Spatial and temporal variability in the relative contribution of king mackerel (*Scomberomorus cavalla*) stocks to winter mixed fisheries off South Florida

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Abstract—King mackerel (*Scomberomorus cavalla*) are ecologically and economically important scombrids that inhabit U.S. waters of the Gulf of Mexico (GOM) and Atlantic Ocean (Atlantic). Separate migratory groups, or stocks, migrate from eastern GOM and southeastern U.S. Atlantic to south Florida waters where the stocks mix during winter. Currently, all winter landings from a management-defined south Florida mixing zone are attributed to the GOM stock. In this study, the stock composition of winter landings across three south Florida sampling zones was estimated by using stock-specific otolith morphological variables and Fourier harmonics. The mean accuracies of the jackknifed classifications from stepwise linear discriminant function analysis of otolith shape variables ranged from 66–76% for sex-specific models. Estimates of the contribution of the Atlantic stock to winter landings, derived from maximum likelihood stock mixing models, indicated the contribution was highest off southeastern Florida (as high as 82.8% for females in winter 2001–02) and lowest off southwestern Florida (as low as 14.5% for females in winter 2002–03). Overall, results provided evidence that the Atlantic stock contributes a certain, and perhaps a significant (i.e., ≥50%), percentage of landings taken in the management-defined winter mixing zone off south Florida, and the practice of assigning all winter mixing zone landings to the GOM stock should be reevaluated.

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King mackerel (*Scomberomorus cavalla*) are large coastal pelagic scombrids distributed from Massachusetts to Brazil in the western Atlantic Ocean, including the Caribbean Sea (McEachran and Fechhelm, 2005). They support important commercial and recreational fisheries throughout the U.S. Gulf of Mexico (GOM) and in the Atlantic Ocean (Atlantic) off the southeastern United States. King mackerel currently are managed in U.S. waters as two migratory groups, one resident in the GOM and one off the southeast U.S. coast. The two-stock migratory group or two-stock model of population structure was adopted in the early 1980s based on tagging data indicating fish from the respective regions had distinct migratory pathways (Sutter et al., 1991). Subsequent studies demonstrated growth differences (DeVries and Grimes, 1997) and genetic distinctiveness (Gold et al., 1997, 2002) between the stocks.

Assessment and management of U.S. king mackerel stocks is complicated because of the seasonal mixing between GOM and Atlantic fish. Mark-recapture (Sutter et al., 1991) and catch-per-unit-of-effort studies (Trent et al., 1987) have indicated that winter migrations of king mackerel occur from both the eastern GOM and Atlantic to south Florida where the mixed stock is targeted by a winter fishery. Thus, an area that stretches from the Volusia-Flagler county line in northeast Florida to the Monroe-Collier county line in southwest Florida was defined in the early 1980s by the Gulf of Mexico and South Atlantic Fishery Management Councils as a mixing zone between the two stocks (GMFMC and SAFMC, 1985; Fig. 1). From April to October, all king mackerel landings in the mixing zone are attributed to the Atlantic stock, and landings from November through March are attributed to the GOM stock. This somewhat subjective stock assignment system was implemented in an effort to protect the GOM migratory group, which was estimated to be overfished. However, assessment and management are complicated by the presence of both Atlantic and GOM fish in the mixing zone during winter.

