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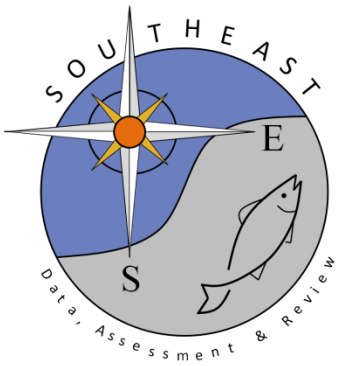

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[Article]

Trends in Atlantic Contribution to Mixed-Stock King Mackerel Landings in South Florida Inferred from Otolith Shape Analysis

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Abstract.—The Atlantic Ocean and Gulf of Mexico (GOM) stocks of king mackerel *Scomberomorus cavalla* are genetically distinct but have overlapping winter ranges around South Florida. Understanding the factors driving the relative contribution of each stock to South Florida winter landings is necessary for effective management. The contribution of the Atlantic stock was estimated for the 2006–2007 and 2007–2008 fishing seasons using otolith shape as a natural tag. Analysis of otolith shapes from king mackerel sampled in summer (when the Atlantic and GOM stocks were presumed to be geographically separated) revealed significant sex and stock effects. Discriminant function analysis conducted with otolith morphometric indices and Fourier harmonic amplitudes as classification variables produced jackknifed classification success rates ranging from 60% to 73%. Maximum likelihood estimates of the Atlantic stock's contribution to winter landings indicated that there was a spatial gradient, the lowest contribution (mean = 25%) occurring off southwestern Florida and the highest (mean = 48%) off southeastern Florida. Estimates of the Atlantic stock's contribution to the easternmost zone increased from December through March, possibly reflecting the northward spring migration of both stocks. A comparison of contemporary and historic estimates dating back to the 1996–1997 fishing season revealed evidence of a long-term increase in the GOM stock's contribution, which may be driven by a dramatic increase in the size of the GOM stock and a gradual decline in that of the Atlantic stock over the time period considered.

King mackerel *Scomberomorus cavalla* is a large, coastal pelagic fish that inhabits waters from Massachusetts to northern Brazil in the Atlantic Ocean (Atlantic), including the Gulf of Mexico (GOM) and Caribbean Sea (Collette and Nauen 1983). Tagging efforts in the 1970s and 1980s provided evidence of three distinct migratory groups, or populations, in U.S. waters: one spawning in summer off the U.S. mid-Atlantic coast, and two spawning in the northern GOM (Fable et al. 1981, 1987; Sutter et al. 1991; Johnson et al. 1994). Western GOM fish migrate south along the Texas coast in late fall and winter, while eastern GOM fish migrate south along the west Florida shelf and mix with Atlantic fish around southern Florida in winter. Analysis of mitochondrial DNA (mtDNA) and nuclear DNA microsatellites later demonstrated that Atlantic fish were genetically distinct from either eastern or western GOM fish, but that no genetic difference was detected between fish sampled in the eastern versus western GOM (Gold et al. 1997, 2002). Therefore, king mackerel in U.S. waters are currently managed as two separate stocks: Atlantic and GOM. While the genetic differences between Atlantic and GOM fish are statistically significant, the two stocks are only weakly divergent (Gold et al. 1997, 2002). Thus, genetic markers are not sufficient for use as natural tags to effectively distinguish winter mixed-stock landings as being contributed by either stock (Broughton et al. 2002).

Important commercial and recreational fisheries exist for king mackerel throughout their range in U.S. waters. Fisheries management is complicated for northeastern GOM and Atlantic stocks due to high catch levels off South Florida during winter when those migratory groups are mixed. In 1985, the Gulf of Mexico and South Atlantic Fisheries Management Councils recognized the existence of separate GOM and Atlantic stocks and, for management purposes, established a winter mixing zone in the waters around South Florida (Figure 1). Until recently, all king mackerel landed in this region from November to March have been attributed to the GOM stock. This

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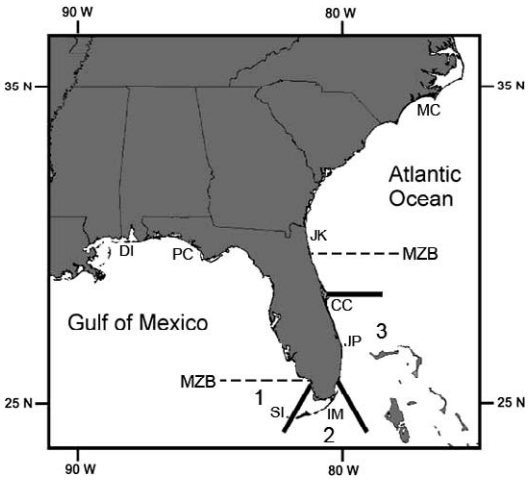

