

# Age and Growth and Stock Mixing in Gulf of Mexico and Atlantic King Mackerel (*Scomberomorus cavalla*)

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## ABSTRACT

King mackerel, *Scomberomorus cavalla*, is one of the more targeted fishes in the US south Atlantic and Gulf of Mexico (GOM). Accurate assessment of the status of Atlantic and GOM stocks requires comprehensive knowledge of population ecology parameters such as growth and population connectivity. We have been conducting research aimed at improving knowledge of those parameters, with a particular emphasis on estimating population connectivity during winter in south Florida. In summer 2006, we sampled 441 individuals from the Atlantic and 502 from the northeastern GOM. Atlantic fish ranged in size from 90 mm to 1,320 mm and age from 0 to 19 years, while ranges for GOM size and age were 91 mm to 1505 mm and 0 to 20 years, respectively. Von Bertalanffy growth equations computed from otolith-based age estimates were different between stocks and sexes. Otoliths of summer sampled fish were digitized and Fourier analysis of their morphology was conducted to compute stock-specific natural tags based on otolith shape. Otolith shape was significantly different between sexes and stocks (MANOVA,  $p < 0.001$ ). Results of linear discriminant function analysis indicated shape parameters distinguished Atlantic and GOM fish but only with modest classification success (mean jackknifed classification accuracy = 66.0%). Natural tags based on otolith shape parameters then were applied to estimate the stock identity of king mackerel harvested in three regions around southern Florida in winter 2006/07 with maximum likelihood stock mixing models. Results indicated a longitudinal gradient existed in Atlantic stock contribution to winter mixed stock fisheries with highest Atlantic contribution in southeastern Florida and lowest in southwestern Florida. Overall, our results provide further evidence that the practice of assigning all south Florida winter landings to the GOM stock is not accurate and should be re-evaluated.

KEY WORDS: Otolith shape analysis, Fourier harmonics, stock mixing

## Edad y Acrecentamiento y Acción Mezclando en Golfo y Atlántico Rey Mackerel

Rey caballa, *Scomberomorus cavalla*, es uno de los más orientados peces en los EE.UU. al sur del Atlántico y el Golfo de México (GOM). La evaluación precisa de la situación de las poblaciones del Atlántico y GOM requiere amplio conocimiento de la ecología de la población, tales como los parámetros de crecimiento de la población y la conectividad. Hemos estado llevando a cabo investigaciones dirigidas a mejorar el conocimiento de los parámetros, con un énfasis particular en la estimación de la población de conectividad en invierno en el sur de la Florida. En el verano de 2006 nos muestra 422 personas en el Atlántico y 501 del noreste de GOM. Atlántico peces tenían entre 90 mm a 1320 mm y la edad de 0 a 19 años, mientras que las gamas de GOM tamaño y edad fueron 91 mm a 1505 mm y 0 a 20 años, respectivamente. Von Bertalanffy de crecimiento calculada a partir de ecuaciones otolith basada en estimaciones de la edad son diferentes entre las poblaciones y sexos. Otoliths verano de los peces muestreados se digitalizaron y análisis de Fourier de su morfología se realizó para calcular población de peces, natural de las etiquetas basadas en otolith forma. Otolith forma fue significativamente diferente entre los sexos y las existencias (MANOVA,  $p < 0.001$ ). Resultados del análisis de la función discriminante lineal de la forma indicada parámetros distinguido GOM Atlántico y peces, pero sólo con modesto éxito la clasificación de los gastos (media jackknifed clasificación exactitud = 66,0%). Natural etiquetas otolith forma sobre la base de parámetros entonces se aplicaron para estimar la identidad de las poblaciones de caballa rey cosechadas en tres regiones de todo el sur de la Florida en el invierno 2006/07 con la máxima probabilidad de existencias modelos de mezcla. Estos resultados indican un gradiente en Atlantic existencias contribución a la pesca un balance mixto de invierno existe con mayor contribución del Atlántico, en el sudeste de Florida, y la más baja en el sudoeste de Florida. En conjunto, estos resultados proporcionan una prueba más de que la práctica de asignar a todos los desembarques de invierno a la GOM balance no es exacta y debe evaluarse de nuevo.

