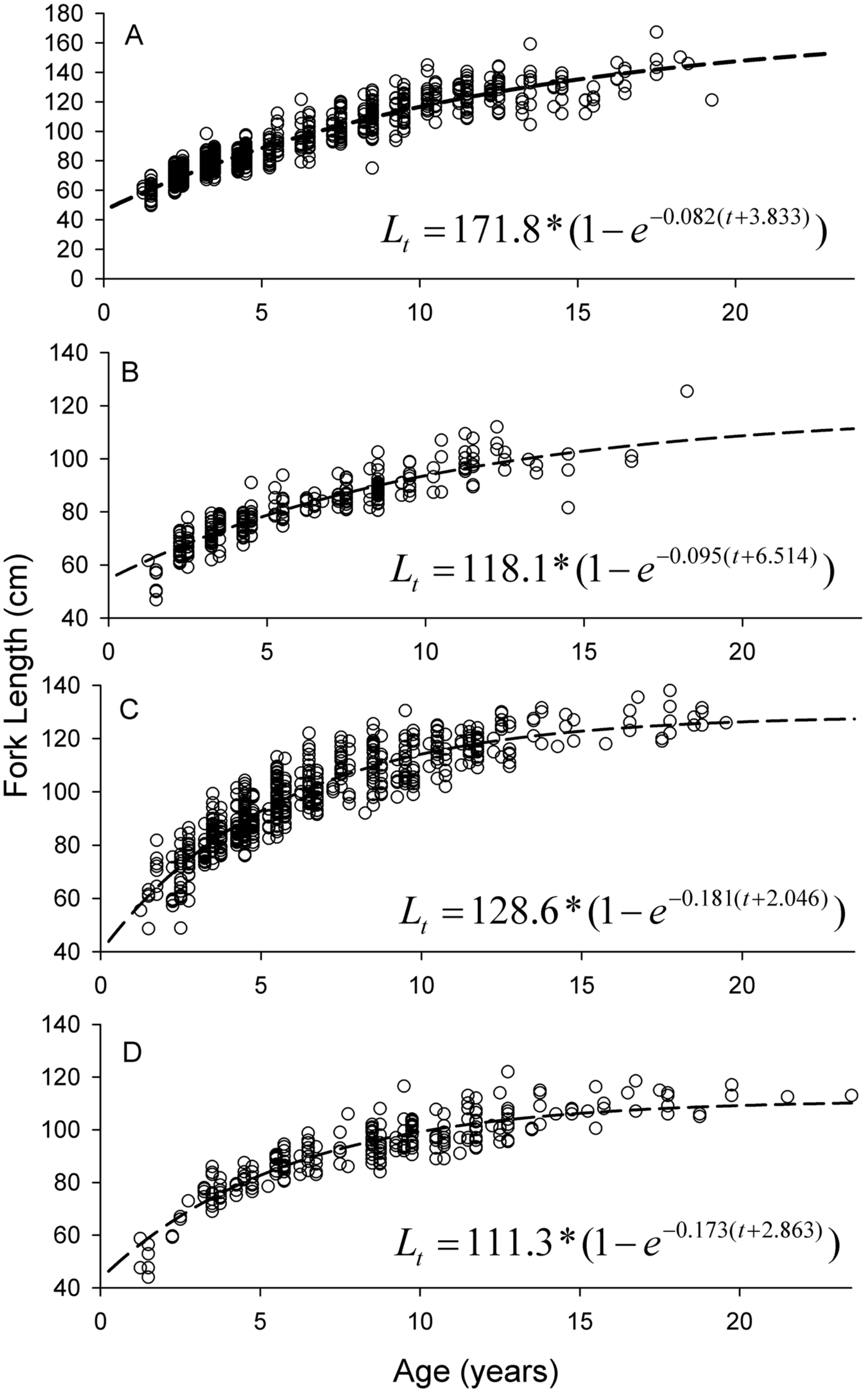

Figure 2. Fishery-dependent size-at-age data for king mackerel, *Scomberomorus cavalla,* sampled during summer 2006 and 2007. Dotted lines and equations are von Bertalanffy growth functions. (A) Gulf of Mexico females, (B) Gulf of Mexico males, (C) Atlantic Ocean females, (D) Atlantic Ocean male. Note that y-axis scale in (A) differs from others.