FIGURE 1.—Map of the southeastern United States depicting the single-stock summer sampling locations (DI = Dauphin Island, Alabama; PC = Panama City, Florida; JK = Jacksonville, Florida; and MC = Morehead City, North Carolina), the management-defined winter mixing zone boundaries (MZB), and the three winter zones (1, 2, and 3) sampled to examine the spatial variability in the percentage contributions of the Atlantic stock of king mackerel to South Florida winter landings. Winter sampling locations are as follows: SI = Stock Island, Florida; IM = Islamorada, Florida; JP = Jupiter, Florida; and CC = Cape Canaveral, Florida.

convention was originally adopted in the 1980s such that conservative winter catch allocations could be assigned to protect the GOM stock. However, simulations conducted by Legault (1998) indicated that assigning all winter mixing zone fish to the GOM stock resulted in overestimates of its biomass, and hence its stock status was designated as being in good condition. The most recent stock assessment (SEDAR16 2008) addressed this issue by assigning 50% of winter landings to each stock. Reliable estimates of the relative contribution of each stock to the mixed-winter landings are essential for accurate stock assessment and effective fisheries management.

Otolith shape analysis is a simple and commonly used method to derive natural tags in stock discrimination studies. Pothin et al. (2006) correctly classified greater than 90% of juvenile yellowstripe goatfish *Mulloidichthys flavolineatus* to their island of origin in the southwestern Indian Ocean. Cardinale et al. (2004) reported success rates between 79% and 85% discriminating between Atlantic cod *Gadus morhua* from Faroe Bank and Faroe Plateau based on otolith shape. An otolith's shape is affected by the rate at which it is deposited (Campana and Neilson 1985). The rate of otolith accretion is linked to somatic growth, and variation in otolith morphology between stocks is driven by stock-specific differences in growth rate (Smith 1992; Campana and Casselman 1993; Cardinale et al. 2004). DeVries et al. (2002) and Clardy et al. (2008) examined the problem of mixed-stock king mackerel fisheries in South Florida by using otolith shape analysis to distinguish Atlantic from GOM fish. DeVries et al. (2002) and Clardy et al. (2008) sampled fish in summer when stocks were separated and estimated how accurately otolith shape parameters distinguished GOM from Atlantic fish with discriminant function analysis. DeVries et al. (2002) reported 78% of GOM females and 71% of Atlantic females were correctly classified to their stock of origin. Clardy et al. (2008) correctly classified 66–76% of fish (both males and females sampled) to their sample regions, the highest classification success resulting from sex-specific discriminate functions.

Both of the earlier studies applied natural tags derived from otolith shape analysis to estimate the stock composition of fish landed off South Florida in winter. DeVries et al. (2002) reported that the Atlantic stock contributed 99.8% of females landed in southeastern Florida during the 1996–1997 fishing season. Clardy et al. (2008) divided the winter mixing area into three zones (Figure 1) and reported that otolith shape analysis indicated a gradient in Atlantic contribution, a lower percentage of Atlantic fish being landed in the west and a higher percentage in the east. This trend was consistent between sexes and years, but the estimated Atlantic contribution decreased between the 2001–2002 and 2002–2003 fishing seasons. The estimated Atlantic contribution to female landings caught off southeastern Florida was 82.8% in 2001–2002 and 40.4% in 2002–2003, both of which are lower than the 99.8% estimated by DeVries et al. (2002) for the 1996–1997 fishing year. It is unclear whether the variation between studies was driven by environmental variability or is representative of a long-term decline in Atlantic contribution. The current study was designed to complete a time series by estimating contemporary Atlantic contribution for each sampling zone defined by Clardy et al. (2008) over two successive fishing seasons. Mixing rates were also estimated for the region off southeastern Florida each month from December to March to assess intraannual variability.

Methods

King mackerel landings were sampled in the northern GOM (Dauphin Island, Alabama, to Panama City, Florida) and Atlantic (Jacksonville, Florida, to Morehead City, North Carolina) in the summers of 2006 and 2007 when GOM and Atlantic stocks were

separated. Data from summer-sampled fish can be used reliably to represent each stock with negligible mixing and thus were used here to derive stock-specific natural tags. For each individual sampled, fork length (FL) and sex were recorded, and both sagittal otoliths were removed.

The management-designated winter mixing area was divided into three sampling zones similar to those defined by Clardy et al. (2008) except that the easternmost zone extended northward to match the sampling region of DeVries et al. (2002; Figure 1). Zone 1 encompassed the southwestern coast of Florida; fish were sampled from a commercial gill-net fishery operating there in January and landed in Stock Island, Florida. Zone 2 included the Florida Keys and was represented by samples collected in January from recreational charter boat landings in Islamorada, Florida. Each month (December–March) individuals from zone 3 off southeastern Florida were sampled from commercial troll landings in Jupiter and Cape Canaveral, Florida. This study was designed to estimate the Atlantic contribution to landings in each zone rather than true mixing rates between the two stocks. Thus, the fishery sector that produces the bulk of king mackerel landings in each zone was sampled.

Otolith shape analysis was performed for all summer- and winter-sampled king mackerel using ImagePro (version 6.0) image analysis software. The distal lateral surface of each left otolith was magnified and digitized according to DeVries et al. (2002). The right otolith was used and the image reversed whenever the left was damaged (Friedland and Reddin 1994). The rather high frequency of otoliths with broken rostra made it necessary to measure and obtain shape parameters from only the posterior portion of the otolith according to methods used by DeVries et al. (2002). A vertical line was drawn from the tip of the antirostrum to the ventral edge, and the otolith perimeter posterior of this line was digitally traced with the auto trace feature in ImagePro.