PALABRAS CLAVES: Otolith análisis de la forma, los armónicos de Fourier, Von Bertalanffy crecimiento funciones

## INTRODUCTION

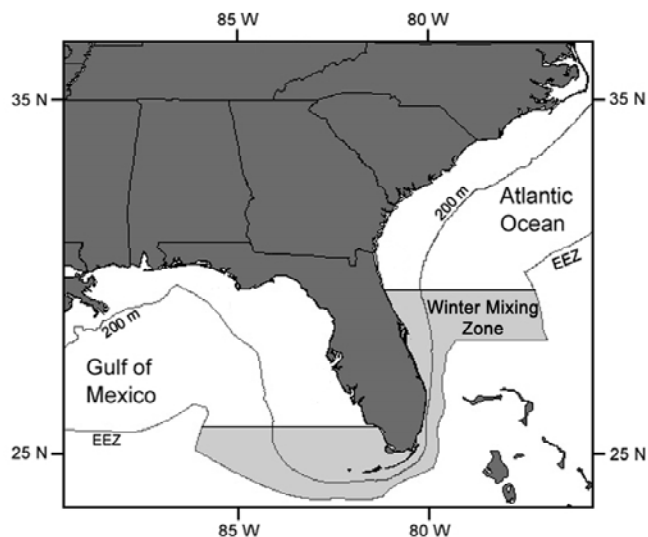
King mackerel, *Scomberomorus cavalla*, are migratory coastal pelagic fish that support significant fisheries in the US Gulf of Mexico (GOM) and south Atlantic. They are moderately long-lived fish whose growth patterns differ among Atlantic, eastern GOM (EGOM), and western GOM (WGOM) contingents (DevVries and Grimes 1997). In fact, differences in growth functions for fish sampled in those three regions between 1977 and 1992 was part of the rationale provided by DeVries and Grimes (1997) that three distinct king mackerel migratory groups exist in US waters. Further

evidence of three distinct migratory groups comes from tagging data that demonstrate WGOM fish migrate southwestwardly in winter, sometimes into Mexican waters, while EGOM fish migrate to the southeast in winter and mix with migrating Atlantic fish in south Florida (Fable 1990, Sutter *et al.* 1991). Despite clear differences in growth and migration pathways that indicate the presence of three distinct king mackerel populations, or migratory groups, population genetic analyses have only shown significant differences exist in haplotype frequencies between Atlantic and GOM fish but none between the two GOM migratory groups (Gold *et al.* 1997, 2002).

Atlantic and GOM king mackerel stocks are jointly managed by the Gulf of Mexico and South Atlantic Fishery Management Councils under the Coastal Pelagics Management Plan (CPMP) (GMFMC and SAFMC 1983). Originally, all king mackerel in US waters were treated as a single stock, but the current management paradigm of two migratory groups (GOM and Atlantic), or stocks, was implemented with Amendment 1 to the CPMP based on tag recapture data (GMFMC and SAFMC 1985, Sutter *et al.* 1991). Subsequent genetic analyses confirmed GOM and Atlantic fish are genetically distinct, although differences between them are weak (Gold *et al.* 1997, Gold *et al.* 2002).

