A Cooperative Research Approach to Estimating Atlantic and Gulf of Mexico: King Mackerel Stock Mixing and Population Dynamics Parameters

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A Cooperative Research Approach to Estimating Atlantic and Gulf of Mexico King Mackerel Stock Mixing and Population Dynamics Parameters

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Abstract

A multidisciplinary study was conducted to examine stock-specific population dynamics and interpopulational mixing in king mackerel sampled from Atlantic Ocean (Atlantic) and eastern Gulf of Mexico (GOM) waters. A total of 4,049 king mackerel was sampled from fishery-dependent and -independent sources in the Atlantic and GOM in summer 2006 and 2007, and from south Florida in winter 2006-07 and 2006-07. Otolith samples were extracted from fish for age and growth analysis, as well as to estimate winter mixing between Atlantic and eastern GOM populations with otolith shape analysis and analysis of otolith chemical signatures. Von Bertalanffy growth functions fit to size-at-age data were significantly different between sexes and between Atlantic and eastern GOM populations (likelihood ratio tests; $p < 0.001$), with females and GOM fish growing faster and achieving larger sizes. There also was a significant difference between contemporary size-at-age estimates and historical estimates from 1977-79 and 1986-92 time periods for ages 2-10 years (ANOVA; $p < 0.05$), with GOM fish being on average 3.9% smaller at age than historical estimates and Atlantic fish being on average 5.0% larger at age than historical estimates. These results are most likely due to density-dependent effects in each population as there has been an estimated 2.5 fold increase in GOM spawning stock biomass (SSB) since the early 1990s, while Atlantic SSB has declined by an estimated 45% over the same time period. Interpopulational winter mixing also likely has been affected by population-specific changes in SSB. Otolith shape parameters and otolith chemical signatures (Ba:Ca, Li:Ca, Mg:Ca, Mn:Ca, Sr:Ca, δ^{13}C, and δ^{18}O) were significantly different between populations and sexes (MANOVA; $p < 0.001$). Jackknifed classification accuracies from stepwise discriminant function analysis revealed that king mackerel populations could be distinguished with a mean accuracy of 65.9% with otolith shape parameters. Otolith chemical signatures yielded a mean classification accuracy of 82.0%, while models parameterized with only δ^{13}C and δ^{18}O values yielded a mean accuracy of 79.0%. Trends in south Florida winter mixing estimates computed with maximum likelihood models parameterized with either otolith shape parameters or otolith chemistry constituents were similar between data types and sampling years. A low percentage (mean = 30.5% among all otolith shape and chemistry models) of winter landings sampled off southwest Florida were estimated to be contributed by the Atlantic population, but the estimated Atlantic contribution increased toward southeast Florida and also increased in the easternmost sampling zone from December to March. Results from both otolith shape and chemistry analysis indicate mixing is spatially and temporally dynamic, but the previous management assumption that 100% of south Florida winter landings are contributed by the GOM population is not supported.

Executive Summary

King mackerel, *Scomberomorus cavalla*, is a large ecologically-important coastal pelagic fish that historically has supported economically-important commercial and recreational fisheries in the US Atlantic Ocean (Atlantic) and Gulf of Mexico (GOM). Fisheries management for king mackerel in US waters is complicated, however, due to seasonal migratory patterns that result in Atlantic and eastern GOM fish mixing in south Florida in winter. Understanding interpopulational mixing dynamics has been considered essential for effective management since the 1970s. Reviewers of the 2004 benchmark assessments of Atlantic and GOM king mackerel stocks also concluded that the assessment models were sensitive to other basic biological parameters, such as growth and fecundity, that were either poorly estimated, based on small samples sizes from studies conducted more than a decade prior to that assessment, or both (SEDAR5 2004). Therefore, this multidisciplinary study was conducted to examine stock-specific population dynamics and interpopulational mixing between Atlantic and GOM king mackerel.

A total of 4,049 king mackerel was sampled from fishery-dependent and -independent sources in the Atlantic and GOM in summer 2006 and 2007, and from south Florida in winter 2006-07 and 2006-07. Otolith samples were extracted from fish for age and growth analysis, as well as to estimate winter mixing between Atlantic and eastern GOM populations with otolith shape analysis and analysis of otolith chemical signatures. Ovaries also were extracted from summer-sampled females, fixed in formalin, and forwarded to the National Marine Fisheries Service (NMFS) Laboratory for fecundity analysis. Therefore, while reproductive biology was not part of this study, sampling efforts did address that critical data need by providing gonad samples to NMFS biologists for analysis (Fitzhugh et al. 2008, 2009).

Von Bertalanffy growth functions fit to size-at-age data were significantly different between sexes and between Atlantic ($n = 869$) and eastern GOM ($n = 1,447$) samples (likelihood ratio tests; $p < 0.001$), with females and GOM fish growing faster and achieving larger sizes (Shepard et al. 2010b). Comparison of contemporary size-at-age estimates with estimates from 1977-79 and 1986-92 for ages 2-10 years revealed that contemporary GOM fish are smaller at age (average decrease in size at age for males = 3.4% and females = 4.3%) than historical estimates, while Atlantic fish are larger at age (average decrease in size at age for males = 4.6% and females = 5.4%) than historical estimates (ANOVA; $p < 0.05$). These results most likely are due to density-dependent effects in each population as there has been an estimated 2.5 fold increase in GOM spawning stock biomass (SSB) since the early 1990s, while Atlantic SSB has declined by an estimated 45% over the same time period.

Shape analysis was performed on a subset ($n = 557$) of otoliths from summer-sampled fish following aging (ages 2-6 were selected) to derive population-specific natural tags for distinguishing Atlantic and GOM fish in south Florida winter landings (Shepard et al. 2010a). Otolith shape was digitized with an image analysis system and then the shape parameters length, width, perimeter, area, roundness, circularity, ellipticity, rectangularity, and the first 19 Fourier series harmonics were computed. Shape parameters were significantly different between populations, sexes, and sampling years (MANOVA; $p < 0.01$). Stepwise discriminant function analysis (DFA) of population-specific shape parameters was performed separately for 2006 and 2007 samples, and for males, females, and combined sexes. Jackknifed classification of DFA models averaged 66.1% among 2006 models and 65.7% among 2007 models. Maximum likelihood models were parameterized with shape parameters (determined with stepwise DFA) from summer-sampled fish to estimate the percentage of winter landings (total sample size = 588 in 2006-07 and 609 in 2007-08) sampled among three south Florida sampling zones that were contributed by the Atlantic population. Spatial trends in the estimated contribution of Atlantic fish to south Florida landings were consistent between years and among models, with a low estimated Atlantic contribution (16-35%) in southwest Florida and a higher contribution (up to 80%) in southeast Florida. Results do not support the previous management assumption that all winter landings are contributed by the GOM stock; however, large standard errors on Atlantic contribution estimates imply high uncertainty with respect to point estimates of Atlantic population contribution to south Florida winter landings.

Interpopulational winter mixing also was estimated based on otolith chemical signatures of summer-sampled ($n = 343$) and winter-sampled ($n = 911$) fish. Otolith chemical signatures (constituents analyzed: Ba:Ca, Li:Ca, Mg:Ca, Mn:Ca, Sr:Ca, δ^{13}C, and δ^{18}O) were significantly different between populations, sexes, and sampling years (MANOVA; $p < 0.001$). Stepwise discriminant function analysis (DFA) of population-specific otolith chemical constituents was performed separately for 2006 and 2007 samples, and for males, females, and combined sexes. A second set of DFA models also was computed with only δ^{13}C and δ^{18}O as classification variables. Jackknifed classification accuracies from stepwise DFA of otolith chemical signatures yielded a mean classification accuracy of 82.0%, while models parameterized with only δ^{13}C and δ^{18}O values yielded a mean accuracy of 79.0%. Trends in estimates of Atlantic population contribution to winter south Florida landings that were computed with maximum likelihood models parameterized with otolith chemistry constituents were similar to results from otolith shape models. However, standard errors of Atlantic contribution estimates were on average 17% lower among the various otolith chemistry estimates versus otolith shape estimates, and 25% lower among the stable isotope only models than shape models. Another key difference is that otolith chemistry models tended to estimate a higher percentage of Atlantic population contribution among all winter sampling zones. Results from both otolith chemistry analysis indicate mixing is spatially and temporally dynamic, but again otolith chemistry-based mixing estimates contradict the previous management assumption that 100% of south Florida winter landings are contributed by the GOM. Furthermore, spatial and temporal variability in king mackerel interpopulational winter mixing implies that a rigid, management-imposed boundary between the two stocks is impractical.

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General Introduction

Background and Rationale:

King mackerel are large, piscivorous scombrids that occur in the western Atlantic Ocean (Atlantic) from Massachusetts to Brazil, including the GOM of Mexico (GOM) and Caribbean Sea (Collette and Nauen 1983). Females may reach fork lengths (FL) greater than 1.5 m and weigh nearly 40 kg, while large males are rarely longer than 1 m FL or heavier than 25 kg (DeVries and Grimes 1997). Maximum longevity for king mackerel appears to be around 25 yr in both the Atlantic and GOM, but GOM fish (both males and females) are larger at age than their Atlantic counterparts (DeVries and Grimes 1997; Sutter et al. 1991). Despite morphological differences between GOM and Atlantic fish, mixing does occur between purported stocks[1]. Tagging studies conducted in the 1970s and 1980s demonstrated king mackerel in the eastern GOM and Atlantic migrate along the Florida peninsula in late fall and overwinter in south Florida where commercial gillnet and recreational hook-and-line fisheries are prosecuted on the mixed stock. As water temperatures warm in spring, fish migrate northward and return to summer spawning grounds (Powers and Eldridge 1983; Sutter et al. 1991).