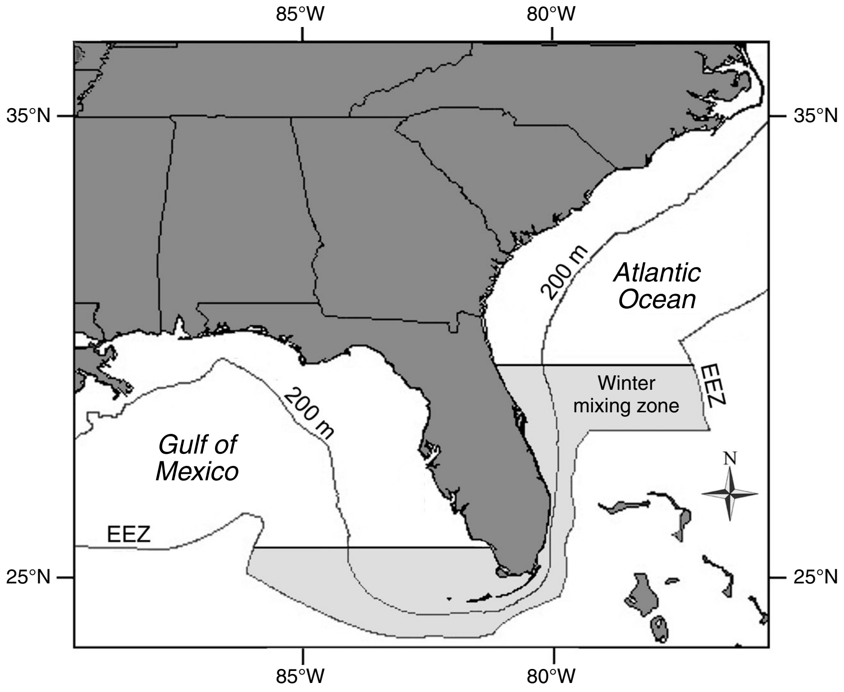

Figure 1

Winter mixing zone established for king mackerel (*Scomberomorus cavalla)* off south Florida. The zone exists throughout the U.S. exclusive economic zone (EEZ) but fish are mostly found over the shelf (200-m isobath). All landings taken from the zone from November through March are attributed to the Gulf of Mexico stock. During the rest of the year, landings are attributed to the Atlantic stock.

Accurate estimation of the contribution of each stock to winter landings is necessary for effective management and conservation. Several different techniques to distinguish these two groups have been explored in various studies. Tagging studies support the current two-stock management approach but have not resolved winter inter-stock mixing proportions. Likewise, although studies of population genetics have confirmed that genetically distinct Atlantic and GOM stocks exist, genetic divergence between the two stocks is weak; thus differences are not robust enough to distinguish winter landings effectively (Broughton et al., 2002; Gold et al., 2002).

Analysis of otolith shape has proven to be a useful technique for stock discrimination in several marine teleosts (e.g., Atlantic cod, *Gadus morhua* [Campana and Casselman, 1993]; Atlantic salmon, *Salmo salar* [Friedland and Reddin, 1994]; and haddock, *Melanogrammus aeglefinus* [Begg et al., 2001]). DeVries et al. (2002) demonstrated that otolith-shape parameters effectively distinguish Atlantic and GOM female king mackerel; classification accuracies from linear discriminant function models ranged from 65.8% to 85.7%. They applied otolith-shape variables as natural markers to estimate the stock identity of female king mackerel landed between Cape Canaveral and West Palm Beach, Florida, in winter 1996–97. A maximum likelihood model parameterized with stock-specific otolith-shape data revealed that Atlantic fish represented 99.8% of the composition of winter mixed fishery landings, thus casting doubt on the management practice of attributing all winter mixing zone landings to the GOM stock.

The objective of this study is to employ otolith-shape analysis to examine temporal and spatial variability in the Atlantic and GOM stock contribution to king mackerel landings around during winter around the southern tip of Florida. We build on the earlier success of DeVries et al. (2002) by examining sex-specific differences in otolith shape and by estimating the contribution of both Atlantic males and females to landings in the winter mixing zone. Temporal and spatial variability in stock mixing also is examined by estimating the Atlantic stock contribution to landings in three south Florida sampling zones distributed across the winter mixing area during two consecutive winters.

Materials and methods

King mackerel were sampled from recreational landings caught in eastern GOM and U.S. south Atlantic waters from April to October 2001 and 2002 when stock distributions did not overlap (Fig. 2); nearly all samples came from summer (June through September) months. Fish were measured to the nearest cm fork length (FL) and sex was determined by macroscopic examination of gonads. When possible, both sagittal otoliths were removed from fish, but for some samples only one sagitta was available. Once extracted, otoliths were cleaned of adhering tissue and placed in plastic vials for storage. Age of fish was estimated by examining whole otoliths for fish less than 80 cm FL and thin sections were prepared for aging larger fish (DeVries and Grimes, 1997). Stratified random sampling was employed once all samples were aged to select up to 15 fish from each of five age categories: ages 2, 3, 4, 5, and 6 years. This age range was selected because winter landings typically are of small, young fish.

King mackerel also were sampled from commercial and recreational landings from three different zones off south Florida from December 2001 to March 2002 and December 2002 to March 2003 (Fig. 2). Zone 1 represented southwest Florida and primarily consisted of samples from the commercial gillnet fishery near and to the east of the Dry Tortugas. Zone 2 represented south central Florida and consisted of samples from the recreational charter boat fishery operating south of Islamorada in the Florida Keys. Zone 3 represented southeast Florida and primarily consisted of samples from the commercial troll fishery from Sebastian Inlet to south of West Palm Beach, Florida. Collection and aging procedures for winter fish otoliths followed the same protocol as summer sampling.

Left sagittal otoliths were digitized sulcus side down with an image analysis system running Image-Pro image analysis software (vers. 4.5, Media Cybernetics Inc., Bethesda, MD). Otolith samples were magnified by 13× with a dissecting microscope before their images were captured with the image analysis system. When left otoliths were damaged or unavailable, right otoliths were digitized and their mirror images were used for shape analysis (DeVries et al., 2002). The autotrace feature in Image Pro then was used to trace the posterior surface of the otolith. Otolith tracing began at the tip of the antirostrum, was directed manually across the base of the rostrum, and then the software traced the posterior portion of the otolith. Thus, rostra were excluded from otolith-shape analysis because the anterior rostrum is fragile and often was broken during otolith collection (DeVries et al., 2002).