King mackerel fisheries management under the two stock model is complicated due to the separate migratory pathways of EGOM and WGOM king mackerel populations and the fact that Atlantic and EGOM populations mix in winter off south Florida. For management purposes, a winter mixing zone off southeast Florida was specified under the CPMP to assign stock identity to mixed-stock landings captured there (Figure 1). Landings taken in this zone from December 1 to March 31 are attributed to the GOM stock, despite information that the Atlantic stock likely contributes a significant percentage of winter landings taken there (DeVries *et al.* 2002, Fable 1990, Patterson *et al.* 2004, Sutter *et al.* 1991). This convention was adopted in the 1980s when the GOM stock was estimated to be overfished and undergoing overfishing such that conservative winter fishery regulations might protect the recovering GOM stock. Subsequent simulation analyses indicated that attributing landings to the GOM stock that were actually contributed by the Atlantic lead to overestimation of GOM stock health and, perhaps, to non-conservative setting of total allowable catch (Legault 1998).

Recent applications of stock-specific natural tags based on king mackerel otolith morphometrics and otolith chemistry to estimate Atlantic stock contribution to mixed-stock fisheries have indicated the current practice of assigning all winter mixing zone landings to the GOM stock is inaccurate and should be re-evaluated (DeVries *et al.* 2002, Patterson *et al.* 2004). The main objective of the current study was to estimate temporal and spatial variability in the contribution of the Atlantic stock to landings taken in three sampling zones around south Florida in winter 2006–2007 with otolith shape analysis. Results effectively extend the time series of winter mixing estimates and allow for examination of interannual variability in mixing estimates. This work is part of a larger study examining temporal and spatial variability in population demographics and mixing between GOM and Atlantic king mackerel populations, and preliminary inter-population growth comparisons also are presented herein.



**Figure 1.** Map of the southeastern USA that indicates the king mackerel winter mixing zone specified by the Coastal Pelagics Management Plan of the Gulf of Mexico and South Atlantic Fishery Management Councils. The seaward boundary is the edge of the exclusive economic zone, but most fish occur and are caught over the shelf (200 m isobath).

## METHODS

Fish were sampled from the northern GOM ( $n = 502$ ) and US south Atlantic ( $n = 441$ ) in summer 2006 when stocks were separate (Figure 2). Juveniles and adults smaller than the legal size limit, as well as legal sized fish, were caught on fishery-independent research cruises. Fish above the legal limit were sampled from recreational charter boat landings, and large fish were sampled at fishing tournaments. Winter samples were collected from three south Florida sampling zones in winter 2006 - 2007 (Figure 2). All winter samples came from the landed catch of various commercial and recreational fisheries operating around southern tip of Florida.

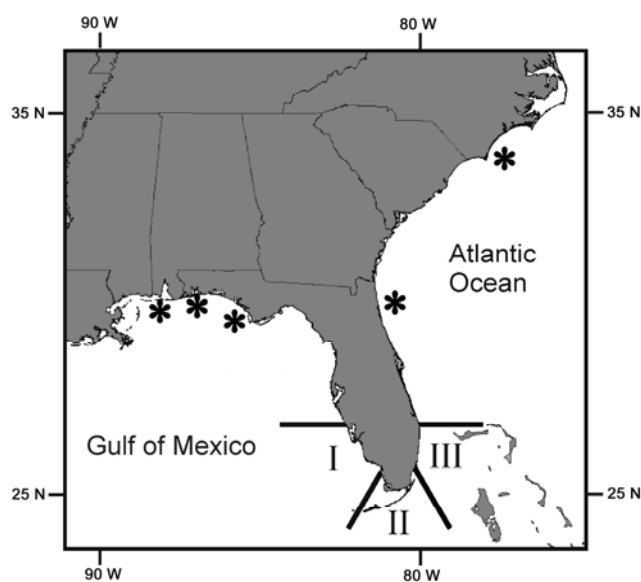
We measured the fork length (FL), determined the sex, and removed both sagittal otoliths for all sampled individuals. Otolith aging analysis was performed according to the methods of DeVries and Grimes (1997). Otoliths from males longer than 800 mm FL and females longer than 900 mm FL were sectioned for aging, while opaque zones were counted in whole otoliths of fish shorter than those lengths. Stock- and sex-specific von Bertalanffy growth functions (VBGF) were fitted to fish size at age data with Proc NLIN in SAS (SAS Institute, Inc. 1996):

$$L_t = L_\infty (1 - e^{-k(t-t_0)}) \quad (1)$$

Where:

- $L_t$  = estimated length at age  $t$ ,
- $L_\infty$  = asymptotic length,
- $k$  = growth coefficient,
- $t$  = age in years, and
- $t_0$  = hypothetical age at zero length.