ImagePro was used to measure the following gross morphometric parameters automatically: length, width, perimeter, and area. Length and width measurements were the dimensions of the smallest enclosing rectangle for the traced portion of the perimeter. The measured geometric parameters were used to calculate roundness, circularity, ellipticity, and rectangularity (i.e., derived parameters), which were calculated as follows:

$$\text{Roundness} = \frac{4\pi \cdot \text{otolith area}}{\sqrt{\text{otolith perimeter}}} \quad (1)$$

$$\text{Circularity} = \sqrt{\frac{\text{otolith area}}{\text{otolith perimeter}}} \quad (2)$$

$$\text{Ellipticity} = \frac{\text{otolith length} - \text{otolith width}}{\text{otolith length} + \text{otolith width}} \quad (3)$$

$$\text{Rectangularity} = \frac{\text{otolith area}}{\text{area of its minimal enclosing rectangle}}. \quad (4)$$

The digitized contour of each otolith posterior was used to calculate Fourier series harmonics. ImagePro determined the mathematical centroid of the traced posterior portion of the otolith and then drew 256 radii at equiangular intervals to the otolith contour to approximate its shape. These radii were used to calculate the first 19 Fourier harmonics, and ImagePro automatically reported the harmonic amplitudes and mean radius. Mean radius was reported as harmonic 1; therefore, harmonics 2–20 represent the first 19 harmonics used in analysis.

Fish size and age can be confounding effects in otolith shape analysis (Castonguay et al. 1991; Campana and Casselman 1993). Thus, several precautions were taken to account for size and age. Only individuals ages 2–6 years were included because approximately 85% of winter landings are derived from those age-classes. All shape parameters were standardized by dividing each parameter by the mean radius (amplitude of the 0th harmonic). Any remaining significant correlation between each standardized parameter and FL was removed by subtracting the product of FL and the slope of the least-squares linear relationship from the standardized parameter. After

TABLE 1.—National Buoy Data Center stations reporting sea surface temperatures in three winter mixed-stock king mackerel sampling zones between December and March during the 1996–1997, 2001–2002, 2002–2003, 2006–2007, and 2007–2008 fishing years.

Station	Sampling zone	Fishing year	Location
SANF1	1	2001–2002, 2002–2003	24.460°N, 81.880°W
KYWF1	1	2006–2007, 2007–2008	24.553°N, 81.808°W
MLRF1	2	2001–2002, 2002–2003, 2006–2007, 2007–2008	25.010°N, 80.380°W
LKWF1	3	1996–1997, 2001–2002, 2002–2003	26.612°N, 80.033°W
4114	3	2006–2007, 2007–2008	27.551°N, 80.225°W

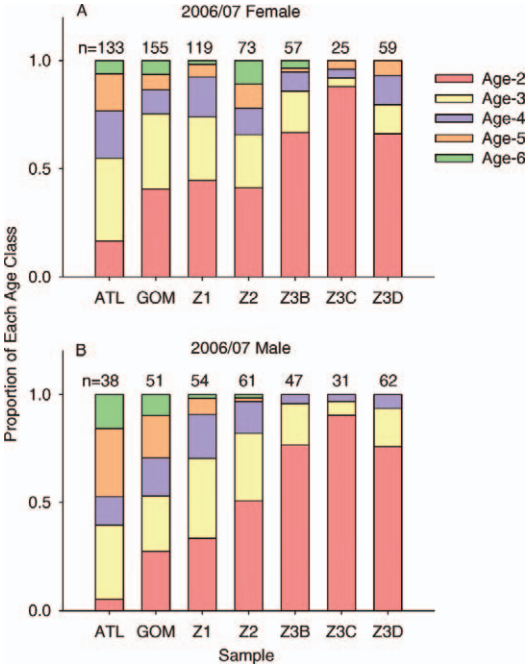

FIGURE 2.—Relative age distributions of **(A)** female and **(B)** male king mackerel collected in the 2006–2007 fishing season from single-stock summer spawning grounds in the Atlantic Ocean (ATL) and Gulf of Mexico (GOM) and as part of South Florida winter mixed-stock landings in sampling zones 1 (Z1), 2 (Z2), 3 in December and January (Z3B), 3 in February (Z3C), and 3 in March (Z3D).

separating by sampling year, all parameters continued to be significantly correlated with FL ($P < 0.001$) and thus were detrended to remove variation due to size.

Otolith shape data were used to derive sex- and stock-specific natural tags, which were used to parameterize maximum likelihood mixing models to estimate the Atlantic contribution to the mixed-winter landings. Standardized parameters were first tested for sex, year, and stock effects with multivariate analysis of variance (MANOVA). Only first-order interactions were tested due to limited degrees of freedom. Stepwise year- and sex-specific discriminant functions (DFs) were computed in SAS (Proc STEPDISC; SAS Institute 1996), the 19 harmonic amplitudes and the gross and derived shape parameters of summer-sampled fish serving as dependent variables. Quadratic DFs were computed because of heterogeneity among variance–covariance matrices. Jackknifed stock- and sex-specific classification accuracies were computed for resultant models (Proc DISCRIM; SAS Institute 1996).