Fourier coefficients were computed with an algorithm within Image-Pro, and we used the mathematically determined centroid as the center of an otolith. The Image-Pro algorithm used 128 vectors at equally spaced polar angles to create an accurate picture of the otolith outline. The amplitudes of the first 20 Fourier harmonics were calculated for analysis because each additional harmonic provides increasingly finer detail of the otolith outline. For example, 97–99% of otolith-shape variability in haddock (*Melanogrammus aeglefinus*) is contained in the first ten harmonics (Begg and Brown, 2000). Fourier amplitudes were standardized to remove the effect of otolith size by dividing each amplitude by the mean radial length of the otolith. In addition to the first 20 standardized Fourier harmonics, the Image-Pro software calculated otolith area, perimeter, rectangularity, circularity, and roundness for a total of 25 shape variables. All variables were tested for univariate normality with the Shapiro-Wilks statistic and for homogeneity of variance with an F_{max} test. Transformations were necessary for perimeter (natural log) and Fourier harmonics 13–16 (square-root) in order to meet parametric statistical analysis assumptions of normality and homogeneity of variances.

Ontogenetic effects on otolith shape were tested by computing the correlations of shape variables with fish length. Ontogenetic effects were removed from each shape variable that was significantly correlated with fish length by subtracting the slope of the least squares linear relationship between length and a given variable. Slope-corrected data were used in all subsequent analyses.

Multivariate analysis of variance (MANOVA) was performed to test for potential shape differences between sides in a subset of 50 left and right sagittal otolith pairs (SAS, vers. 6.11, SAS Inst., Inc., Cary, NC). A second MANOVA also was performed to test for stock-specific differences in summer samples. The effect of other factors, including sex, age, and sampling year, on otolith shape parameters also was tested within this second MANOVA.

Stepwise linear discriminant function (LDF) analysis was performed separately for sexes and years on otolith-shape variables from summer sampled fish with the PROC STEPDISC procedure in SAS. The LDF procedure selected variables that were effective predictors of stock identity. Jackknife cross-validation was used to evaluate the performance of resultant discriminant functions. Classification suc-

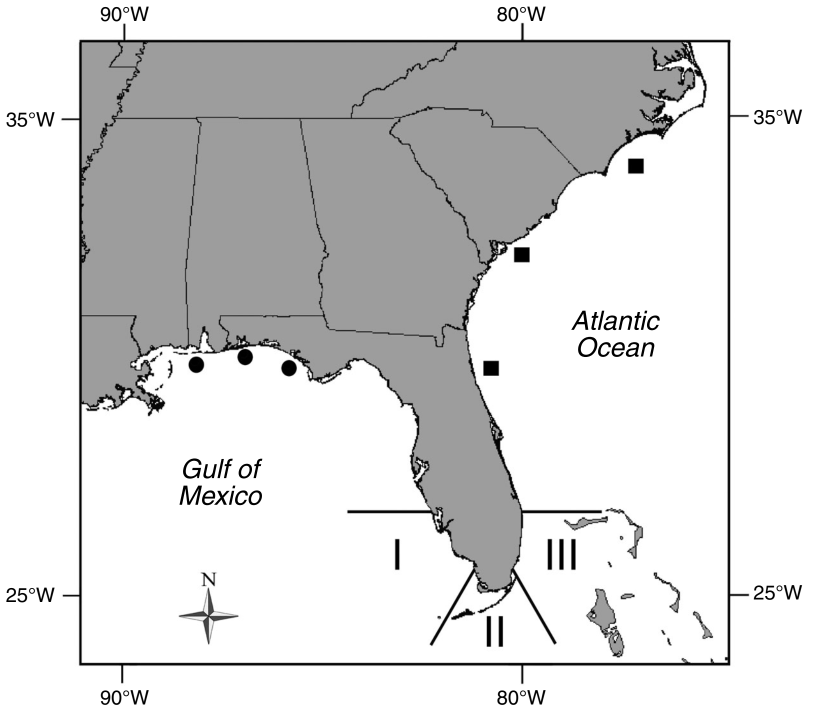

Figure 2

Map of sampling locations for king mackerel (*Scomberomorous cavalla*) in summers 2001 and 2002 in U.S. Atlantic Ocean waters (squares) and the Gulf of Mexico (circles). The map also shows the three winter sampling zones around southern Florida from which fish were sampled in winter 2001–02 and 2002–03 for estimates of the Atlantic stock contribution to winter landings.

cess was estimated as the percentage of individuals correctly classified to stock.