King mackerel support important commercial and recreational fisheries throughout their US range. Concerns over fluctuations and declines in US landings in the late 1970s and early 1980s lead to the creation of the Coastal Pelagics Management Plan (CPMP), which originally treated the species as a single stock in US waters (GMFMC and SAFMC 1983). Currently, king mackerel in US waters are assumed to constitute two separate migratory groups (GOM and Atlantic), but remain jointly managed by the Gulf of Mexico and South Atlantic Fishery Management Councils (GMFMC and SAFMC, respectively). This division into two migratory groups, or stocks, was implemented with Amendment 1 to the CPMP (GMFMC and SAFMC 1985) and was based on tag recapture data that indicated two distinct migratory groups existed (Powers and Eldridge 1983; Sutter et al. 1991). Subsequent genetic analyses have confirmed GOM and Atlantic fish are genetically distinct (Gold et al. 1997; Gold et al. 2002).

Estimates that king mackerel stocks were subjected to overfishing in the 1970s was the impetus for creating a federal management plan for the species. Regulations were implemented to decrease fishing mortality and increase spawning stock biomass (SSB) beginning in the mid 1980s. The Atlantic stock experienced increased SSB through the late 1990s and is estimated to be above its target biomass level (Anon 2004b). Routine overruns of total allowable catch (TAC) coupled with the absence of a clearly defined rebuilding strategy for the GOM migratory group, however, resulted in it not recovering above an overfished threshold during the 1990s (MSAP 1999, 2000; Powers 1996).

Stock assessment and management of US king mackerel is complicated due to mixing between eastern GOM and Atlantic stocks in winter. Although mixing was not well understood at the time, a winter mixing zone in southeast Florida was defined in the mid 1980s from the Collier/Monroe County line in the southwest to the Flagler/Volusia County line in the northeast as a conservation measure to aid recovery of the overfished GOM migratory group (Fig.

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[1] The Gulf of Mexico and South Atlantic Fishery Management Councils adopted the term “migratory group” in the 1980s to refer to king mackerel populations in the GOM and Atlantic Ocean that had unique migratory pathways as inferred from tagging data. More recent population genetics evidence suggests at least two genetic stocks exist: Atlantic and GOM. Here the term “migratory group” is used when referring to historical management measures and assessments. Otherwise, “stock” is used.

2). Amendment 1 of CPMP prescribed that all fish harvested in the mixing zone from November through March were attributed to the GOM migratory group such that management regulations could limit winter mixing zone landings as added protection for that group. Results of simulation modeling demonstrated, however, that estimates of GOM migratory group SSB and health (relative to a benchmark SPR of 30%) actually were overestimated when the Atlantic migratory group was assumed not to contribute to winter mixing zone landings (Legault 1998). Legault (1998) estimated that increasing the percentage of fish in the winter mixing area attributed to the Atlantic migratory group had no effect on the status of the Atlantic group (i.e., no effect on transitional SPR), but both estimated Atlantic group SSB and allowable biological catch (ABC) increased as the percentage of fish in the mixing area assigned to it increased. Conversely, estimated GOM group SSB and ABC decreased as Atlantic contribution to the mixed fishery increased. Worse yet, estimated SPR for the GOM group decreased as the percentage of fish assigned to the Atlantic increased.

During the assessment workshop for the 2004 SEDAR5 assessments for Atlantic and Gulf king mackerel, Ortiz (2004a) conducted additional simulations to test the effect of the Atlantic migratory group contributing to winter mixing zone landings. He simulated the effect of assuming 0% (base 2004 VPA model), 50%, and 98% of winter mixing zone landings were Atlantic fish. The estimated SSB of the Atlantic migratory group increased as the percentage of winter landings contributed by it increased. Atlantic group stock status estimates were unaffected by the simulation values because it was not otherwise estimated to be overfished or undergoing overfishing. However, increasing the contribution of the Atlantic group to winter landings had a negative effect on GOM group stock status and ABC.

Other sensitivity analyses beyond stock mixing scenarios also were considered by the king mackerel SEDAR5 assessment and review workshop panels. Intensive review of assessment inputs revealed historically used growth functions computed from fishery-dependent samples yielded such poorly estimated t_0 values (the hypothetical age when length is zero) that length at age zero was estimated to be between 35 and 60 cm for various models (Brooks and Ortiz 2004). Updated growth models with a sample size of nearly 30,000 aged fish (combined between Atlantic and GOM) suffered this bias even more so than the older models due to almost no age-1 or age-0 samples in the fishery-dependent samples. The poor fitting of t_0 resulted in extreme differences in estimated catch-at-age matrices (CAA) when a stochastic ageing method was used to estimate age from length of measured landings, which was done throughout the time series whenever sample sizes were too small to compute area/time-specific age length keys (Brooks and Ortiz 2004; Ortiz 2004b, Ortiz et al. 2004). In turn, changes in the CAAs had significant effects on estimates of stock production and status.

An additional effect of changes in the growth functions by adding more recent data was a significant shift in fecundity at age estimates (Brooks and Ortiz 2004). More rigorous review of reproductive biology data revealed current fecundity estimates for both stocks are based on data from small samples sizes (n = 86 fish) that are over two decades old (Finucane et al. 1986). Thus, both the SEDAR5 review workshop panel stressed the point raised by the data workshop panel that reproductive biology parameters for both Atlantic and GOM king mackerel stocks desperately need updating (Anon 2004a,b,c).

The implications of SEDAR5 stock mixing, age and growth, and reproductive biology sensitivity analyses are significant for the assessment and management of king mackerel. Stock mixing sensitivity model runs indicated that if the Atlantic migratory group contributed significantly to winter landings off south Florida, an ABC recommended for the GOM stock assuming 100% GOM contribution of winter landings in the mixing zone would lead to overfishing (Ortiz 2004a). Conversely, the Atlantic migratory group could be fished harder than it currently is being fished and still remain healthy. Sensitivity analyses addressing growth parameter and fecundity estimation also indicated VPAs were sensitive to seemingly subtle differences in parameters. This highlighted the need to update biological parameters using fishery-independent samples to compute precise and accurate estimates, which was strongly recommended by all three SEDAR5 panels (Anon 2004a,b,c). Furthermore, while the assessment and review workshop panels both stated stock discrimination techniques based on otolith shape and chemistry analyses offered promising tools to estimate winter mixing proportions, the consensus view of the review panel was that it was imprudent to abandon the base model scenario in favor of incorporating mixing estimates into the assessment given 1) mixing estimates were computed for only two years of the fishery and 2) the uncertainty in other biological parameters and the sensitivity of the assessment models to those parameters (Anon 2004b). Clearly, research was needed to update growth and reproductive biology parameter estimates, as well as to further examine mixing between Atlantic and GOM stocks.

Study Objectives and Components:

There were three main objectives of this study, all of which were focused on filling critical data needs for effective assessment and management of Atlantic and GOM king mackerel. The first main objective was to collect fishery-dependent and -independent king mackerel otolith samples to examine contemporary age and growth. Secondary age and growth objectives were to test for differnce in growth between sexes and between Atlantic and GOM stocks, as well as to test for differences in size at age between contemporary and historical samples.

The second main objective of this study was to estimate mixing between Atlantic and GOM king mackerel with natural tags derived from otolith shape parameters and otolith chemical consituents. For both the otolith shape and chemistry components, natural stock-specific signatures of Atlantic and GOM stocks were computed with data collected from summer-sampled fish. Stock-specific otolith shape or chemical signatures then were applied to samples of winter south Florida landings to estimate the percentage contribution of the Atlantic stock. A secondary objective of both the otolith shape and chemistry components was to estimate the temporal variability in Atlantic stock contribution to winter landings off southeast Florida.

The third main objective of this study was to sample ovaries from female king mackerel to improve reproductive biology information for both the Atlantic and GOM stocks. Therefore, ovaries were dissected from summer-sampled females and fixed in formalin. Histological analysis of ovarian tissue was beyond the scope of this study, but we did forward samples we collected to the National Marine Fisheries Service's (NMFS) Panama City Laboratory where they were analyzed by NMFS biologists (Fitzhugh et al. 2008, 2009).

Each component of the study, age and growth, otolith shape, and otolith chemistry, is presented in a separate section below. Results of the age and growth component of the study are published in the peer-reviewed literature (Shepard et al. 2010b) but are detailed in the first study component section below. Results of the otolith shape component also are published in the peer-reviewed literature (Shepard et al. 2010a) but are detailed below along with the otolith chemistry component.

Age and Growth Component

Objectives:

The objective of the age and growth component of the study was to estimate contemporary sex- and stock- specific VBGFs for eastern Atlantic and GOM king mackerel. We included fishery-independent as well as fishery-dependent samples in an effort to improve estimates of VBGF parameters. A secondary objective was to test for differences in von Bertalanffy growth functions (VBGF) between Atlantic and GOM fish, as well as between sexes. Lastly, we compared contemporary and historical age and growth data to test if long term changes in size-at-age had occurred.

Methods:

King mackerel were sampled during 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 tournament and recreational charter boat landings between Panama City, Florida and Dauphin Island, Alabama for the GOM stock and in Jacksonville, Florida and Beaufort, North Carolina for the Atlantic stock (Fig. 3). 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. Sex was determined for each fish macroscopically, fork length (FL) was measured to the nearest centimeter, and both saggital otoliths were removed. Juveniles were defined as individuals that were below the minimum size limit (Atlantic: 50.8 cm; GOM: 61.0 cm) and could not be sexed macroscopically

Otolith opaque zones were counted to determine age (Johnson et al. 1983; DeVries and Grimes 1997). Analysis of 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 et al. 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 (~0.5mm) 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 10x magnification with transmitted light. Otoliths from males < 800 mm FL and females < 900mm FL were immersed in water in an opaque, black dish and aged whole under a dissection microscope at 7x 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 annuli). The margin was classified as nonexistent if the last opaque zone was on the edge of the otolith. A small margin was less than 1/3 the width of the previous increment. An average margin was 1/3 to 2/3 the width of the previous increment, and a large margin was greater than 2/3 the width of the previous increment. Annuli count was converted to age based on margin classification and timing of sampling with the method of 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 for the two sets of age estimates (Beamish and Fournier 1981). The calculated APE served as a measure of between-reader agreement and aging precision.

Length at capture and estimated age were used to fit stock- and sex-specific von VBGFs using a maximum likelihood procedure with a normal left-truncated error distribution to account for the minimum size limits (GOM: 61.0 cm; Atlantic: 50.8 cm) for fishery-dependent samples (Ortiz and Palmer 2008). The minimum size for fishery-independent samples was set to 0 cm FL. The model fitting procedure also assumed a constant coefficient of variation (CV) to account for heterogeneous variance across ages.