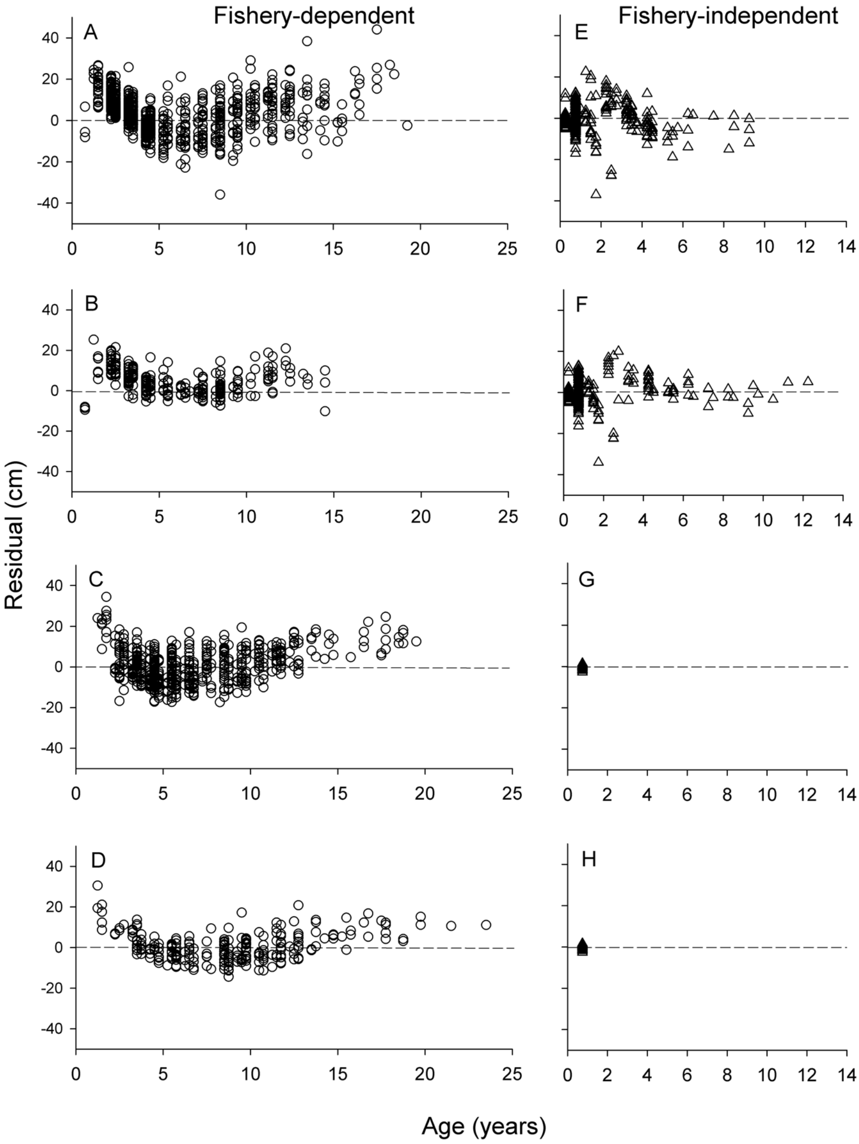

Figure 3. Residual distributions for combined-source von Bertalanffy growth functions estimated from king mackerel, *Scomberomorus cavalla,* samples collected from fishery-dependent (panels A–D) and fishery–independent (panels E–H) sources for (A,E) Gulf of Mexico females, (B,F) Gulf of Mexico males, (C,G) Atlantic Ocean females, and (D,H) Atlantic Ocean males.

ness, and there was no evidence of heterogeneous variances. Thus, we decided transformation was not appropriate. All effects and interactions were highly significant ($P < 0.001$) for females. All effects and interactions except population ($P = 0.836$) and age*population ($P = 0.458$) were highly significant ($P < 0.001$) for males. The large number of significant interactions would seem to complicate interpretation. However, one would expect age and population, as well as their interactions, to be significant based on differences in the growth functions. In the GOM population,