Maximum likelihood stock mixing models were parameterized with the significant shape variables and applied to the mixed-winter samples to estimate the percentage of landings contributed by the Atlantic stock in each sampling zone (and month for zone 3; DeVries et al. 2002; Clardy et al. 2008). The SE of estimates was calculated from 500 bootstraps. All maximum likelihood modeling was conducted in S-Plus (version 6.0).

Spatial and temporal patterns in estimated Atlantic contribution were explored using winter sea surface temperature (SST) data from the National Buoy Data Center (NBDC; Table 1). Differences in SST among sampling zones, fishing years, and months in zone 3 were tested with analysis of variance based on daily mean SST, subsequent multiple comparisons being done with a Tukey–Kramer adjustment. The NBDC stations used to represent zone 1 are south of the king mackerel fishing grounds; however, all buoys represent the nearest stations for which SST data were available during the time periods considered. Temperature data were analyzed for fishing years that also had otolith shape-based estimates of Atlantic contribution to king mackerel landings and included 1996–1997 (zone 3 only), 2001–2002, 2002–2003, 2006–2007, and 2007–2008.

Results

Totals of 965 and 1,309 king mackerel were sampled in the 2006–2007 and 2007–2008 fishing years, respectively. Fish were between ages 2 and 6, and yielded at least one otolith with the posterior portion intact for shape analysis. The 11 samples collected in zone 3 in December of 2006 were added to the samples collected in January 2007 for analysis. Totals of 588 and 609 king mackerel were sampled from the South Florida sampling zones in winter 2006–2007 and 2007–2008, respectively.

Atlantic and GOM samples from summer 2006 had similar sample sizes and somewhat similar age distributions, with the exception of a higher proportion of age-2 fish from the GOM and a higher proportion of age-4 and age-5 fish from the Atlantic (Figure 2). The 2007 summer samples were subsampled to mitigate bias due to uneven sample sizes and age distributions (Figure 3). Wherever possible, ten samples from 2007 were randomly selected for each age-class in each sex and stock, resulting in a sample size of 50 individuals for each sex–stock combination except for the Atlantic males, which were not subsampled due to already low sample sizes. The majority of 2006–2007 winter-sampled fish were ages 2 and 3, the former making up the bulk of the zone 3 landings sampled (Figure 2). The 2007–2008 winter samples displayed a broader age distribution, the majority being between ages 2 and 4

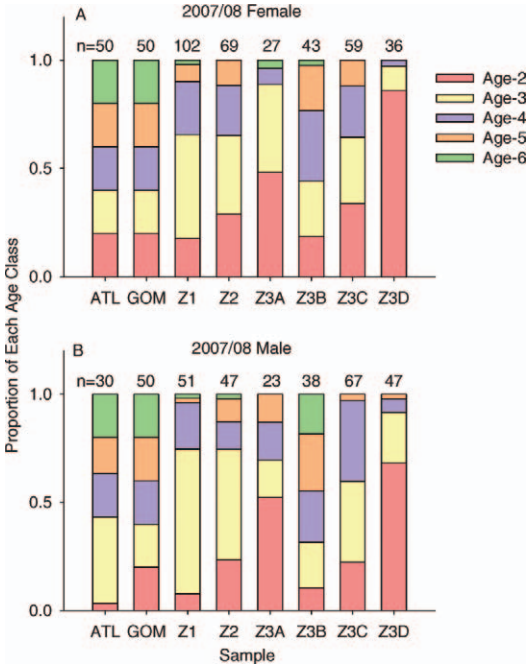

FIGURE 3.—Relative age distributions of **(A)** female and **(B)** male king mackerel collected in the 2007–2008 fishing season from single-stock summer spawning grounds in the Atlantic Ocean (ATL) and Gulf of Mexico (GOM) and as part of South Florida winter mixed-stock landings in sampling zones 1 (Z1), 2 (Z2), 3 in December (Z3A), 3 in January (Z3B), 3 in February (Z3C), and 3 in March (Z3D). Females from the ATL ($n = 130$) and GOM ($n = 399$) and males from the GOM ($n = 141$) were subsampled (50 fish).

except for zone 3 March samples (the majority of which were age 2; Figure 3).

All 27 otolith shape parameters were significantly correlated with FL (all $P < 0.001$), and each parameter was detrended to remove the size effect. Variance–covariance matrices were heteroscedastic, and area, perimeter, roundness, and harmonic 8 were leptokurtic, thus violating normality. Several common transformations were attempted to normalize the data, but these resulted in further deviation from normality. Pillai's trace was used as the test statistic in the MANOVA because it is robust to violations of homoscedasticity and normality (Scheiner 2001).