Differences VBGFs were tested between between sexes and stocks with likelihood ratio tests (Cerrato 1990). The likelihood ratio (χ^2) statistic was calculated:

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

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 was clearly 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, stocks, and time stanzas, as described below. A conservative significance level (α=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.

Tests were conducted to test for differences in growth between contemporary and historical (1977-79 and 1986-92) fishery-dependent data reported by DeVries and Grimes (1997). Growth functions from fish collected in the 1970s, 1980s, and 1990s 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, historical 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. Likelihood ratio tests were performed for each sex/stock combination to test for differences in the fitted growth functions among the three time stanzas (1977-79, 1986-92, and 2006-07). As above, α=0.01 was used to control for Type I error.

Lastly, differences in mean size among time stanzas were tested with an analysis of variance (ANOVA). The test was conducted with a 3-factor (sex, stock, and time stanza) model with a Scheffe adjusted multiple comparisons procedure sliced by age*sex*stock to determine which age/sex/stock combinations were displaying significant time stanza effects. Analysis of mean size was conducted on the fishery-dependent data directly rather than from VBGF model predictions.

Results and Discussion:

A total of 2,316 king mackerel was sampled for age and growth analysis in 2006-08 (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. Maximum observed age was 19, 20, 19, and 23 y for GOM females, GOM males, Atlantic females, and Atlantic males, respectively. The APE computed between age estimates for 237 individuals read independently by two readers was 3.4%.

Contemporary VBGFs were significantly different among all sex/stock combinations (Fig. 4). All parameters, as well as overall functions, were significantly different in each of the four comparisons (likelihood ratio tests, $p < 0.001$). The models displayed lower estimates of L_∞, higher estimates of k, and more negative estimates of t_0 than models reported by Shepard et al. (2010b) that were fit to fishery-dependent data alone, which was also true with respect to models to landings data during SEDAR5. We infer that including fishery-independent samples modeled growth more effectively for the stocks as a whole than did fitting functions to size-at-age of only the landed catch. In particular, incorporation of age-0 and age-1 fishery-independent samples in the data set resulted in fitting t_0 closer to the origin than the fishery-dependent only models cited above. The improved fit of t_0 further served to constrain estimates of L_∞ due to correlation among the VBGF parameters.

As expected, contemporary fishery-dependent growth functions displayed differences between sexes and stocks that are consistent with historical patterns (DeVries et al. 1997). Females achieved larger size at age than males in both stocks, and individuals from the GOM stock grew larger than those from the Atlantic stock. Contemporary fishery-dependent growth functions differed significantly from historical functions for all sex/stock combinations (likelihood ratio tests, $p < 0.001$). 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 of minimum size limits. It is also possible that the differences in VBGF fit are a function of sample size, as the 1986-92 data set had the largest sample sizes (n = 3,624 for the GOM and 5,709 for the Atlantic) followed by the 1977-79 data set (n = 1,336 for the GOM and 541 for the Atlantic). 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 stanzas provided a more direct test for stock-specific changes over time. 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 stocks or sexes (Fig. 5). The only non-significant effects in the analysis were the time*sex and age*time*sex interaction terms. The large number of significant interactions would seem to complicate interpretation. However, one would expect age, stock, and sex, as well as their interactions, to be significant based on differences in the growth functions. In the GOM stock, contemporary mean size-at-age was consistently lower than historical estimates for ages 2 through 7 and similar to historical estimates for ages 8 through 10. Contemporary mean size-at-age in the Atlantic stock was greater than historical estimates for ages 4-10, similar to historical estimates for age 3, and less than historical 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.

The GOM stock had been heavily exploited as early as 1980, which continued until 1996 (SEDAR16 2009; Powers 1996). 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 king mackerel 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 stock 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 stock size was increasing most rapidly in the GOM.

The trend in estimated SSB in the Atlantic king mackerel stock has been counter to the trend in the GOM, with SSB in the Atlantic stock 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 stock also is a density-dependent response to stock 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 stock because that system is less productive than the GOM. However, without evidence that individual growth had been limited historically by stock density it is difficult to attribute the increase in size-at-age entirely to a density-dependent response (Sinclair et al. 2002).

While it remains somewhat unclear whether the trends in king mackerel size-at-age since the 1970s result from a genetic effect due to size-selective harvesting (Conover and Munch 2002), or a compensatory response to changes in stock density (Hilborn and Minte-Vera 2008), it appears that the preponderance of evidence favors that latter versus former explanation. Part of the rationale for the age and growth component of the current study was to determine if there is 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 a increase in Atlantic size-at-age during a period of declining stock size estimates, indicate density-dependence as a simpler and more logical explanation for observed trends. These two stocks with their contrasting biomass trajectories present an interesting opportunity to further study the relationship between changes in stock size and growth rates. Furthermore, this study highlights the importance of constantly examining stock growth rates over time, especially for GOM and Atlantic king mackerel, 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). Lastly, this study component highlights the importance of including fishery-independent samples into age and growth analysis.

Otolith Shape Analysis Component

Objectives:

The objective of the otolith shape component of this study was to estimate mixing between Atlantic and GOM king mackerel with natural tags derived from otolith shape parameters. A secondary objective was to examine within season temporal variability in the Atlantic stock's estimated contribution to winter landings off southeastern Florida. To accomlish these objectives, natural stock-specific signatures of Atlantic and GOM stocks first were computed with data collected from summer-sampled fish. Stock-specific otolith shape signatures then were applied to samples of winter south Florida landings to estimate the percentage contribution of the Atlantic stock.

Methods:

Stock-specific king mackerel otolith shape parameters were measured from a sub-sample of otoliths collected in the northeastern GOM and Atlantic in summer 2006 and 2007 when GOM and Atlantic stocks were separated. Only individuals aged from 2 to 6 years were included in otolith chemical analyses because approximately 85% of winter landings are derived from those age classes (SEDAR 16 2009). Data from summer-sampled fish could be used to represent each stock reliably due to negligible mixing in summer. Therefore, summer samples were used here to derive stock-specific natural tags. As stated above, FL and sex were recorded and both sagittal otoliths were removed from each sampled individual.

The management-designated winter-mixing area was divided into three sampling zones similar to those defined by Clardy et al. (2008), with the exception that the easternmost zone extended northward to match the sampling region of DeVries et al. (2002) (Fig. 3). Zone 1 encompassed the southwest coast of Florida, and fish were sampled from a commercial gill-net fishery prosecuted 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 fishery 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 produced 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 Image Pro (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 anti-rostrum to the ventral edge and the otolith perimeter posterior of this line was digitally traced with the auto trace feature in Image Pro.

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:

$$\text{Roundness} = \frac{4\pi * \text{otolith area}}{\sqrt{\text{otolith perimeter}}} \qquad \text{(equation 2)}$$

$$\text{Circularity} = \sqrt{\frac{\text{otolith area}}{\text{otolith perimeter}}} \qquad \text{(equation 3)}$$

$$\text{Ellipticity} = \frac{\text{otolith length - otolith width}}{\text{otolith length} + \text{otolith width}} \qquad \text{(equation 4)}$$

$$\text{Rectangularity} = \frac{\text{otolith area}}{\text{area of its minimal enclosing rectangle}} \qquad \text{(equations 5).}$$

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). Therefore, several precautions were taken to account for size and age. Only individuals ages 2 to 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 separating by sampling year, all parameters continued to be significantly correlated with FL ($p < 0.001$), 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, Inc. 1996) with 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, Inc. 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 standard error (SE) of estimates was calculated from 500 bootstraps. All maximum likelihood modeling was conducted in S-Plus® (version 6.0).

Results and Discussion:

Totals of 965 and 1,309 king mackerel were sub-sampled for shape analysis from otoliths sampled from the 2006/07 and 2007/08 fishing years, respectively (Table 2). Fish were between ages 2 and 6 and yielded at least one otolith with the posterior portion intact for shape analysis. Totals of 588 and 609 king mackerel were sampled from the south Florida sampling zones in winter 2006/07 and 2007/08, respectively (Table 2).

All 27 otolith shape parameters were significantly correlated with FL (all $p<0.001$), thus each 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).

Results from otolith shape MANOVA indicated sex, year, and stock effects all were significant (Pillai's Trace, $p < 0.001$). 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 2006/07 and 2007/08 summer samples to account for variation in otolith shape between fishing years. The significant sex effect also supported sex-specific analysis to improve classification success and precision in estimates of Atlantic contribution.

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%, with higher rates for the Atlantic than GOM fish, 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 (Fig. 6). (Note: The 11 samples collected in Zone 3 in December of 2006 were added to the samples collected in January 2007 for analysis due to small December 2006 sample size.) The 2006/07 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, with lower contributions 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 2006/07 and March in 2007/08). Sex-specific results for 2007/08 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 2007/08 than 2006/07 in all models except for females in Zone 3B. Zone 3A 2007/08 estimates could not be compared directly because they were combined with Zone 3A in 2006/07 due to low sample size. The mean standard error 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 creates uncertainty about spatial and intra-annual temporal trends in the Atlantic stock's estimated contribution to south Florida winter landings.

A comparison between otolith shape-based estimates of Atlantic contribution to winter landings reported here and historical 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 southeast Florida (Cape Canaveral to Palm Beach) in 1996/97 were from the Atlantic stock. This estimate is striking considering the majority of 1996/97 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 2001/02 and 40% in 2002/03 (Clardy et al. 2008). Mixed-stock 2001/02 and 2002/03 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 2006/07 and 32% in 2007/08. Zone 3 male landings also declined from 76% in 2001/02 and 72% in 2002/03 (Clardy et al. 2008) to 70% and 37% in 2006/07 and 2007/08, respectively.