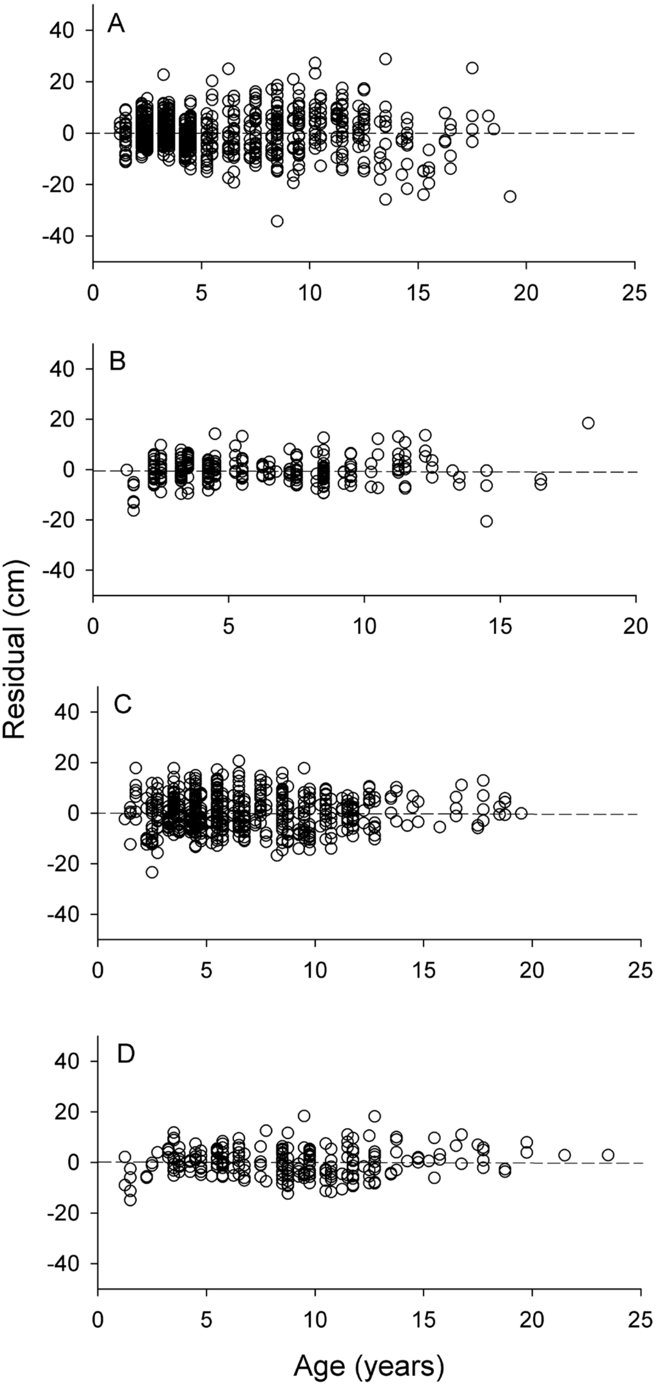

Figure 4. Residual distributions for von Bertalanffy growth functions estimated from king mackerel, *Scomberomorus cavalla,* samples collected from fishery-dependent sources alone for (A) Gulf of Mexico females, (B) Gulf of Mexico males, (C) Atlantic Ocean females, and (D) Atlantic Ocean males.

Table 3. Results of likelihood ratio tests for differences in the estimated von Bertalanffy growth functions for female and male king mackerel, *Scomberomorus cavalla*, from the Gulf of Mexico and Atlantic Ocean populations during three time stanzas (2006–07, 1986–92, and 1977–79). Models were fit to fishery-dependent data assuming a normal left-truncated distribution with a constant CV. Where the sum of squares for the combined model was less than the sum of squares for the models fit separately, the parameters were assumed to be not significantly different and no test was conducted ("na" in the table).