The MANOVA revealed that effects due to fishing year, sex, stock, age, and the year × age interaction were all significant (Table 2). The significant stock effect confirmed the potential of otolith shape for use as a natural tag in GOM and Atlantic king mackerel. Separate rule functions were developed from the 2006–2007 and 2007–2008 summer samples to account for variation in otolith shape between fishing years, and for the significant year × age interaction, which was likely driven by differences in the age distributions between years. The significant sex effect supported sex-specific analysis to improve classification success and precision in estimates of Atlantic contribution. The significant age effect confirmed the importance of using uniform sample age distributions between stocks.

Stepwise DF analysis of detrended shape data by fishing year revealed that both gross and fine-scale otolith shape parameters were significant in discriminating between GOM and Atlantic king mackerel. Classification success ranged from 60% to 73%, rates being higher for the Atlantic than the GOM stock and for sex-specific than combined sex DFs (Table 3). Estimates of Atlantic stock contribution to winter landings exceeded zero across all zones and among all models (Figure 4). The 2006–2007 male and combined sex models, as well as the 2007/08 combined sex model, displayed a consistent spatial pattern in the estimated percentage of landings contributed by the Atlantic stock, lower contributions occurring in zone 1 and higher contributions in zones 2 and 3. Results from combined sex models also showed Atlantic contribution to zone 3 landings increased late in the fishing season (February and March in 2006–2007 and March in 2007–2008). Sex-specific results for 2007–2008 did not display any apparent trends in the percentage of landings estimated to have been contributed by the Atlantic stock. Atlantic contribution was lower in 2007–2008 than 2006–2007 in all models except for females in zone 3B. Zone 3A 2007–2008 estimates could not be compared directly because they were combined with Zone 3A in 2006–2007 due to low sample size. The mean SE about estimates of Atlantic contribution was fairly high (17.2 percentage points). This low precision likely reflects the low classification success of the rule functions and made it difficult to

TABLE 2.—Results of multivariate analysis of variance of otolith shape data from summer-sampled king mackerel to determine differences between the 2006–2007 and 2007–2008 fishing years, Gulf of Mexico and Atlantic Ocean stocks, sexes, and ages 2–6.

Source	Pillai's trace	*F*	df	*P*
Year	0.912	1.82	27, 508	0.008
Stock	0.170	3.86	27, 508	<0.001
Sex	0.186	4.31	27, 508	<0.001
Age	0.452	2.41	108, 2,044	<0.001
Year × stock	0.070	1.42	27, 508	0.082
Year × sex	0.047	0.93	27, 508	0.565
Year × age	0.299	1.53	108, 2,044	<0.001
Stock × sex	0.050	0.99	27, 508	0.486
Stock × age	0.236	1.19	108, 2,044	0.099
Sex × age	0.238	1.2	108, 2,044	0.084