Otolith shape analysis was performed with Image Pro<sup>®</sup> 6.0 image analysis software. The distal lateral surface of each otolith was magnified 7x and a high-resolution digital image was captured with an image analysis system. Left otoliths were analyzed whenever possible; however, the right otolith was used and the image reversed when the left otolith was damaged (Friedland and Reddin 1994). Otolith contours were digitized with the auto-trace feature in Image Pro. The rostrum of king mackerel otoliths is fragile and often broken during extraction, thus a vertical line was drawn toward the ventral edge from the tip of the anti-rostrum and only the posterior portion of the otolith was used to calculate shape descriptors (DeVries *et al.* 2002).



**Figure 2.** Sampling locations (\*) for king mackerel sampled in summer 2006 from US northern GOM and south Atlantic waters. South Florida winter sampling zones (I-III) also are labeled.

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Image Pro automatically measured otolith morphometric descriptors: area, perimeter, length, width, and roundness. These measurements were used to calculate indices of circularity, ellipticity, and rectangularity:

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

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

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

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

Several steps are involved in computing Fourier harmonics. First, a number of radii are drawn from the calculated centroid of the otolith to coordinates along the contour at regular angular intervals. The radii then are unrolled from a distinct landmark and the radii lengths are plotted against the angle at which they were drawn. A cosine wave is fitted to the undulation in radii lengths. Successively higher frequency cosine waves are added to the first to explain radii length undulation in finer detail (Campana and Casselman 1993). Each cosine wave added to the Fourier series is referred to as a harmonic and can be described in terms of its amplitude and phase angle. The height of radius  $R$  at polar angle  $\theta$  is explained by

$$R(\theta) = A_0 + \sum_{n=1}^{\infty} A_n \cos(n\theta - \phi_n) \quad (6)$$

where  $\theta$  is the angle from the chosen landmark,  $A_0$  is the amplitude of the 0<sup>th</sup> harmonic (the mean radius),

$A_n$  is the amplitude of the  $n^{\text{th}}$  harmonic, and  $\phi_n$  is the phase angle of the  $n^{\text{th}}$  harmonic (Bird, *et al.* 1986).

Phase angles are difficult to normalize for use in statistical comparisons. Therefore, studies of Fourier harmonics typically only use the amplitudes (Campana and Casselman 1993). In this study, Fourier amplitudes were calculated from the digitized contour with the Radial Fast Fourier Transformation macro in Image Pro. The first 20 harmonics were retained for subsequent statistical analysis.

Fish size and age can confound otolith shape-based stock discrimination because otolith shape is determined by the rate of deposition, which is related to somatic growth. Several precautions were taken to control for these effects. First, only individuals from two to six years old were included in shape analysis. This age range was selected because nearly 90% of the landed catch is less than or equal to 6 years old (Patterson *et al.* 2004). Second, all shape variables for a given otolith were standardized by dividing them by the otolith's mean radius. Lastly, any

significant correlations that existed between standardized variables and FL were removed by subtracting the slope of the linear relationship between the variable and FL.