Similar declines exist between estimated Atlantic contribution reported by Clardy et al. (2008) for Zones 1 and 2 in 2001/02 and 2002/03 and those reported here for 2006/07 and 2007/08. Mixed-stock Zone 1 and Zone 2 samples were collected in January in both studies. Zone 1 female Atlantic contribution dropped from 61% in 2001/02 to 15% in 2002/03 then increased to 32% in 2006/07 and fell to 26% in 2007/08. Estimated Atlantic contribution to Zone 1 male landings declined from 61% in 2001/02 and 45% in 2002/03 to 24% in 2006/07 and 14% in 2007/08. The estimated Zone 2 female Atlantic contribution remained fairly stable at 49, 41, and 42% in 2001/02, 2002/03, and 2006/07, respectively, but declined to 25% in 2007/08. Finally, the percentage of Atlantic Zone 2 male landings was estimated as high as 99% in 2001/02 and then dropped to 83% in 2002/03, 80% in 2006/07, and 54% in 2007/08.

Current estimates of Atlantic stock contribution to winter landings are consistently lower than historical 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 the Atlantic stocks' presence, or both. During the period between 1996 and 2008, the estimated GOM SSB increased 2.5 fold in response to conservation measures and decreased consumption due to public concern over mercury warnings (Powers 1996; SEDAR16 2008). The estimated Atlantic SSB declined 45% over the same period. Therefore, the shift in Atlantic contribution is likely a function of changes in relative stock size, particularly the increase in the GOM stock's biomass.

The estimated Atlantic contribution of king mackerel landings was >0 in each zone for all model results, thus indicating the historical 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 (Clardy 2008; DeVries et al. 2002), 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). The spatial and temporal variability (both inter- and intra-annual) in estimates of Atlantic contribution reported herein 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. However, uncertainty in point estimates of the Atlantic stock's contribution to winter landings implies that categorizing mixing more precisely, especially with respect to spatial and temporal variability across south Florida in winter, would be precarious with otolith shape analysis. Benefits of continuing to perform otolith shape analysis are that otoliths can be digitized easily and rapidly prior to aging; otolith shape analysis is a relatively inexpensive approach to estimating stock mixing; and, the longest time series of Atlantic stock contribution to south Florida winter landings are based on shape analysis.

Otolith Chemistry Component

Objectives:

The objective of the otolith chemistry component of this study was to estimate mixing between Atlantic and GOM king mackerel with natural tags derived from otolith chemical signatures. A secondary objective was to examine the with-in season temporal variability in the Atlantic stock's estimated contribution to winter landings off southeastern Florida. To accomlish these objectives, natural stock-specific signatures of Atlantic and GOM stocks first were computed with data collected from summer-sampled fish. Stock-specific otolith chemical signatures then were applied to samples of winter south Florida landings to estimate the percentage contribution of the Atlantic stock.

Methods:

Stock-specific king mackerel otolith chemical signatures were measured from a sub-sample of otoliths collected in the northeastern GOM and Atlantic in summer 2006 and 2007 when GOM and Atlantic stocks were separated (Fig. 3). Likewise, winter mixing around south Florida was estimated from sub-samples of otoliths collected in the three south Florida winter sampling zones (Fig. 3). As with the shape analysis component, only individuals aged to be 2 to 6 years old were included in otolith chemical analyses. A sub-sample of 45 males and 45 females (where sample sizes were sufficiently large) were selected for each stock and mixed-stock sampling zone (and each month for zone 3) in each sampling year. An effort was made to randomly select 9 individuals from each age class (2-6), but when 9 individuals were not available for a particular age class samples were chosen from the closest age class with more than 9 individuals. For each sub-sampled individual, the otolith that was not randomly selected for aging (see above) was used for chemical analysis.

All otolith chemistry sample preparations were conducted under a laminar flow class-10 clean hood to prevent contamination. An otolith's rostrum was removed if it survived the extraction process intact in order to maintain consistency among samples; otoliths were weighed following rostrum removal. Otolith samples were cleaned with 1% nitric acid and rinsed with ultrapure water. After drying, otoliths were reweighed to determine the amount of material lost during cleaning. Clean otoliths were pulverized with acid-leached mortar and pestles. The pulverized material then was either dissolved in ultrapure 1% nitric acid (dilution factor ~1,000x) in an acid-leached high-density polyethylene bottle for sector field-inductively coupled plasma-mass spectrometry (SF-ICP-MS) analysis, or transferred to a centrifuge tube and stored dry for subsequent stable isotope ratio-mass spectrometry (SIR-MS) analysis.

Aliquots (5 mL) of otolith solutions were analyzed with a Finnigan MAT Element2 sector field-inductively coupled plasma-mass spectrometer (SF-ICP-MS) by Dr. Alan Shiller in the Department of Marine Sciences at the University of Southern Mississippi. Otolith solutions were spiked with Indium at a concentration of 2.5 ppb as an internal standard and then analyzed for ^{137}Ba, ^{48}Ca, ^{7}Li, ^{55}Mn, ^{25}Mg, and ^{86}Sr. Blank solutions were prepared from 1% ultrapure HNO_3 and processed through the same stages of sample preparation as sample solutions. They were analyzed consecutively with sample solutions to estimate the instrument's limit of detection (LOD) for individual elements; LOD was estimated as 3 standard deviations of mean blank values. Instrument performance and matrix effects were checked by assaying elemental concentrations of an otolith standard reference material (SRM; National Research Council of

Canada FEBS-1) prepared from adult red snapper otoliths (Sturgeon et al. 2005). Solutions of the SRM were prepared and analyzed similarly to red snapper otolith samples.

Stable isotope analysis was conducted with a Finnigan MAT 251 stable isotope ratio-mass spectrometer (SIR-MS) by Mr. David Winter at the University of California-Davis. The machine was calibrated daily against the International Atomic Energy Agency's carbonate standard, NBS-19. Accuracy of analytical runs was measured through routine analysis of an in-house check standard which had been stringently calibrated against NBS-19. Results were reported as $\delta^{18}O$ and $\delta^{13}C$ expressed as per mil (‰) relative to the international carbonate standard: Vienna Peedee Belemnite.

Otolith element:Ca ratios and stable isotope values from the GOM and Atlantic samples collected in summer were used to derive sex- and stock-specific natural tags, which were subsequently used to parameterize maximum likelihood mixing models to estimate the Atlantic contribution to the mixed winter landings. Significant correlations between each constituent (Ba:Ca, Li:Ca, Mg:Ca, Mn:Ca, Sr:Ca, $\delta^{13}C$, and $\delta^{18}O$) and FL were removed by subtracting the product of FL and the slope of the least squares linear relationship from the variable. The data then were tested for stock, sex, and year effects with multivariate analysis of variance (MANOVA), as well as each constituent individually being tested for those effects with ANOVA. Stepwise year- and sex-specific discriminant functions (DFs) were computed in SAS (Proc STEPDISC; SAS Institute, Inc. 1996) with all constituents loaded as classification variables. Year- and sex-specific DFs also were computed with only $\delta^{13}C$ and $\delta^{18}O$ as classification variables. Jackknifed classification accuracies were computed for resultant models with Proc DISCRIM in SAS.

Maximum likelihood stock mixing models were parameterized with constituents identified in stepwise DFA, as well as with $\delta^{13}C$ and $\delta^{18}O$ values, and applied to winter samples to estimate the percentage of landings contributed by the Atlantic stock in each sampling zone (and month for zone 3). The standard error (SE) of estimates was calculated from 500 bootstraps (DeVries et al. 2002). All maximum likelihood modeling was conducted in S-Plus (version 6.0).

Results and Discussion:

Totals of 600 and 654 king mackerel were selected for otolith chemistry analysis from the samples collected in the 2006/07 and 2007/08 fishing years, respectively (Table 4). Of those, 343 were summer-sampled fish and 911 were sampled in winter. The 12 samples collected in zone 3 in December of 2006 were combined with the samples collected in January 2007 for analysis due to low sample size.

Otolith $\delta^{18}O$ and $\delta^{13}C$ values from summer 2007 deviated from normality; however, this deviation appears to have been driven by one or two samples with particularly low $\delta^{18}O$ and $\delta^{13}C$ values. All attempted transformations resulted in worse violation of parametric assumptions. Also, the variance-covariance matrices were heteroscedastic. Thus, Pillai's Trace was used as the MANOVA test statistic, and quadratic, rather than linear, DFs were estimated. Otolith chemical signatures were significantly different among years, stocks, and sexes (Pillai's Trace, $p < 0.001$; Table 5, Fig. 7). All individual otolith chemistry constituents were significantly different between stocks, but year was only significant for 3 of 7 constituents and sex was only significant for 2 of 7 (ANOVA, $p < 0.05$; Table 5).

Stepwise DFs computed with all otolith chemistry constituents as classification variables yielded jackknifed classification accuracies that ranged from 60% to 90% (Table 6), while models based on just $\delta^{13}C$ and $\delta^{18}O$ yield accuracies between 66% and 91% (Table 7). Despite the significant sex effect in the MANOVA, the sex-specific analyses did not consistently produce higher classification success rates than combined sex models. This was likely due to the fact that the significant sex effect was driven by significant differences in only Li:Ca and Sr:Ca (Table 5).

Otolith stable isotope signatures appear to provide a more powerful stock-specific tag than either otolith shape parameters or otolith chemical signatures that include element:Ca ratios. Clearly, both otolith chemical and stable isotope signatures both provided more accurate discrimination of king mackerel stocks than did shape parameters, as they both averaged 14-15% higher classification accuracies than did shape models. While stable isotope classification from DF models were only slightly more accurate than those from models that included element:Ca data, what is important to consider is the temporal, spatial, and inter-sex consistency of stable isotope signatures (Table 6), combined with the fact that adding element:Ca ratios did not improve classification. A final consideration is that ICP-MS analysis of otolith chemistry is a process were contamination effects are always a concern, while SIR-MS is much less likely to suffer from contamination effects and also is typically less expensive to perform.