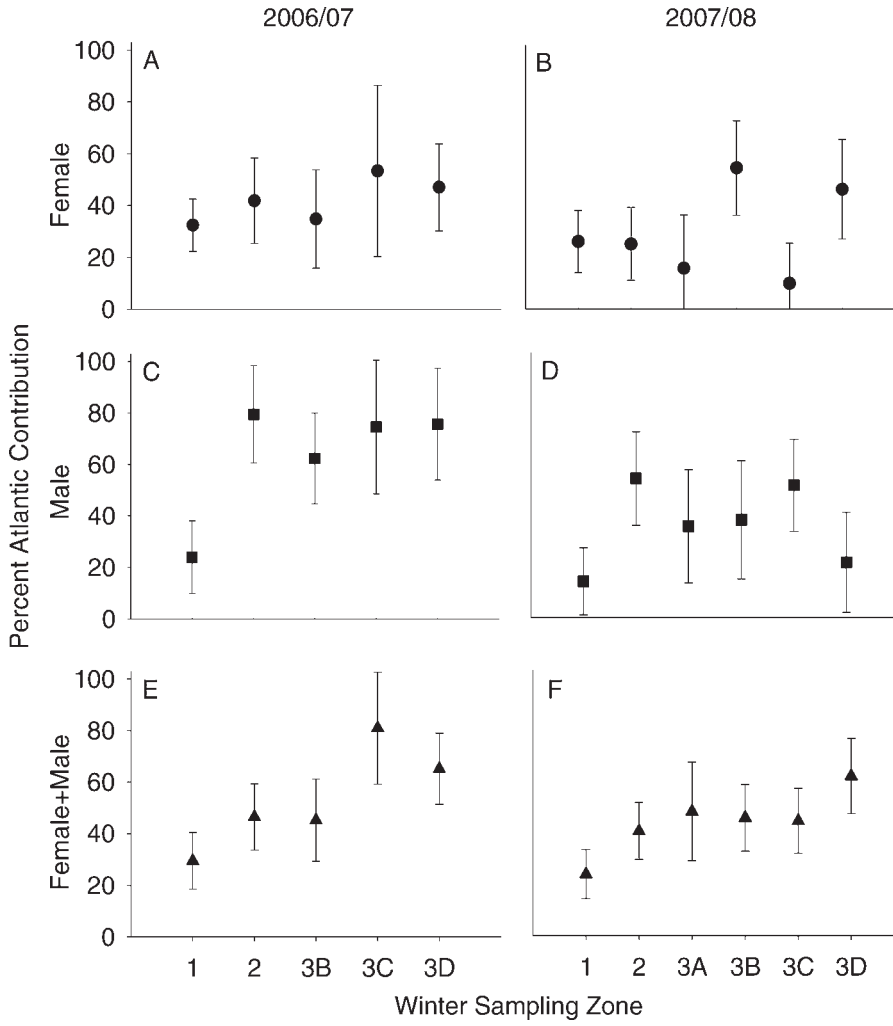

FIGURE 4.—Otolith-shape-based maximum likelihood estimates of the proportions of **(A)–(B)** female king mackerel landed in 2006–2007 and 2007–2008), **(C)–(D)** male king mackerel landed in 2006–2007 and 2007–2008, and **(E)–(F)** both female and male king mackerel landed in 2006–2007 and 2007–2008 contributed by the Atlantic Ocean stock to each South Florida sampling zone. Zone 3 samples were collected in December (3A), January (3B), February (3C), and March (3D). Error bars = SEs.

TABLE 3.—Results of year- and sex-specific stepwise discriminant function analysis for king mackerel identifying otolith shape variables capable of distinguishing between single-stock Gulf of Mexico (GOM) and Atlantic Ocean samples collected from geographically distinct summer spawning grounds and the associated jackknifed classification success rates.

		Classification success (%)	
Sex	Significant variables	GOM	Atlantic
	2006		
Female	Roundness, circularity, harmonics 3, 4, 12, 15, 16, 18	62	67
Male	Harmonics 4, 9, 14, 17	71	73
Combined	Harmonics 4, 5, 10, 12, 15, 16	61	63
	2007		
Female	Area, harmonics 2, 14, 16	70	70
Male	Harmonics 2, 4, 12, 13	60	66
Combined	Width, ellipticity, rectangularity, harmonics 4, 7, 12, 16	63	65

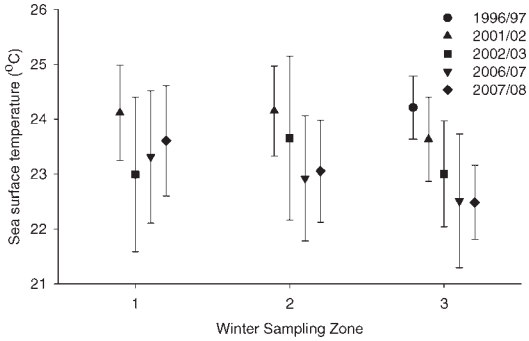

FIGURE 5.—Mean winter (December–March) sea surface temperature in each of the South Florida sampling zones, with standard deviations calculated from the hourly temperature measurements reported by National Buoy Data Center stations SANF1 (zone 1; 2001–2003), KYWF1 (zone 1; 2006–2008), MLRF1 (zone 2), LKWF1 (zone 3; 1996–2003), and 4114 (zone 3; 2006–2008).

identify spatial and intraannual temporal trends more conclusively.

Sea surface temperature varied significantly by sampling zone ($F_{2,\ 1,530} = 4.76$; $P = 0.009$), fishing year ($F_{4,\ 1,528} = 28.36$; $P < 0.001$), and month in zone 3 ($F_{3,\ 239} = 25.39$; $P < 0.001$). The difference among sampling zones was driven by a lower SST in zone 3 (23.18°C) than zones 1 (23.42°C; $P = 0.050$) and 2 (23.46°C, $P = 0.013$; Figure 5). Among fishing years, SST was significantly higher in 1996–1997 and 2001–2002 (24.21°C and 23.90°C, respectively) than 2002–2003, 2006–2007, and 2007–2008 (23.24, 22.95, and 23.04°C, respectively; $P < 0.001$; Figure 5). Finally, in 2006–2007 and 2007–2008, SST was higher in December than all other months considered (23.54°C; $P < 0.001$) and higher in January (22.59°C) than February (21.93°C; $P = 0.013$) and March (21.95°C, $P = 0.013$; Figure 6).

Discussion

A comparison between otolith shape-based estimates of Atlantic contribution to winter landings reported here and historic estimates indicates a long-term decline in Atlantic contribution to mixed-stock winter landings. DeVries et al. (2002) estimated that 99.8% of female king mackerel in southeastern Florida (Cape Canaveral to Palm Beach) in 1996–1997 were from the Atlantic stock. This estimate is striking considering the majority of 1996–1997 mixed-stock samples were collected in December when Atlantic contribution would be lowest based on current temporal trends. Estimated Atlantic contribution to zone 3 female landings declined to 83% in 2001–2002 and 40% in 2002–2003 (Clardy et al. 2008). Mixed-stock 2001–2002 and 2002–2003 samples were collected in February and March when Atlantic contribution is expected to be highest. In the current study, the average percentage across all winter months of zone 3 female landings contributed by the Atlantic stock was 45% in 2006–2007 and 32% in 2007–2008. Zone 3 male landings also declined from 76% in 2001–2002 and 72% in 2002–2003 (Clardy et al. 2008) to 70% and 37% in 2006–2007 and 2007–2008, respectively.