The contribution of the Atlantic stock to winter fishery landings in each winter sampling zone was estimated by using the maximum likelihood (ML) modeling approach described in DeVries et al. (2002). Mixing estimates were calculated for males and females separately by sample year. Otolith-shape variables were used in a two-step expectation-maximization (EM) algorithm written for the S-Plus statistical package (Insightful Corp., Seattle, WA) (Millar, 1987; DeVries et al., 2002). Sex- and year-specific ML models first were parameterized with otolith-shape data from summer-sampled fish. Then, the EM algorithm computed estimates of the percentage of landings within a given winter sampling zone that were members of the Atlantic stock based on their otolith shape parameters. A bootstrap procedure (n=500 bootstraps) was used to compute bias-corrected ninety percent confidence intervals around the maximum likelihood estimate (MLE) of Atlantic stock contribution.

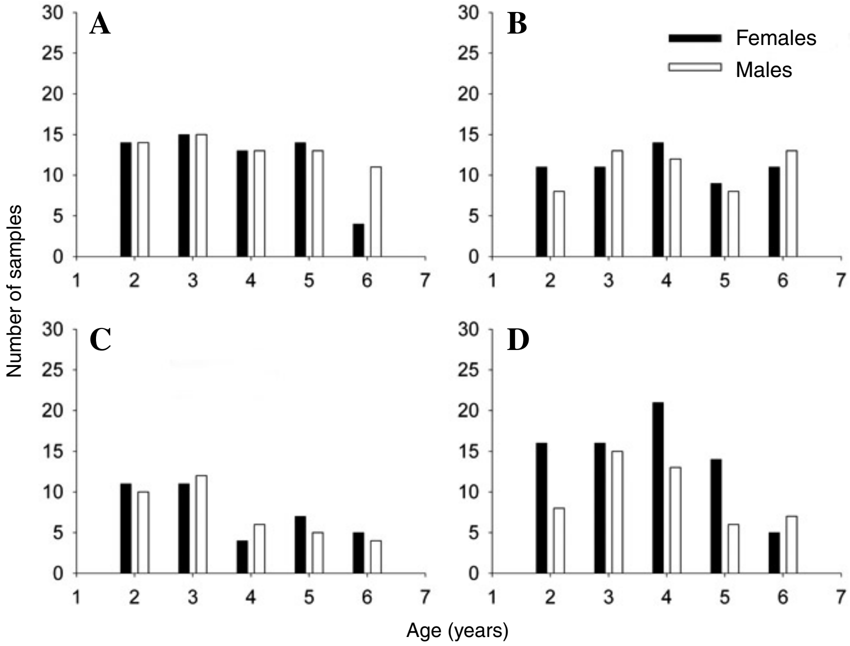

Figure 3

Age distribution of king mackerel (*Scomberomorus cavalla)* in samples collected in summers 2001 and 2002. (**A**) Atlantic 2001; (**B**) Atlantic 2002; (**C**) Gulf of Mexico (GOM) 2001; and (**D**) GOM 2002.

Results

Summer sample sizes differed somewhat between stocks, sexes, and sampling years. One hundred twenty-six king mackerel (60 females, 66 males) were sampled in summer 2001, and 110 fish (56 females, 54 males) were sampled in summer 2002 from Atlantic waters. Seventy-three fish (37 females, 36 males) were sampled in summer 2001, and 120 fish (71 females, 49 males) were sampled in summer 2002 from the GOM. The age distributions of summer-sampled king mackerel generally were similar between sexes, migratory groups, and years (Fig. 3).

Sex-specific sample sizes were more variable from south Florida sampling zones during winter than during summer. In winter 2001–02, 153 fish (85 females, 68 males) were sampled in zone 1, 50 fish (44 females, 6 males) were collected in zone 2, and 142 fish (67 females, 75 males) were sampled in zone 3. In winter 2002–03, 158 fish (85 females, 73 males) were collected in zone 1, 72 fish (50 females, 22 males) were collected in zone 2, and 153 fish (86 females, 67 males) were collected in zone 3. The age distributions of winter-sampled king mackerel were skewed toward younger fish in comparison to summer samples (Fig. 4).

Correlation analysis indicated some ontogentic effects on otolith shape may have been present. Several shape variables were significantly correlated with fish length (area, perimeter, roundness, rectangularity, circularity, Fourier harmonics 1–9, 11–14, 17, 19, and 20); the method described above was applied to remove the correlation of those variables with respect to fish length. MANOVA results indicated there were no significant differences in otolith shape between left otoliths and right otoliths (MANOVA, $P<0.601$).