Maximum likelihood results for both years indicated some level of Atlantic stock contribution in all zones for both the chemical signature (including element:Ca ratios) models and the models with only stable isotope signatures ($\delta^{13}C$ and $\delta^{18}O$ only). The estimated percentage of Atlantic fish in the landings increased from west to east with the lowest percentage in zone 1 and the highest in zone 3 (Figs. 8 and 9). Many of the 2007/08 models estimated the Atlantic stock's contribution to zone 3 December landings to be lower than Zone 2, but zone 1 and 2 landings were sampled in January, and zone 3 estimates were consistently higher than zones 2 in that month. Atlantic stock contribution estimates also increased in zone 3 over the course of the winter (December-March). The spatial and temporal patterns were consistent between models incorporating element:Ca ratios and those only using $\delta^{13}C$ and values. However, mean SE about mixing estimates was 8% lower among the stable isotope models than the SE among estimates from otolith chemistry models that included element:Ca ratios, and 25% lower than the SE about mixing estimates from otolith shape models (Figs. 6, 8, and 9).

Atlantic stock contribution to winter landings in south Florida was estimated to be much greater than 0% in all models, with spatial and temporal trends consistent with historical results (Patterson et al. 2004, Clardy et al. 2008, Shepard 2008). In response to preliminary results from this study and other recent estimates, the assumption that all mixed-stock winter landings were from the GOM was replaced by a 50:50 ratio of GOM to Atlantic contribution in the most recent stock assessment (SEDAR 2008), as well as in management adopted by the GMFMC and SAFMC. While this decision is more reflective of natural stock dynamics than the historical assumption, it still does not fully account for the spatial and temporal variability in Atlantic contribution to mixed-stock winter landings. While uncertainty in point estimates of Atlantic stock contribution to winter landings based on otolith shape analysis clearly is too great to incorporate spatially-explicit winter mixing dynamics into stock assessment models, variance about otolith chemistry-based Atlantic contribution estimates is perhaps tight enough to begin to consider that option, or at least might indicate that stock assessment sensitivity analyses should be conducted to assess the effect of incorporating spatially-explicit winter mixing among the various regions and fisheries in south Florida on model results.

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Tables and Figures

Table 1. Samples sizes for female, male, and juvenile king mackerel, *Scomberomorus cavalla*, sampled from the northern Gulf of Mexico (GOM) and Atlantic Ocean (Atlantic) in 2006-08 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	0	0	0
Fishery-Independent	17	13	2	0	0	22
Recreational	137	64	0	279	118	0
Tournament	166	28	0	0	0	0
2007						
SEAMAP	0	0	85	0	0	0
Fishery-Independent	86	46	1	0	0	0
Recreational	341	146	0	7	7	0
Tournament	173	43	0	306	120	0
Commercial	0	0	0	10	0	0
2008						
SEAMAP			62			
Total	921	340	186	602	245	22

Table 2. King mackerel samples sizes for otolith shape analysis from 2006-08 in the Gulf of Mexico (GOM), Atlantic Ocean (Atlantic), and in south Florida winter sampling zones. For zone 3, monthly samples are given as D = December, J = January, F = February, and M = March.

	Summer samples		Winter mixed stock samples					
	GOM	Atlantic	Zone 1	Zone 2	Zone 3D	Zone 3J	Zone 3F	Zone 3M
2006/07								
Female	155	133	119	73	8	49	25	59
Male	51	38	54	61	3	44	31	62
2007/08								
Female	399	130	102	69	27	43	59	36
Male	141	30	51	47	23	38	67	47

Table 3. King mackerel year- and sex-specific stepwise discriminant function analysis (DFA) results identifying otolith shape parameters selected for DFA discrimination between Gulf of Mexico (GOM) and Atlantic Ocean (Atlantic) populations, along with the models' associated jackknifed classification success rates.

	Significant parameters	Classification success (%)		
		GOM	Atlantic	Overall
2006				
Female	Roundness, Circularity, Harmonics 3, 4, 12, 15, 16, 18	62	67	65
Male	Harmonics 4, 9, 14, 17	71	73	72
Combined	Harmonics 4, 5, 10, 12, 15, 16	61	63	62
2007				
Female	Area, Harmonics 2, 14, 16	70	70	70
Male	Harmonics 2, 4, 12, 13	60	66	63
Combined	Box width, Ellipticity, Rectangularity, Harmonics 4, 7, 12, 16	63	65	64

Table 4. King mackerel samples sizes by sex (F = Female, M = Male) selected for otolith chemistry analysis from 2006/07 and 2007/08 Gulf of Mexico (GOM) and Atlantic Ocean summer samples and winter samples from sampling zones 1-3. For zone 3, monthly samples are given as D = December, J = January, F = February, and M = March.

		Summer Samples				Winter South Florida Sampling Zone Samples											
		GOM		Atlantic		Zone 1		Zone 2		Zone 3D		Zone 3J		Zone 3F		Zone 3M	
Year	Sex:	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M
2006/07	n:	45	45	45	38	45	45	45	45	7	5	45	45	25	30	45	45
2007/08	n:	45	45	45	35	45	45	44	43	27	23	45	40	45	45	37	45

Table 5. Results of MANOVA and ANOVA models computed to test for differences in otolith chemical signatures among king mackerel stocks, sampling years, and sexes for fish sampled in the Gulf of Mexico and Atlantic Ocean in summer 2006 and 2007. The statistic computed in MANOVA was Pillai's Trace and mean square error (from Type III sum of squares) in ANOVA models.

Model	Statistic Value	F-Value	Degrees of Freedom	Prob > F
MANOVA				
Stock	0.423	32.24	7; 327	<0.001*
Year	0.185	10.59	7; 327	<0.001
Sex	0.143	7.79	7; 327	<0.001*
Stock*Year	0.126	6.72	7; 327	<0.001*
Stock*Sex	0.047	2.32	7; 327	0.025*
Year*Sex	0.011	0.51	7; 327	0.830
Stock*Year*Sex	0.014	0.67	7; 327	0.696
Ba:Ca ANOVA				
Stock	3.419	18.80	1; 333	<0.001*
Year	0.602	3.31	1; 333	0.070
Sex	0.058	0.32	1; 333	0.574
Stock*Year	0.817	4.49	1; 333	0.035*
Stock*Sex	1.617	8.89	1; 333	0.003
Year*Sex	0.027	0.15	1; 333	0.702
Stock*Year*Sex	0.028	0.16	1; 333	0.693
Li:Ca ANOVA				
Stock	0.817	8.39	1; 333	0.004*
Year	0.131	1.34	1; 333	0.247
Sex	0.574	5.89	1; 333	0.016*
Stock*Year	1.854	19.03	1; 333	<0.001*
Stock*Sex	0.176	1.80	1; 333	0.180
Year*Sex	0.001	0.01	1; 333	0.909
Stock*Year*Sex	0.040	0.41	1; 333	0.521
Mg:Ca ANOVA				
Stock	0.533	6.56	1; 333	0.019*
Year	0.615	7.57	1; 333	0.006*
Sex	0.269	3.31	1; 333	0.070
Stock*Year	0.689	8.49	1; 333	0.004*
Stock*Sex	0.188	2.31	1; 333	0.130
Year*Sex	0.047	0.58	1; 333	0.449
Stock*Year*Sex	0.003	0.03	1; 333	0.860

Table 5. continued.

Model	Statistic Value	F-Value	Degrees of Freedom	Prob > F
Mn:Ca ANOVA				
Stock	0.533	6.56	1; 333	0.011*
Year	0.615	7.57	1; 333	0.006*
Sex	0.269	3.31	1; 333	0.070
Stock*Year	0.689	8.49	1; 333	0.004*
Stock*Sex	0.187	2.31	1; 333	0.130
Year*Sex	0.047	0.58	1; 333	0.449
Stock*Year*Sex	0.003	0.03	1; 333	0.860
Sr:Ca ANOVA				
Stock	1.244	39.81	1; 333	<0.001*
Year	0.004	0.12	1; 333	0.729
Sex	0.878	28.09	1; 333	<0.001*
Stock*Year	0.539	17.25	1; 333	<0.001*
Stock*Sex	0.033	1.05	1; 333	0.306
Year*Sex	0.002	0.06	1; 333	0.801
Stock*Year*Sex	0.074	2.36	1; 333	0.126
δ^{13}C ANOVA				
Stock	2.100	18.42	1; 333	<0.001*
Year	0.022	0.19	1; 333	0.662
Sex	0.007	0.06	1; 333	0.805
Stock*Year	0.045	0.39	1; 333	0.532
Stock*Sex	0.120	1.05	1; 333	0.307
Year*Sex	0.115	1.01	1; 333	0.316
Stock*Year*Sex	0.012	0.11	1; 333	0.744
δ^{18}O ANOVA				
Stock	8.472	167.38	1; 333	<0.001*
Year	1.640	32.41	1; 333	<0.001*
Sex	0.767	15.16	1; 333	0.242
Stock*Year	0.070	1.37	1; 333	<0.001*
Stock*Sex	0.029	0.57	1; 333	0.451
Year*Sex	0.022	0.43	1; 333	0.511
Stock*Year*Sex	0.054	1.07	1; 333	0.303

Table 6. Stock-specific and overall jackknifed classification success from stepwise discriminant function models computed with otolith chemical signatures of king mackerel sampled in the Gulf of Mexico (GOM) and Atlantic Ocean in summer 2006 and 2007.

Year	Sex	Parameters	GOM % Success	Atlantic % Success	Overall % Success
2006	Male	Li:Ca, Mg:Ca, Mn:Ca, $\delta^{18}O$	60.0	79.0	69.5
	Female	Ba:Ca, Mg:Ca, Mn:Ca, Sr:Ca, $\delta^{18}O$	71.1	86.4	78.7
	Both Sexes	Ba:Ca, Mg:Ca, Mn:Ca, $\delta^{18}O$	72.2	90.2	81.2
2007	Male	$\delta^{13}C$, $\delta^{18}O$	88.6	91.4	90.0
	Female	O, Li, Sr	75.6	88.9	82.2
	Both Sexes	O, Li, Sr	85.4	92.5	88.9

Table 7. Stock-specific and overall jackknifed classification success from stepwise discriminant function models computed with otolith $\delta^{13}C$ and $\delta^{18}O$ values of king mackerel sampled in the Gulf of Mexico (GOM) and Atlantic Ocean in summer 2006 and 2007.