Similar declines can be seen between estimated Atlantic contribution reported by Clardy et al. (2008) for zones 1 and 2 in 2001–2002 and 2002–2003, and those reported here for 2006–2007 and 2007–2008. Mixed-stock zone 1 and 2 samples were collected in January in both studies. Zone 1 female Atlantic contribution dropped from 61% in 2001–2002 to 15% in 2002–2003, then increased to 32% in 2006–2007 and fell to 26% in 2007–2008. Estimated Atlantic contribution to zone 1 male landings declined from 61% in 2001–2002 and 45% in 2002–2003 to 24% in 2006–2007 and 14% in 2007–2008. The estimated zone 2 female Atlantic contribution remained fairly stable at 49, 41, and 42% in 2001–2002, 2002–2003, and 2006–2007, respectively, but declined to 25% in 2007–2008. Finally, the percentage of Atlantic zone 2 male landings was estimated as high as 99% in 2001–2002 and then dropped to 83% in 2002–2003, 80% in 2006–2007, and 54% in 2007–2008.

Current estimates of Atlantic contribution are consistently lower than historic otolith-shape-based estimates for all zones and both sexes. The decline in Atlantic contribution may reflect an increase in the GOM stock's presence in the mixing area, a decline in

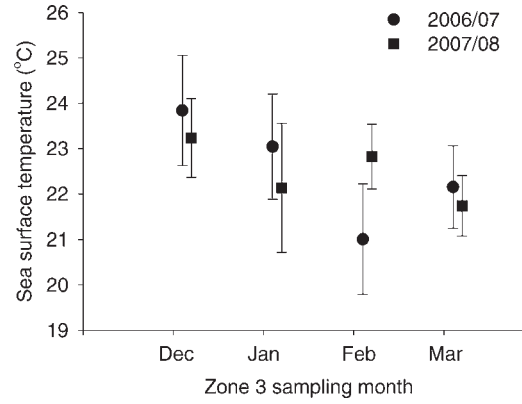

FIGURE 6.—Mean monthly winter (December–March) sea surface temperatures in sampling zone 3, with standard deviations calculated from the hourly temperature measurements reported by National Buoy Data Center station 4114.

the Atlantic stock's presence, or both. During the period between 1996 and 2008, the estimated GOM stock biomass increased in response to conservation measures and decreased consumption due to public concern over mercury warnings (Powers 1996; SEDAR16 2008). The Atlantic stock's estimated biomass declined somewhat over the same period. The shift in Atlantic contribution is likely a function of changes in relative population size, particularly the increase in the GOM stock's biomass.

It is also possible that the decline in the Atlantic stock's contribution has been in response to long-term environmental changes affecting king mackerel migration patterns. King mackerel are known to migrate along isotherms between 20°C and 26°C (Manooch 1979). Analysis of SST in the winter mixing zone indicates a drop in mean water temperature occurred between the 2001–2002 and 2002–2003 fishing seasons. However, all estimated mean SSTs were within the optimal 20–26°C range and within 1.26°C of one another. Thus, a long-term thermal shift is not likely motivating the monotonic decline in the Atlantic contribution to mixed-stock landings.

The estimated Atlantic contribution of king mackerel landings was greater than 0 in each zone for all model results, thus indicating the historic management strategy, which assigned all landings from the winter mixing area to the GOM stock, did not accurately reflect king mackerel migratory patterns. Based on similar evidence from earlier work (DeVries et al. 2002; Clardy et al. 2008), as well as preliminary results from this study, a mixing rate of 50% was assumed in the most recent stock assessment to account for the presence of Atlantic king mackerel in the mixed-winter landings (SEDAR16 2008). However, the spatial and temporal variability (both inter- and intraannual) in estimates of Atlantic contribution reported herein, as corroborated by Clardy et al. (2008), indicate that dividing mixed-winter landings according to a single set mixing rate does not fully account for the complexity of king mackerel migratory behavior.

Our results suggest a pattern of lower Atlantic contribution in the west (zone 1) and higher Atlantic contribution in the east (zones 2 and 3), a pattern consistent with earlier otolith shape-based mixing estimates (Clardy et al. 2008). The absence of any spatial pattern in the sex-specific 2007–2008 models may be due to the smaller sample sizes used to generate the rule function. Spatial trends in Atlantic contribution do not appear to be driven by variation in SST across the three sampling zones. The lower mean SST in zone 3 compared with zones 1 and 2 was not surprising considering it ranges over more northern latitudes, but this does not provide evidence for a thermal mechanism for the reported lower Atlantic contribution in zone 1 than zones 2 and 3. Furthermore, the maximum difference in mean SST among zones was ~0.3°C, which, while statistically significant, is not likely to be biologically relevant.