Morphological features of otoliths proved to be different between stocks, but several other factors also significantly affected otolith shape. Sex and age, as well as stock, significantly affected otolith shape (MANOVA, $P<0.001$), but sampling year did not (MANOVA, $P=0.964$). Six of 25 shape variables were significantly different between sexes (ANOVA, $P<0.05$). Most of the shape differences were in variables that described gross otolith morphological features (area, perimeter, roundness, circularity, and rectangularity), and only one of the significantly different variables was a Fourier harmonic. Twelve of 25 shape variables were significantly different among ages (ANOVA, $P<0.05$), and most of the differences were in Fourier harmonics. Nine of 25 shape variables were significantly different between stocks (ANOVA, $P<0.05$). Most of the stock-specific shape differences were in gross otolith morphological features or low-order Fourier harmonics.

Sex and year-specific linear discriminant functions yielded a range of shape variables selected, and the mean accuracy of classifications ranged from 65.8% to 76.4% among models (Table 1). Discriminant functions included between five and seven variables. The highest classification accuracies from a given model were 71.1% for GOM females and 81.7% for Atlantic females in 2001 (mean accuracy 76.4%). The lowest classification accuracies were 61.2% for GOM males and 70.4% for Atlantic males in 2002 (mean accuracy 65.8%). Classification accuracies were slightly higher for Atlantic fish (67.9–81.7%) than for GOM fish (61.2–71.1%) for most models.

Atlantic stock king mackerel contributed to landings in all three winter sampling zones. Maximum likelihood models estimated that the contribution of Atlantic fish to winter landings ranged from 14.5% for females in zone 1 in 2002 to 99.9% for males in zone 2 in 2001 (Table 2). Bias-corrected bootstrapped 90% confidence intervals varied among zones and between years but generally were on the order of point estimates ±20%. Bootstrap cumulative frequency distributions demonstrated that although the majority of bootstraps fell near point estimates, wide confidence intervals resulted from long upper and lower distribution tails (Figs. 5 and 6).

The estimated contribution of the Atlantic stock to 2001–02 winter landings was similar between males and females among all three winter sampling zones, except for zone 2 where few males were sampled (Table 2). In winter 2002–03, Atlantic females contributed less than males and also had lower contribution estimates than females in 2001–02. Atlantic males had similar contribution estimates during both sampling years. Overall, a gradient in contribution estimates was observed; there were higher Atlantic stock percentages in southeast Florida (zone 3) and declining Atlantic stock presence in southwest Florida landings (zone 1).

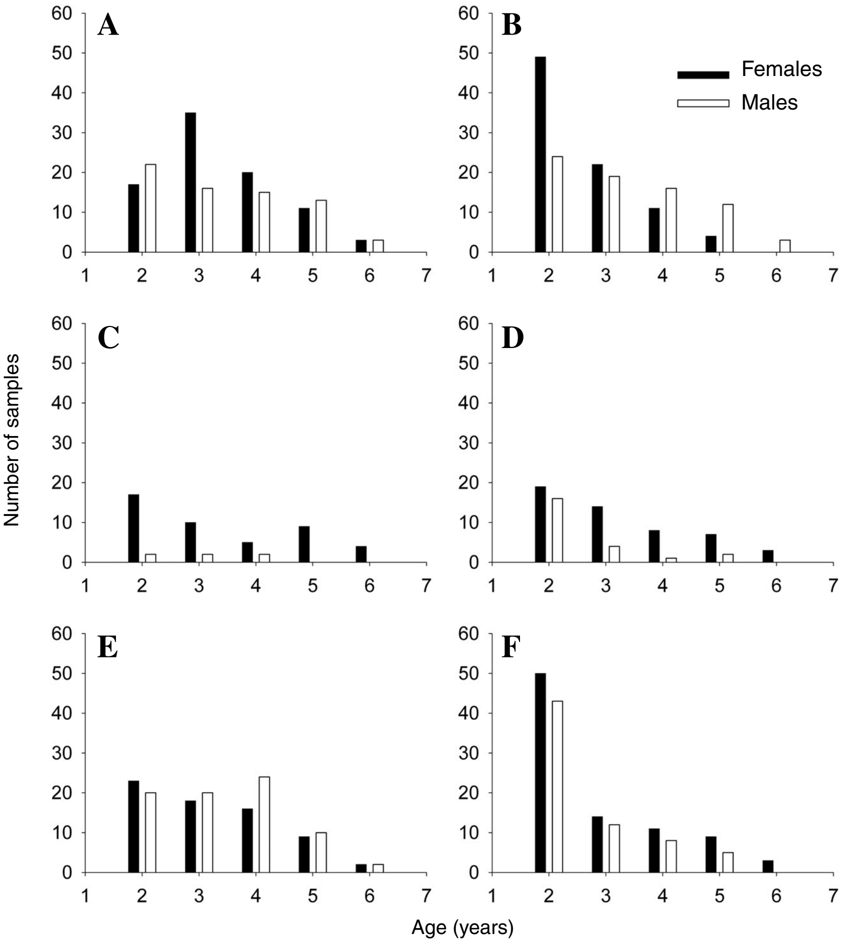

Figure 4

Age distribution of king mackerel (*Scomberomorus cavalla)* in samples collectged in winters 2001–02 and 2002–03. (**A**) = 2001 zone 1 ; (**B**) = 2002 Zone 1 ; (**C**) = 2001 zone 2 ; (**D**) = 2002 zone 2 ; (**E**) = 2001 zone 3 ; and (**F**) = 2002 zone 3.