		Model (df = 3)	L_∞ (df = 1)	k (df = 1)	t_0 (df = 1)
Female vs male (2006–07)					
GOM	χ^2	700.4	9.7	0.5	4.2
	p	< 0.001*	0.002*	0.464	0.041
Atlantic	χ^2	488.3	24.2	0.1918	2.6
	p	< 0.001*	< 0.001*	0.661	0.107
GOM vs Atlantic (2006–07)					
Female	χ^2	117.3	82.3	56.6	21.7
	p	< 0.001*	< 0.001*	< 0.001*	< 0.001*
Male	χ^2	69.8	na	2.3	6.2
	p	< 0.001*	na	0.126	0.013
2006–07 vs 1986–92					
GOM female	χ^2	139.2	58.1	81.9	60.8
	p	< 0.001*	< 0.001*	< 0.001*	< 0.001*
GOM male	χ^2	59.9	na	6.7	15.53
	p	< 0.001*	na	0.009*	< 0.001*
Atlantic female	χ^2	116.8	na	na	na
	p	< 0.001*	na	na	na
Atlantic male	χ^2	228.7	201.6	64.5	30.122
	p	< 0.001*	< 0.001*	< 0.001*	< 0.001*
2006–07 vs 1977–79					
GOM female	χ^2	61.5	46.2	47.4	29.8
	p	< 0.001*	< 0.001*	< 0.001*	< 0.001*
GOM male	χ^2	24.5	10.2	17.724	20.935
	p	< 0.001*	0.001*	< 0.001*	< 0.001*
Atlantic female	χ^2	346.1	1.6	8.4	23.9
	p	< 0.001*	0.212	0.004*	< 0.001*
Atlantic male	χ^2	121.2	9.7	na	na
	p	< 0.001*	0.002*	na	na

contemporary mean size-at-age was consistently lower than historic estimates for ages 2 through 7 and similar to historic estimates for ages 8 through 10. Contemporary mean size-at-age in the Atlantic population was greater than historic estimates for ages 4–10, similar to historic estimates for age 3, and less than historic estimates for age 2. The average percent difference in size-at-age between contemporary and 1986–92 samples for ages 2–10 were −4.3%, −3.4%, 5.2%, and 4.6% for GOM females, GOM males, Atlantic females, and Atlantic males, respectively.

Discussion

Fitting VBGFs to combined fishery-dependent and -independent samples appear to model growth more effectively for the population as a whole than did fitting functions to size-at-age of only the landed catch. In particular, incorporation of age-0 and

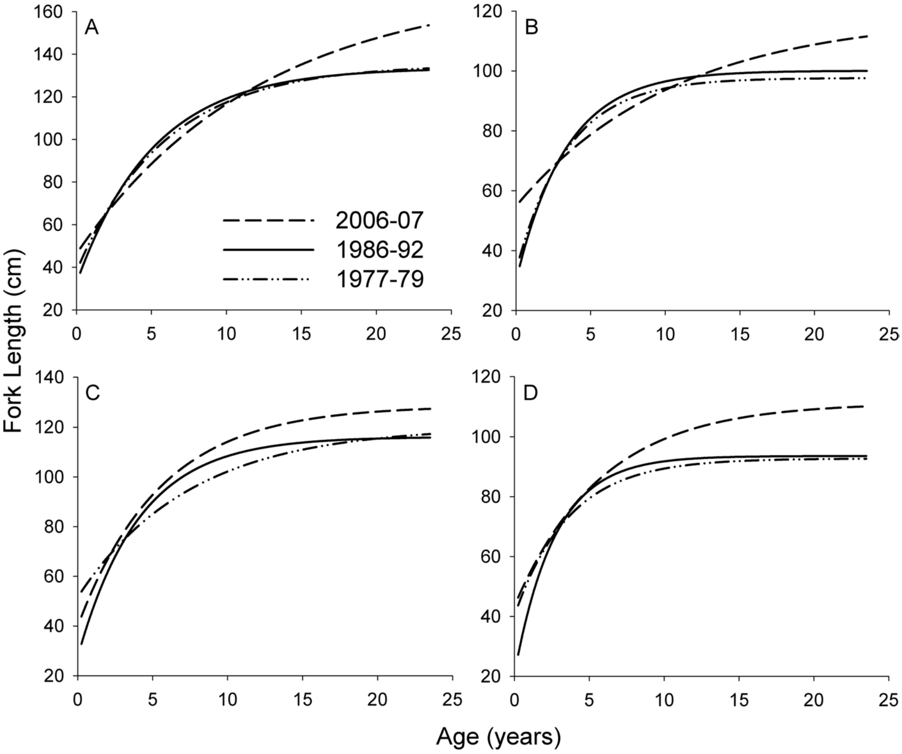

Figure 5. Von Bertalanffy growth functions estimated for king mackerel, *Scomberomorus cavalla,* collected from fishery landings during the summer spawning seasons over three time periods for (A) Gulf of Mexico females, (B) Gulf of Mexico males, (C) Atlantic Ocean females, (D) Atlantic Ocean males. Data for 1986–1992 and 1977–1979 originally reported by DeVries and Grimes (1997). Note y-axis scales differ among panels.

age-1 fishery-independent samples in the data provided information to the model to estimate t_0 more accurately than fishery-dependent models. The improved fit of t_0 further served to constrain estimates of $L_{\infty,}$ in part, due to correlation among the VBGF parameters.