The estimated Atlantic contribution to combined-sex zone 3 landings was higher in March (and February in 2006–2007) than estimates from earlier in the season. A higher percentage of Atlantic fish landed later in the season is likely evidence of early spring migration of both stocks to their respective summer spawning grounds. Thus, the period of time in which mixed-stock landings were collected should be taken into account when interpreting any mixing estimates for Zone 3. The decline in mean SST in Zone 3 across months is evidence of a possible seasonal migratory cue. However, that colder water temperatures would cue the spring northward migrations is not necessarily intuitive. One explanation is that Atlantic king mackerel move into the warm, northward flowing Gulf Stream in response to decreasing water temperatures. It is also possible that the seasonal thermal trend is correlated with other, more proximate, environmental (e.g., dorsal light response) or biological (e.g., prey migration) cues that are stimulating king mackerel migration in February and March.

The significant otolith shape parameters identified by the stepwise discriminant function routine varied between sexes and fishing years. Sex-specific shape signatures shared only one harmonic amplitude each fishing year. Female king mackerel grow faster and to larger sizes than males, and the dissimilar shape signatures between the sexes probably reflect this difference in somatic growth rate. The significant difference in shape signatures between years could be driven by a number of factors, such as year classes entering and leaving the stock or inter-annual variation in environmental conditions. Regardless of the reason, it appears that rule functions calculated from samples collected in 1 year cannot be accurately applied to classify samples collected in another year. The variation in significant shape parameters between years and sexes reported here is consistent with the results of Clardy et al. (2008), indicating these patterns are persistent.

The otolith shape-based classification success rates of 60–73% reported here are similar to, but somewhat lower than, previous mean classification success: 75% (DeVries et al. 2002) and 69% (Clardy et al. 2008). The higher classification success using sex-specific over combined-sex models is likely caused by the removal of variation in otolith shape from sex-specific differences in growth rate. Classification success for the Atlantic stock was higher than the GOM in all cases,

which is unexpected considering samples sizes were greater for the GOM stock in 2006. It is possible that this pattern is due to greater variability in individual growth rate in the GOM than the Atlantic. Overall, consistently low classification success rates indicate otolith shape is not a powerful stock-specific tag. Classification success was similar between fishing years in this study, but 2007–2008 point estimates of Atlantic contribution displayed higher precision than 2006–2007 estimates, as evidenced by lower SEs. This increase in precision may have been the result of larger mixed-stock sample sizes in 2007–2008. Increasing stock-specific sample sizes might also increase the robustness of otolith shape as a natural tag by permitting separate year-class models.

Variation in otolith shape due to fishing year, sex, and age complicate its use as a natural stock-specific tag. The effects of fishing year and sex are easily accounted for by modeling years and sexes separately. However, age continued to be a significant factor in determining otolith shape even after the data were detrended to correct for fish size, implying there may be a year-class effect. Such an effect could result from interannual variation in somatic growth due to periods of poor or favorable environmental conditions, prey availability, and competition. The age range of samples included for analysis was limited to reduce any age effect, but it appears that examining individual year-class models would be necessary to fully account for variation due to age. Sample sizes were deemed insufficient to examine that in the current study. Begg and Brown (2000), however, found no significant year-class effect in otolith shape of haddock *Melanogrammus aeglefinus* from the same region and age-class.

Combining age-classes for analysis may reduce the resolution of otolith shape signatures, likely contributing to the low classification success rates in this and earlier studies of king mackerel mixing (DeVries et al. 2002; Clardy et al. 2008). An otolith shape-based stock discrimination study of Atlantic mackerel *Scomber scombrus* produced an average classification success of 82% when year-classes were tested individually (Castonguay et al. 1991). However, it is also possible that classification success might be inflated in a combined age analysis if sample age distributions vary between stocks (Castonguay et al. 1991). In such a case, stock-specific otolith shape signatures would reflect both variation due to stock and variation due to age. The consistency in classification success rates between 2006–2007, when age distributions varied slightly, and 2007–2008, when the data were subsampled to create uniform age distributions, suggests classification success was not inflated by combining ages in this study.

It is possible that variation between fishing years and ages might simultaneously be accounted for by developing cohort-specific rule functions, which could be applied across fishing years (Bergenius et al. 2006). However, before applying a cohort-based method to estimate Atlantic contribution to mixed-stock king mackerel landings, one would need to demonstrate the interannual stability of cohort-specific otolith shape signatures. As previously stated, however, sample sizes were not sufficient to test the validity of such a method in the current study.

The analysis presented here completes a decade-long series of otolith shape-based estimates of Atlantic contribution to mixed-stock king mackerel landings. Although otolith shape is not a superlative natural tag for discriminating between GOM and Atlantic king mackerel (as evidenced by low classification success and imprecision about mixing estimates), shape analysis is inexpensive, simple to perform, and allows for comparisons to be made over a longer time series. Analysis of otolith elemental and stable isotope chemistry may provide a more powerful natural tag for producing more precise estimates of Atlantic contribution (Shepard 2008), but such methods are expensive and labor intensive, and samples are subject to contamination when collected by field-based, fishery-dependent sampling programs. Furthermore, by developing a time series of otolith shape-based estimates, it has now become possible to detect long-term trends in the relative contribution of each stock to winter landings. Also, the relative stability over years of the east–west trend in Atlantic contribution indicates this pattern will likely persist as the interactions between the two stocks continue to change.

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