Discussion

Classification accuracies from stepwise linear discriminant function analysis confirm the feasability of using otolith-shape parameters to distinguish king mackerel stocks but also demonstrate that stock-specific otolith-shape parameters provide natural tags that are far from perfect (i.e., <=100% stock discrimination success). The classification success that we report (61.2% to 81.7%) is similar to the range reported in shape-based stock or population discrimination for other fishes (e.g., 54.9% to 89.3% for lake whitefish, *Coregonus clupeaformis* [Casselman et al., 1981]; 63.9% to 87.5% for Atlantic salmon [Friedland and Reddin, 1994]; 61% to 83% for haddock [Begg et al., 2001]; and, 63.6% to 83.3% for coral trout, *Plectropomus leopardus* [Bergenius et al., 2006], as well as that previously reported by DeVries et al. [2002] for female king mackerel [65.8% to 85.7%]). However, the lack of more distinct differences in otolith shape between stocks likely contributed significantly to the wide confidence intervals estimated

Table 1

Accuracies of jackknifed classifications from stepwise linear discriminant function models computed with otolith shape parameters to estimate summer king mackerel (*Scomberomorus cavalla*) stock identity. The model column identifies which sex- and year-specific models are examined. Numbers in the parameters column represent Fourier harmonics; *Ro* = Roundness, *Re* = Rectangularity, and *P* = Perimeter. Remaining columns indicate the percentage of fish correctly classified to the Atlantic and Gulf of Mexico (GOM) stocks with the jackknife algorithm.

Model	Parameters	Accuracy (%) for Atlantic region	Accuracy (%) for GOM region	Mean accuracy (%)
Females 2001	*Ro*, *Re*, 3, 7, 20	81.7	71.1	76.4
Males 2001	3, 5, 6, 8, 9, 10	69.7	67.6	67.8
Females 2002	*P*, *Ro*, 2, 9, 13, 15, 16	67.9	70.8	69.4
Males 2002	*P*, *Re*, 2, 8, 11, 13	70.4	61.2	65.8

Table 2

Maximum likelihood estimates (MLE) of the contribution (%) of Atlantic stock king mackerel (*Scomberomorus cavalla*) to winter landings in each of three south Florida winter sampling zones by sex and year, with 90% bias-corrected confidence intervals (CI) provided. The model column indicates which zone and year was estimated.

Model	MLE females	90% CI	MLE males	90% CI
Zone 1, 2001–02	61.0	32.2–82.7	61.0	40.2–73.9
Zone 2, 2001–02	48.6	20.1–67.2	99.9	60.9–100.0
Zone 3, 2001–02	82.8	62.8–99.8	76.0	57.0–99.7
Zone 1, 2002–03	14.5	0.0–28.9	45.0	21.2–70.0
Zone 2, 2002–03	41.3	20.9–68.9	83.1	49.4–100.0
Zone 3, 2002–03	40.4	24.2–59.5	71.9	51.5–99.4

from bootstrapped MLEs of Atlantic stock contribution to south Florida winter king mackerel landings. Imprecision in those estimates prohibits more definitive conclusions about the relative contribution of GOM and Atlantic stocks to winter fisheries off south Florida. Nonetheless, it is possible to infer from our results that the Atlantic stock contributes substantially more than the zero percent of winter south Florida landings that is currently assumed by fishery management groups.

Most of the otolith-shape differences between king mackerel stocks were observed in gross morphological variables and low-order Fourier harmonics. Low-order Fourier harmonics are related to general otolith shape, whereas high-order Fourier harmonics are related to increasingly fine-scale variation (Bird et al., 1986). DeVries et al. (2002) reported that gross otolith morphological parameters and low-order Fourier harmonics are significant contributors to otolith-shape variability in female king mackerel in southwest Florida, but they also reported many high-order Fourier harmonics to be significant as well.