We tested for significant sex and stock differences in otolith morphology with multivariate analysis of variance (MANOVA). Morphometric variables, shape indices, and harmonic amplitudes from summer samples then were used to compute sex- and stock-specific stepwise linear discriminant functions with Proc STEPDISC in SAS. Variables entered and retained by the stepwise discriminant function models were used to re-compute linear discriminant functions with Proc DISCRIM (SAS Institute, Inc. 1996) such that the crossvalidate option could be used to compute jackknifed classification success rates for each model. Maximum likelihood models were parameterized in S-Plus® (version 6.0) with the variables selected by the stepwise model building algorithm and applied to the mixed winter samples to estimate the percentage of winter landings contributed by the Atlantic stock to each winter sampling zone. Bootstrapped 90% confidence intervals were computed around point estimates (DeVries *et al.* 2002).

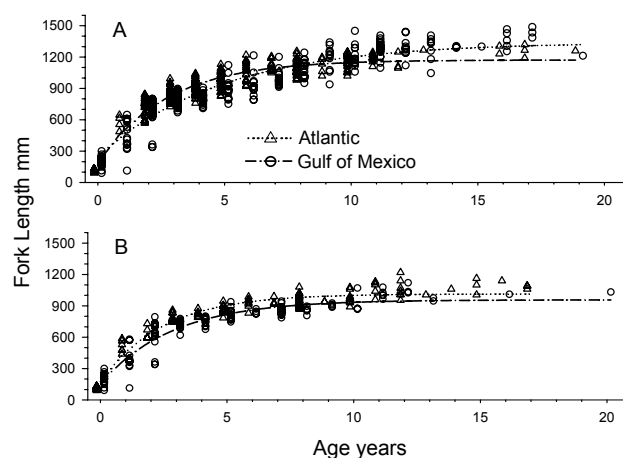
## RESULTS

A total of 943 king mackerel was sampled and aged in summer 2006; 441 from the Atlantic and 502 from the GOM. Size at age data demonstrate GOM females achieved greater lengths than did Atlantic females, while differences in males were less distinct (Figure 3). The estimated value of  $L_{\infty}$  was greater for GOM females than Atlantic females, but  $k$  and  $t_0$  were greater in the Atlantic (Table 1). Point estimates for all VBGF parameters were greater in Atlantic versus Gulf males, although the confidence limits around estimates of  $k$  overlap.

Shape analysis was performed on 377 summer-sampled fish that met the age criterion (ages 2 - 6; Table 2). There were significant difference in otolith morphology between sexes and stocks (MANOVA;  $p < 0.001$ ).

Shape variables retained in models included roundness, circularity, and harmonics 3, 4, 12, 15, 16, 18 for females; harmonics 4, 9, 14, and 17 for males; and, harmonics 4, 5, 10, 12, 15, and 16 for the combined sex model. Stepwise discriminant function models resulted in mean jackknifed classification accuracies of 64.5%, 71.9%, and 61.9% for female, male, and combined sex models.

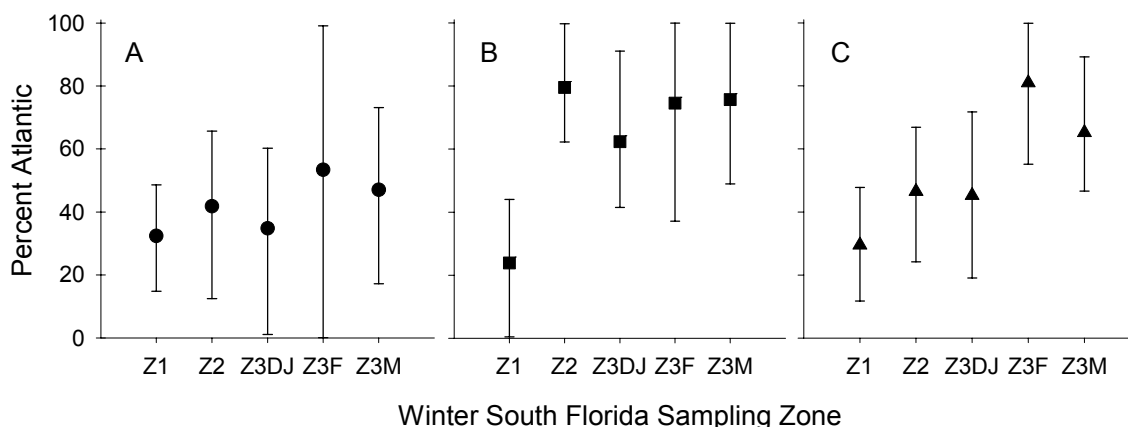
A total of 588 individuals was sampled among our south Florida sampling zones in winter 2006/07, with zone 3 being sampled monthly across the winter mixing period (Table 2). Estimates of Atlantic stock contribution to winter landings were lowest in zone 1, the westernmost zone, and highest in zone 3, the easternmost zone, regardless of the model (Figure 4).