Positive fishery-dependent residuals about the combined-source VBGFs in the youngest age classes may be both artifacts of the model and a reflection of gear selectivity. Simulations have shown size-selective sampling gears lead to biased estimates of size-at-age (Goodyear, 1995). In this study, samples were collected with a variety of gear types to reduce the impact of size-selective sampling. The VBGFs were intentionally fit below observed size-at-age data for the youngest fish by assuming a normal left-truncated distribution to account for individuals absent due to the minimum size limit. Positive residuals for the youngest individuals also may reflect the dome-shaped selectivity pattern of the commercial and non-tournament recreational hook and line gear, which can lead to overestimating size-at-age for the youngest age classes because the fastest growing young fish are the first to recruit to the gear (Goodyear, 1995; DeVries and Grimes, 1997; Taylor et al., 2005).

Positive residuals for the oldest fishery-dependent samples were likely also affected by both the model itself and by the sampling methods. Correlation between VBGF

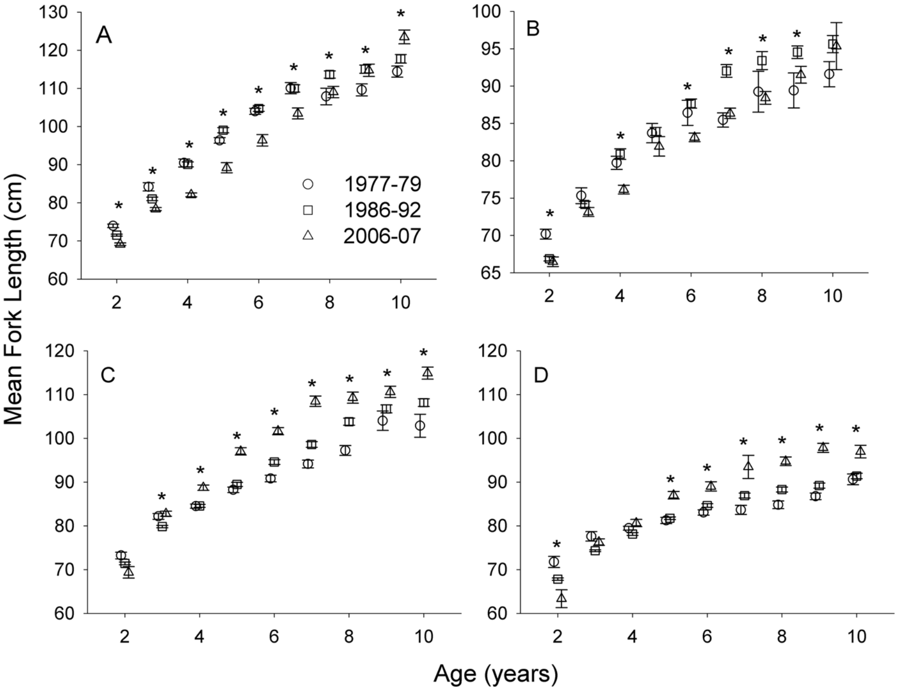

Figure 6. Mean (± SE) size-at-age for Gulf of Mexico (A) female and (B) male, and Atlantic Ocean (C) female and (D) male king mackerel, *Scomberomorus cavalla,* ages 2–10 yrs sampled from fishery landings during the summer spawning seasons over three time periods (2006–2007, 1986–1992, 1977–1979). Data for 1986–1992 and 1977–1979 originally reported by DeVries and Grimes (1997). * indicates a significant difference among time periods ($P < 0.05$), and time periods are offset by 0.15 yrs for clarity.

parameters requires a balance between achieving the best estimates of k and L_∞. The sparseness of data for the oldest age classes and the abundance of observations from younger and intermediate ages may have resulted in better estimates of k and limited the ability of old, large observations to draw L_∞ upward. Positive residuals for the oldest fish may also reflect the fact that most of these samples were collected from fishing tournament landings. Predicted size-at-age of tournament landings tend to be upwardly biased, but exclusion of tournament samples in our region can result in the absence of large, old fish from a dataset (Patterson et al., 2001; Fischer et al., 2004).