Sex effects on king mackerel otolith shape were significant for every gross morphological variable but for only one Fourier harmonic; this results indicates that sex-specific shape differences exist at a general level. Sex effects are not surprising given that sexually dimorphic growth occurs in king mackerel; females achieve higher growth rates than males (Johnson et al., 1983; Manooch et al., 1987; Sturm and Salter, 1989; DeVries and Grimes, 1997). DeVries et al. (2002) examined only female king mackerel as a precaution against potential sex effects due to sexually dimorphic growth observed in this species. Most otolith shape studies that have tested for sex effects have found no significant differences between males and females (Bird et al., 1986; Castonguay et al., 1991; Bolles and Begg, 2000; Begg et al., 2001). In studies where sex effects were significant, other factors were deemed more influential (Campana and Casselman, 1993).

Otolith-shape variables in the models that best classified king mackerel migratory groups were not consistent between sampling years. This result indicates that new shape-analysis models should be developed each summer and used only to estimate the migratory group composition of landings of the next winter. It is unclear why parameters in a discriminant function model may be important one year but of little value in distinguishing stocks the next year. However, interannual variability in growth rates between stocks may explain why LDFs do not perform well from one year to

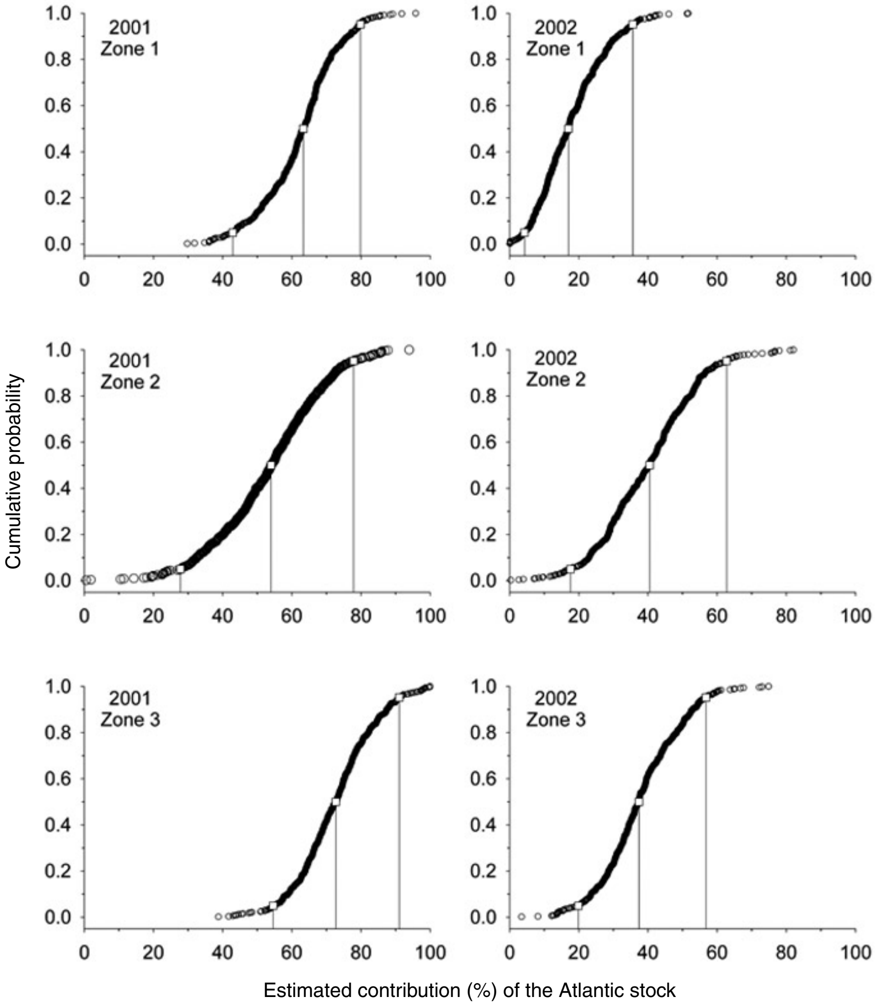

Figure 5

Cumulative probability distributions of bootstrapped estimates of the contribution of Atlantic stock female king mackerel (*Scomberomorus cavalla)* to landings at three south Florida sampling zones. Drop-lines indicate the 5th, 50th, and 95th percentiles of bootstrap distributions.

the next (Campana and Casselman, 1993). For example, cohort-specific discriminant function models computed for coral trout sampled on the Great Barrier Reef did a poor job distinguishing fish from another cohort to sampling region (34.3% to 39.7% classification success), a percentage that Bergenius et al. (2006) attributed to differences in growth rates ultimately caused by variability in oceanographic conditions.

Maximum likelihood estimates indicated that some percentage of winter landings in all three zones originated from the Atlantic stock in both study years. However, bootstrapped confidence intervals indicated considerable imprecision around point estimates. Cumulative probability distributions of bootstraps (n=500) were broad for females and males in both study years. However, even at the lower end of the confidence intervals, Atlantic fish were estimated to have contributed greater than 20% of landings in all three zones, except for females sampled in zone 1 during winter 2002–03.