Year	Sex	Parameters	GOM % Success	Atlantic % Success	Overall % Success
2006	Male	$\delta^{13}C$, $\delta^{18}O$	66.7	86.8	76.8
	Female	$\delta^{13}C$, $\delta^{18}O$	71.1	90.9	81.0
	Both Sexes	$\delta^{13}C$, $\delta^{18}O$	65.6	85.4	75.5
2007	Male	$\delta^{13}C$, $\delta^{18}O$	84.1	85.7	84.9
	Female	$\delta^{13}C$, $\delta^{18}O$	64.4	84.4	74.4
	Both Sexes	$\delta^{13}C$, $\delta^{18}O$	68.5	88.8	78.6

Figure 1. Migratory pathways for Atlantic and eastern Gulf of Mexico king mackerel populations inferred from tagging data.

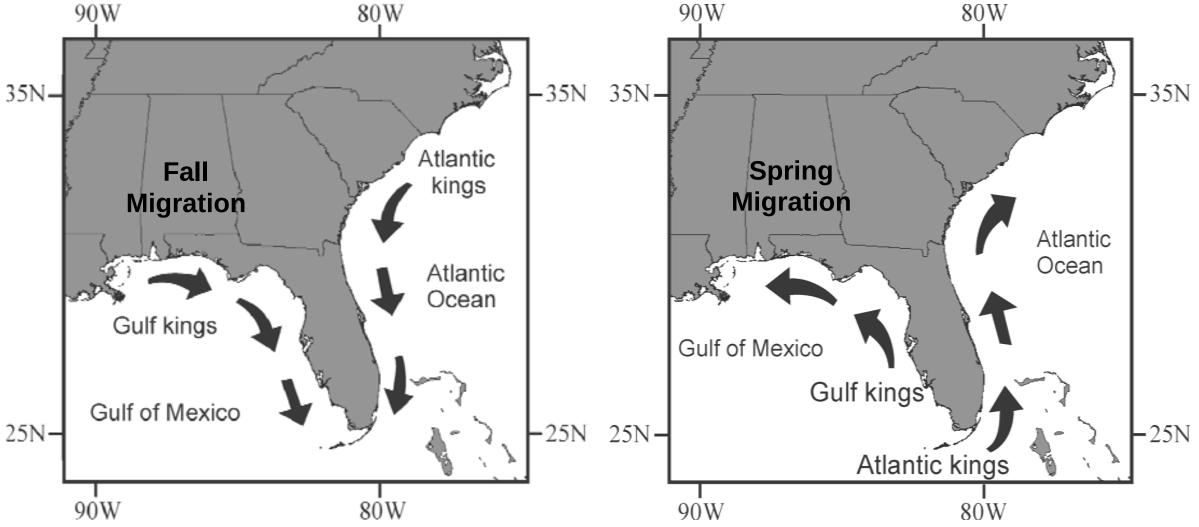

Figure 2. Boundaries of the king mackerel mixing zone that was originally defined in Amendment 1 of the Coastal Pelagics Management Plan in the 1985. The seaward boundary of the mixing zone is the edge of U.S. exclusive economic zone. However, most fish are caught over the continental shelf, the edge of which is denoted by the 200 m isobath.

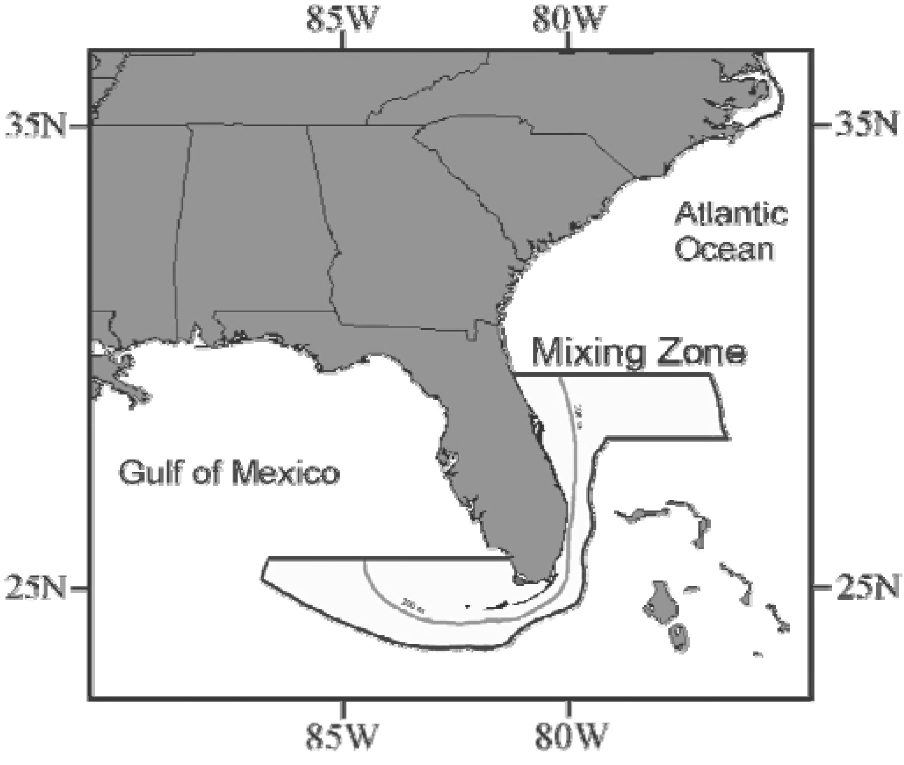

Figure 3. Map of the southeastern United States depicting summer sampling locations in the Gulf of Mexico (DI = Dauphin Island, Alabama; OB = Orange Beach, Alabama; PC = Panama City, Florida) and Atlantic Ocean (JK = Jacksonville, Florida; and MC = Morehead City, North Carolina), the management-defined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

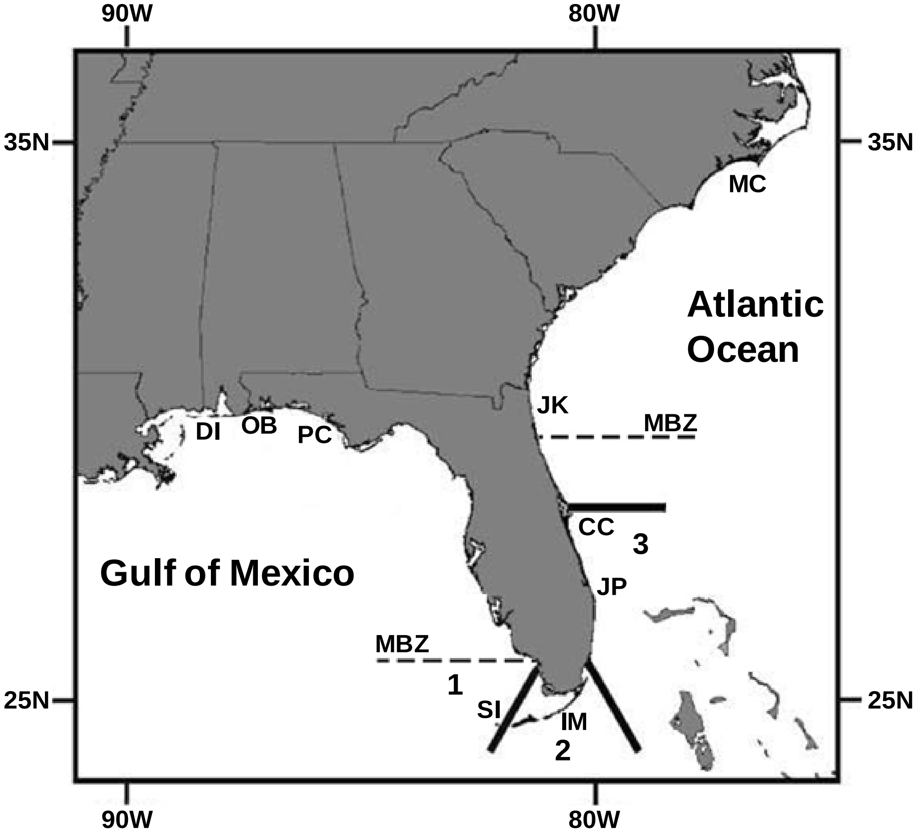

Figure 4. Fishery-dependent and -independent size-at-age data for king mackerelsamples during summer 2006-08. Fitted lines and equations are von Bertalanffy growth functions. (A=Gulf of Mexico females, B=Gulf of Mexico males, C=Atlantic Ocean females, D=Atlantic Ocean males).