Contemporary fishery-dependent growth functions displayed differences between sexes and populations that are consistent with historic patterns (DeVries and Grimes, 1997). Females achieved larger size-at-age than males in both populations, and individuals from the GOM population grew larger than those from the Atlantic population. The residuals of the VBGF fits to fishery-dependent data were randomly distributed, but L_∞ and t_0 were poorly fit due to the truncated size distribution that resulted from excluding the smaller, fishery-independent samples. Despite potential biases, comparisons of growth among time periods were conducted on the fishery-dependent data to maintain consistency with historic methods.

Contemporary fishery-dependent growth functions differed significantly from historic functions for all sex/population combinations. That contemporary L_∞ estimates were generally higher, and k and t_0 estimates lower, than for fits to historic data might be a function of changes in fishing regulations over the time period considered, but all VBGFs were fit assuming a truncated distribution to account for minimum size limits. It is also possible that the differences in VBGF fit are a function of sample size. The 1986–92 data set has the largest sample sizes followed by the 1977–79 data set and the contemporary data set had the smallest sample sizes. The fact that sample sizes and parameter estimates did not increase or decrease consistently over time supports an explanation based on the fit of the growth functions rather than a biologically significant change in king mackerel growth.

Analysis of size-at-age among time periods with ANOVA provided a more direct test for population-specific changes over time. Changes in size-at-age observed in both the GOM and Atlantic populations may be driven by a number of environmental and anthropogenic factors. Because this analysis was conducted on fishery-dependent data, it is also possible that shifts in gear selectivity have influenced our estimates of size-at-age over time. Unfortunately, specific information on sector and gear-type no longer exist for the historic data sets, making it impossible to test for a selectivity effect. The fact that the trends were not consistent across all ages also indicates temporal variability may exist in the suite of factors affecting king mackerel growth. The complex nature of phenotypic expression complicates any attempt to attribute these trends to any one factor; however, it is possible that exploitation of king mackerel has contributed to the adaptive landscape that led to these changes.

Changes in size-at-age in fish populations have been linked to exploitation, population density, temperature, and prey availability. Assessing the effects of any one of these factors in isolation can lead to spurious conclusions (Sinclair et al., 2002; Hilborn and Minte-Vera, 2008). Many of these factors, such as population density and prey availability, may both produce immediate phenotypic effects and impact the direction or strength of natural selection processes, resulting in gradual long-term genotypic changes (Lorenzen and Enberg, 2002; Edeline et al., 2007). Fishing has been shown to act as an artificial selection pressure with the strength and direction of the selection determined by the degree of exploitation and selectivity of the gear (Carlson et al., 2007; Edeline et al., 2007; Swain et al., 2007; Kuparinen et al., 2009). However, fishing also reduces population density, and growth is often negatively correlated with population density (Lorenzen and Enberg, 2002; Sinclair et al., 2002; Edeline et al., 2007; Swain et al., 2007). Temperature has been shown to be positively correlated with growth, but this effect is often weak compared to fishery and density-dependent responses (Sinclair et al., 2002; Swain et al., 2007). Finally, high prey availability has been shown to favor rapid growth, while low prey availability favors slow growth and a lower metabolic rate (Edeline et al., 2007). It is possible that the effect of prey availability on size-at-age has the greatest impact of the factors discussed here, but little work has been done to directly study this relationship (Edeline et al., 2007; Hilborn and Minte-Vera, 2008).