Results potentially indicate that a distribution gradient may exist; more Atlantic king mackerel may contribute to landings from the Atlantic side (zone 3) and fewer Atlantic stock king mackerel contribute toward the GOM (zone 1). Mixing estimates for zone 2 are somewhere in the middle, with the exception of zone 2 males in 2001–02. However, the sample size of king mackerel in zone 2 in 2001–02 generally was low, particularly for males, and this shortage could account for the higher estimate for the Atlantic stock contribution.

Atlantic male and female king mackerel appear to have had similar contributions across all three south Florida sampling zones in winter 2001–02, but this

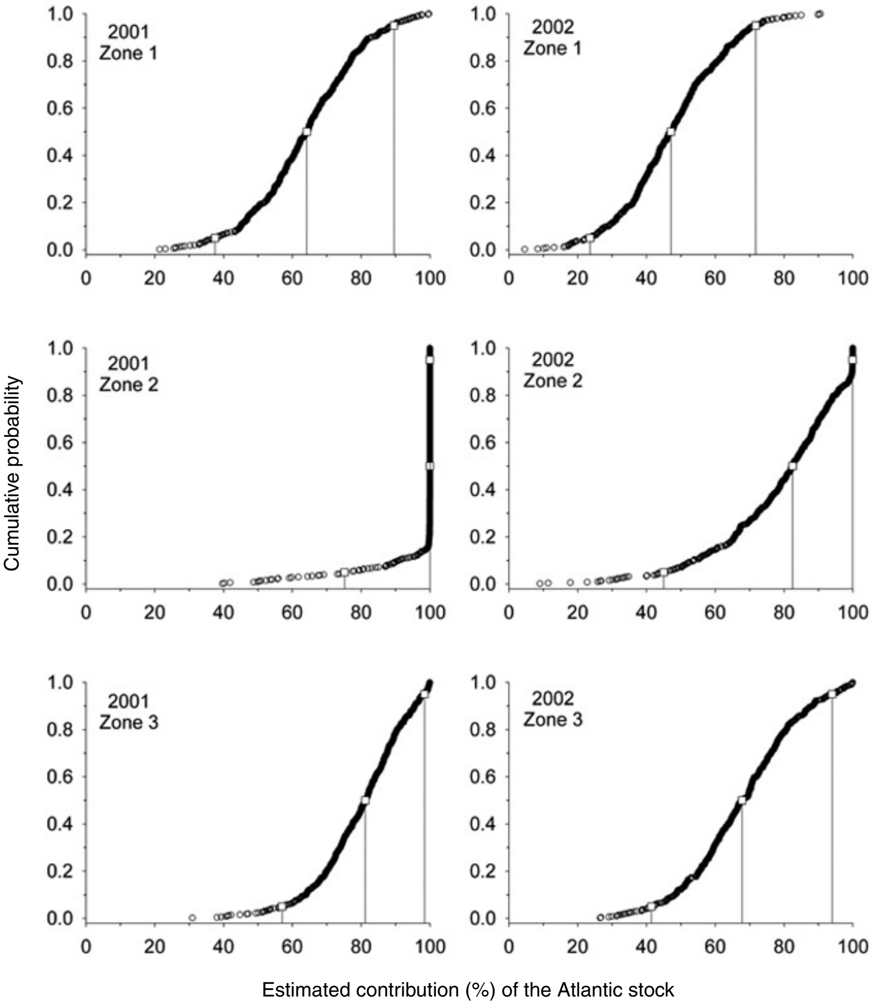

Figure 6

Cumulative probability distributions of bootstrapped estimates of the contribution of Atlantic stock male king mackerel (*Scomberomorus cavalla)* to landings at three south Florida sampling zones. Drop-lines indicate the 5th, 50th, and 95th percentiles of bootstrap distributions.

was not the case in winter 2002–03. Zone 1 and zone 3 in particular showed reductions of 35% and 45%, respectively, in the contribution of Atlantic females in 2002–03. It is unclear why Atlantic females were estimated not to have contributed as significantly to landings in these zones. Differences in classification accuracies between summer 2001 and summer 2002 females may have affected landings contribution estimates, but discriminant function classification accuracies differed by only 7% between years. The reduced contribution of Atlantic females in winter 2002–03 most likely reflects temporal variability in stock mixing.

Overall, results of this study provide further evidence that the U.S. Atlantic king mackerel stock contributes a certain, and perhaps a significant, percentage of landings taken in the management-defined winter mixing zone off south Florida. Based on our results, fisheries managers should consider adopting some form of a gradient approach in attributing south Florida winter landings to GOM and Atlantic stocks. An alternative, and perhaps more easily defended, management approach may be to assign 50% of winter mixing zone landings to the Atlantic stock in the absence of annual estimates of stock-specific landing contributions.

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