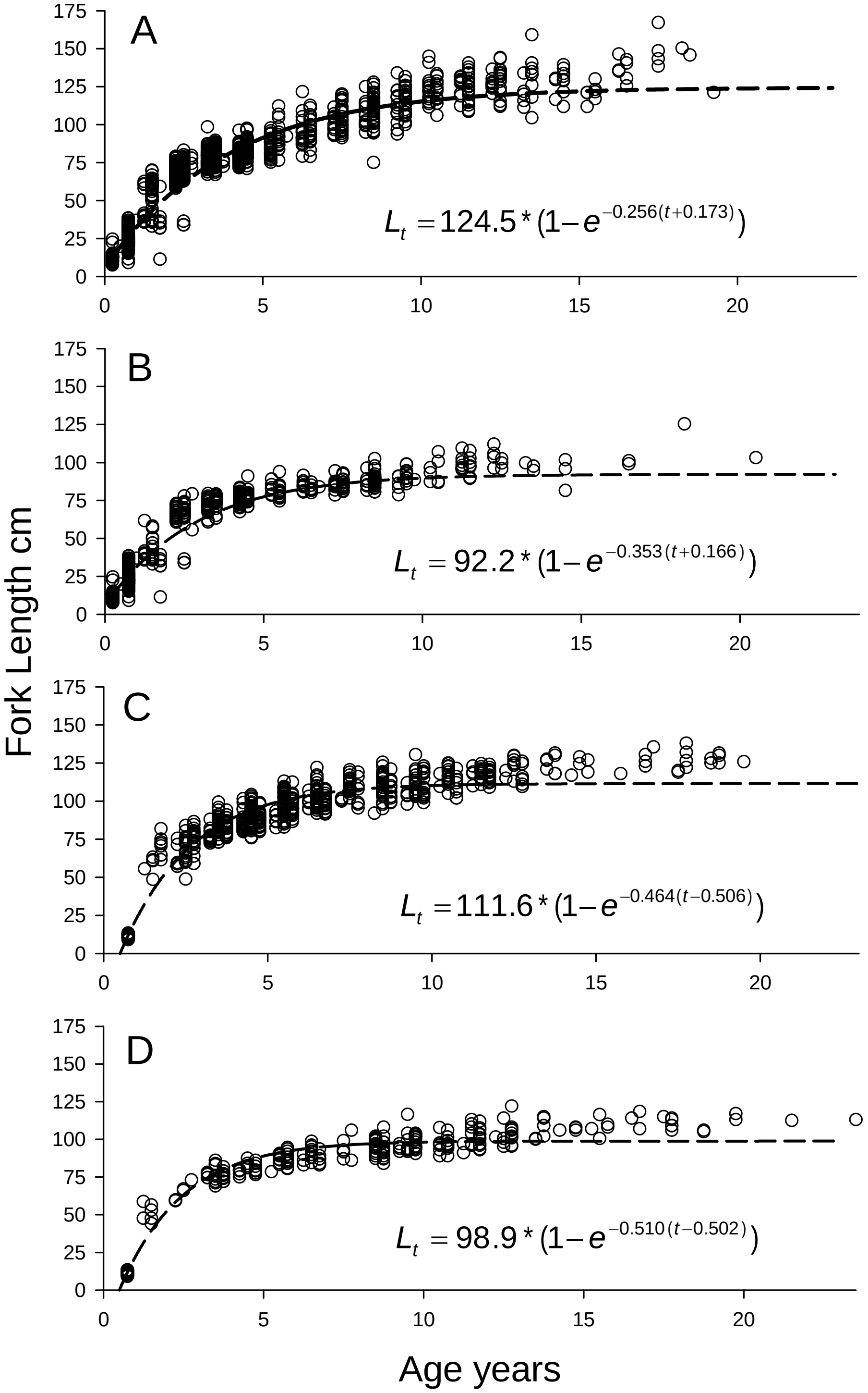

Figure 5. Mean (± SE) size-at-age of Gulf of Mexico female (A) and male (B) and Atlantic Ocean female (C) and male (D) king mackerel ages 2-10 years that were sampled from fishery landings during the summer spawning seasons over three time stanzas (2006-2007, 1986-1992, 1977-1979). Data for 1986-1992 and 1977-1979 were originally reported by DeVries and Grimes (1997). * indicates a significant difference among time stanzas (p<0.05).

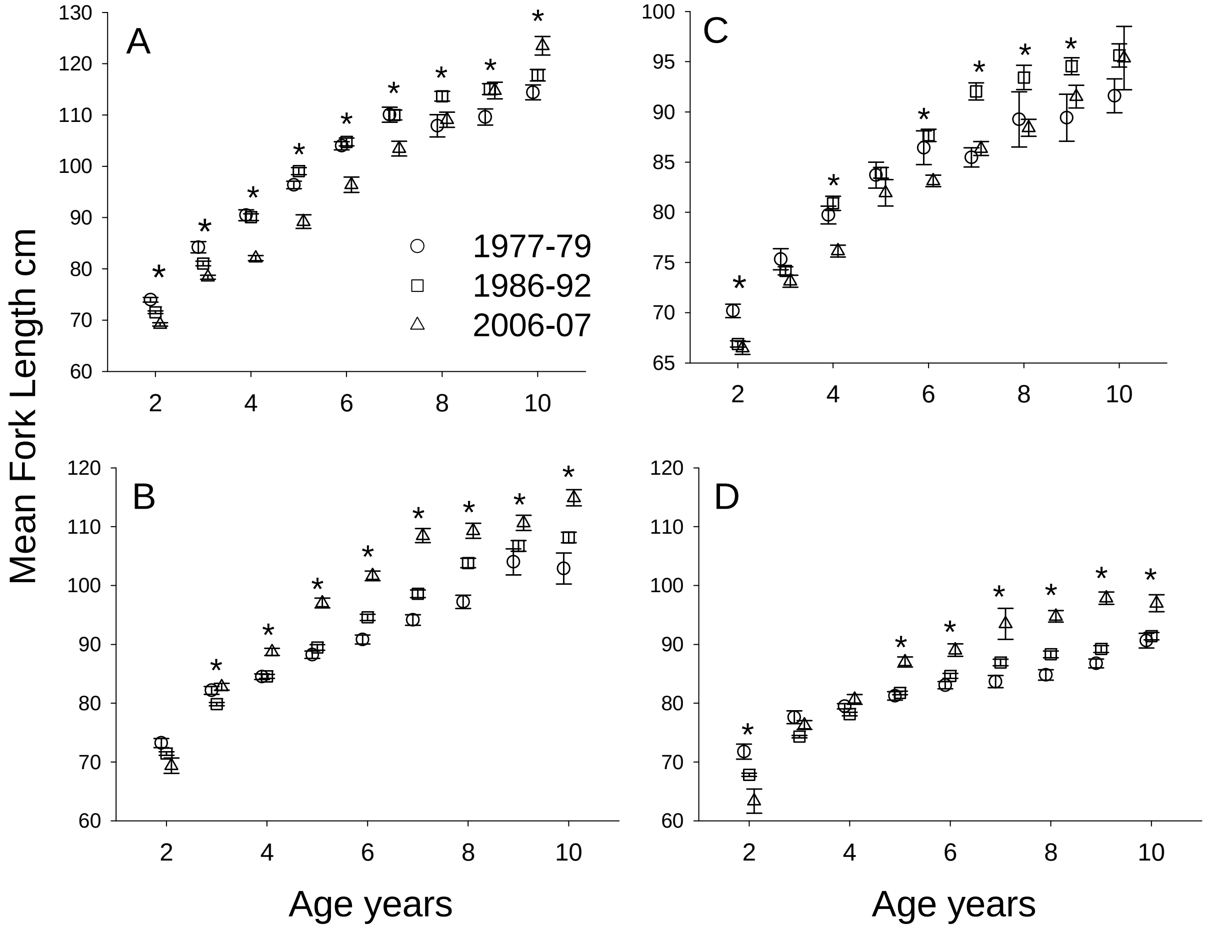

Figure 6. Otolith shape based maximum likelihood estimates of the percentage (±SE) of female (A=2006/07, B=2007/08), male (C=2006/07, D=2007/08), and combined sex (E, F) king mackerel landings that were contributed by the Atlantic population to each south Florida sampling zone (and month in Zone 3). Zone 3 samples were collected in December (3D), January (3J), February (3F), and March (3M).

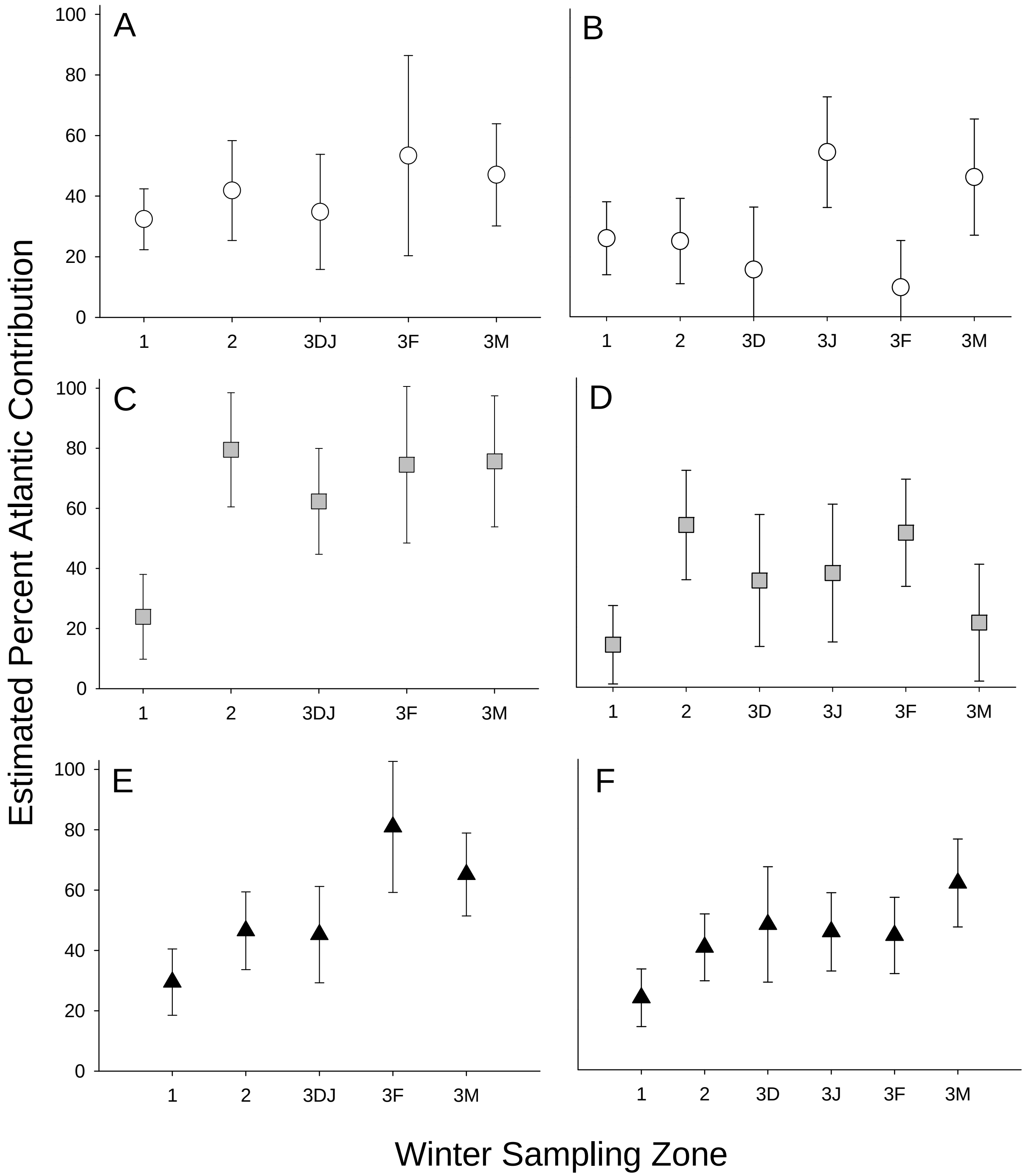

Figure 7. Mean (±SE) otolith chemistry values for constituents measured in king mackerel otoliths for fish sampled in the Atlantic Ocean and Gulf of Mexico during summer 2006 and 2007. Labels along x-axes indicate stock, sex, and year (e.g., AF06 = Atlantic stock, female, summer 2006).