The GOM king mackerel population had been heavily exploited as early as 1980, and continued to be until 1996 (Powers, 1996; SEDAR16, 2009). Therefore, declines in size-at-age observed in contemporary samples may be due to an artificial selection effect resulting from the chronic overfishing that GOM fish experienced in the preceding decades (Conover and Munch, 2002), but that explanation seems unlikely given other information available. If artificial selection were the cause, then its seems likely that the shift to smaller size-at-age would have occurred at least by the mid-

1990s, when the fishery had been overexploiting the GOM population for well more than a decade, and not only apparent after a decade of stock recovery. Estimated king mackerel spawning stock biomass (SSB) in the GOM has increased approximately 2.5 times since the late 1980s (SEDAR16, 2009), thus it seems more likely that a density-dependent feedback depressed growth rates in the 2000s (Hilborn and Minte-Vera, 2008). This explanation has further traction given that age-7 and younger individuals among contemporary samples would have been spawned during the period when population size was increasing most rapidly in the GOM. Hilborn and Minte-Vera (2008) suggest that any increase in growth rate as a population is fished down would occur soon after the increase in exploitation. Because GOM king mackerel were already heavily exploited when the earliest historic data (1977–1979) were collected, it is likely any associated increase in growth rate had already occurred.

Counter to the biomass trend in the GOM, SSB in the Atlantic population is estimated to have decreased by approximately 45% since the late 1980s (SEDAR16, 2009). Therefore, it is likely that the increase in mean size-at-age observed among several ages in that population is also a density-dependent response to population size, albeit in the opposite direction as the trend in the GOM. Such a density-dependent effect is even more likely in the Atlantic than the GOM population because that system is less productive than the GOM (Grimes, 2001). However, without evidence that individual growth had been limited historically by population density it is difficult to attribute the increase in size-at-age entirely to a density-dependent response (Sinclair et al., 2002).

Clearly, it would not be possible to invoke density-dependence in explaining the smaller size-at-age observed in contemporary vs historic samples of Atlantic 2 yr-olds. Perhaps this decrease in size-at-age indicates the beginning of an artificial selection response to fishing, but that inference seems like a bit of a reach given the single year class affected, and the different patterns observed between Atlantic females and males. Instead, the apparent decline in size-at-age for 2 yr-olds might have resulted from a larger proportion of samples being collected earlier in the year in the contemporary vs historical data sets, given that king mackerel grow rapidly in the first few years of life. However, this does not appear to be the case, as the percentage of Atlantic age-2 samples assigned to each of four fractional ages (2, 2.25, 2.5, and 2.75) was comparable between the contemporary (0, 25.0, 35.7, and 39.3%, respectively) and combined historic (9.6, 26.5, 35.8, and 28.1%, respectively) data sets. The decline in size-at-age-2 might also be due to fluctuations in prey abundance or environmental factors affecting growth. As in the GOM population, a more directed effort would be necessary to tease apart the suite of factors driving the variability in size-at-age reported here.

The combination of natural and fishery selection has shown the potential to produce a maladaptive environment where phenotypes with reduced fitness can be preserved in the population (Carlson et al., 2007). Natural selection tends to favors larger size and is stabilizing when prey abundance is not limiting (Carlson et al., 2007; Edeline et al., 2007). Large size is associated with high fecundity, large egg size, and increased egg and larval survival (Walsh et al., 2006). Fishery selection with hook-and-line gear, on the other hand, typically favors small size and is disruptive (Carlson et al., 2007). A population depleted as a result of fishing and experiencing a fishery selection response toward slower growth may be slow to recover once overfishing has ceased (Walsh et al., 2006). The GOM population has rebounded in recent years, indicating reduced size-at-age has not inhibited its recovery. This rapid recovery may be due in part to the high productivity of the region. If the Atlantic population continues to decline, then understanding the mechanisms driving variation in size-at-age and the possible evolutionary consequences of size-selective fishing may become increasingly important for effective management.

It is unclear whether the trends in king mackerel size-at-age reported here are a genetic effect due to size-selective harvesting (Conover and Munch, 2002), or a compensatory response to changes in population density (Hilborn and Minte-Vera, 2008), but it appears that the preponderance of evidence favors the latter vs the former explanation. Part of the rationale for the current study was to determine if there was evidence for artificial selection having occurred in GOM king mackerel. However, the decrease in GOM size-at-age during a period when estimated SSB has been increasing rapidly, coupled with an increase in Atlantic size-at-age during a period of declining population size estimates, indicate density-dependence as a simpler and more logical explanation for observed trends. These two populations with their contrasting biomass trajectories present an interesting opportunity to further study the relationship between changes in population size and growth rates. Furthermore, this study highlights the importance of constantly examining population growth rates over time as projections of long-term productivity and fishery yield may be greatly affected by incorporating density-dependence into population dynamics parameters (Lorenzen and Enberg, 2002; Minto et al., 2008).

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