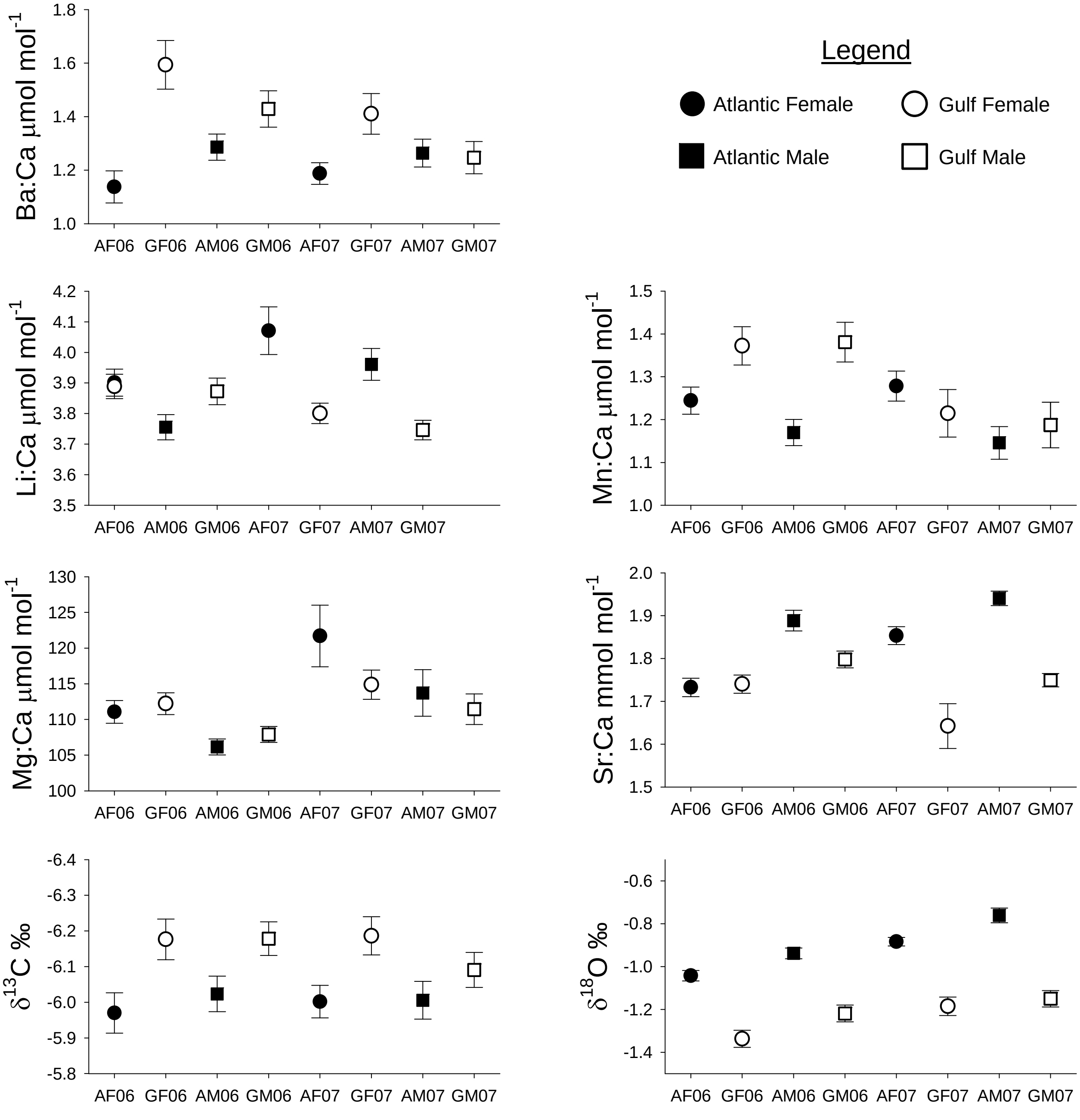

Figure 8. Maximum likelihood (±SE) estimates of the percentage of winter 2006-07 south Florida landings contributed by the Atlantic stock. Models were computed for A) males (Li:Ca, Mg:Ca, Mn:Ca, and δ^{18}O), B) Females (Ba:Ca, Mg:Mn, Sr:Ca, and δ^{18}O), and combined sexes (Ba:Ca, Mg:Ca, Mn:Ca, and δ^{18}O) with the suite of constituents that resulted from stepwise discriminant function analysis of the chemical signatures of summer sampled fish. Models also were computed for D) males, E) females, and F) combined sexes with only stable isotope data (δ^{13}C and δ^{18}O). Winter sampling zones are zones 1-3 shown in Figure 1. 3DJ = zone 3 in December 2006 and January 2007; 3F = zone 3 in February 2007; and, 3M = zone 3 in March 2007.

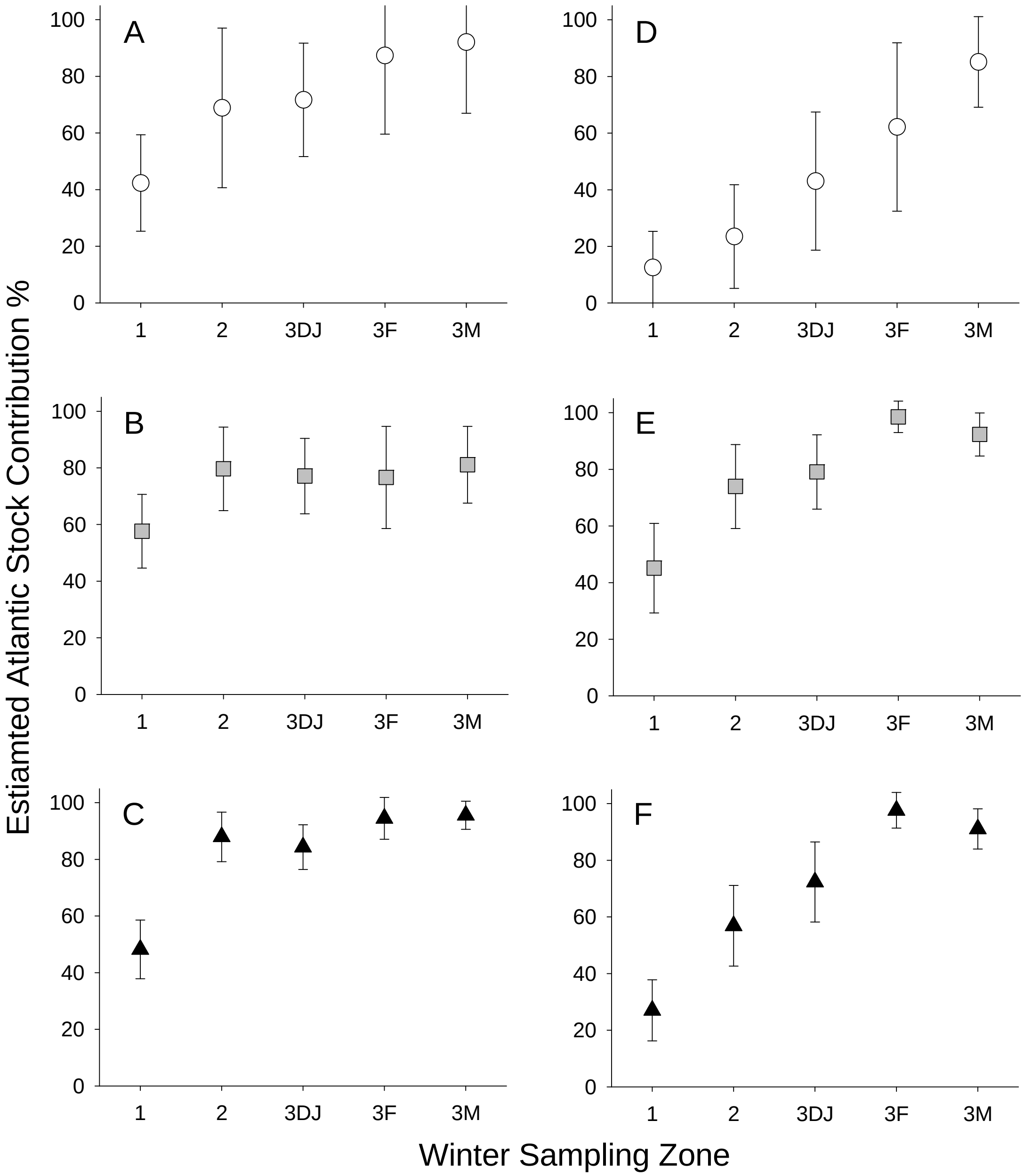

Figure 9. Maximum likelihood (±SE) estimates of the percentage of winter 2007-08 south Florida landings contributed by the Atlantic stock. Models were computed for A) males (Li:Ca, Mg:Ca, Mn:Ca, and $\delta^{18}O$), B) Females (Ba:Ca, Mg:Mn, Sr:Ca, and $\delta^{18}O$), and combined sexes (Ba:Ca, Mg:Ca, Mn:Ca, and $\delta^{18}O$) with the suite of constituents that resulted from stepwise discriminant function analysis of the chemical signatures of summer sampled fish. Models also were computed for D) males, E) females, and F) combined sexes with only stable isotope data ($\delta^{13}C$ and $\delta^{18}O$). Winter sampling zones are zones 1-3 shown in Figure 1. 3D = zone 3 in December 2007; 3J = zone 3 in January 2008; 3F = zone 3 in February 2008; and, 3M = zone 3 in March 2008.