**Figure 3.** Size at age data from king mackerel sampled in the Atlantic and northern Gulf of Mexico during summer 2006. Integer ages are offset by 0.15 years for viewing. Fitted lines are von Bertalanffy growth functions for (A) females and (B) males of each population. Function parameters are provided in Table 1. The legend applies to both panels.

**Table 1.** Estimated von Bertalanffy growth function parameters for GOM and Atlantic male and female king mackerel sampled in summer 2006.

Population	Parameter	Point Estimate	95% Confidence Limits
GOM Females (n=359)	$L_{\infty}$	1341.4	1298.6 – 1384.3
	$k$	0.2042	0.182 – 0.226
	$t_0$	-1.1729	-1.401 – -0.944
Atlantic Females (n=301)	$L_{\infty}$	1172.1	1150.9 – 1193.2
	$k$	0.3671	0.343 – 0.391
	$t_0$	-0.3455	-0.433 – -0.258
GOM Males (n=143)	$L_{\infty}$	956.8	921.8 – 991.8
	$k$	0.3528	0.303 – 0.403
	$t_0$	-0.6817	-0.846 – -0.518
Atlantic Males (n=140)	$L_{\infty}$	1013.6	994.8 – 1032.5
	$k$	0.4096	0.373 – 0.446
	$t_0$	-0.3360	-0.417 – -0.256



**Figure 4.** Maximum likelihood estimates of the percentage of (A) female, (B) male, and (C) combined king mackerel landings contributed by the Atlantic stock to each south FL sampling zone (Z1=Zone 1, Z2=Zone 2, Z3DJ=Zone 3 Dec and Jan, Z3F=Zone 3 Feb, and Z3M=Zone 3 Mar). Intervals bracketing point estimates are 90% bootstrapped confidence intervals.

**Table 2.** King mackerel sample sizes utilized in sex-specific and combined sex linear discriminant function analysis models (summer samples only), and samples sizes from south Florida winter sample zones.

Time/Location	Female	Male	Combined
Summer GOM	155	51	206
Summer Atlantic	133	38	171
Winter Zone 1 Jan	118	54	172
Winter Zone 2 Jan	74	61	135
Winter Zone 3 Dec and Jan	57	47	104
Winter Zone 3 Feb	25	31	56
Winter Zone 3 Mar	59	62	121

## DISCUSSION

Otolith aging was an important component of this study, but growth functions computed from size at age data should be viewed as preliminary due to small sample sizes. That caveat aside, preliminary VBGFs presented here suggest GOM and Atlantic king mackerel growth functions have not changed appreciably since the early 1990s (DeVries and Grimes 1997). With the exception of the Atlantic males, point estimates of  $L_{\infty}$  were slightly higher and  $k$  and  $t_0$  were slightly lower for each of the growth functions relative to historic values reported by DeVries and Grimes (1997), but that pattern likely resulted from greater numbers of age-0 fish in our data set that led to a better fit of  $t_0$  rather than actual changes in growth dynamics (Fischer *et al.* 2004). Overall, our results are fairly consistent with the functions reported by DeVries and Grimes (1997). Data presented here suggest female king mackerel of both populations reach greater lengths than males, and GOM females reach larger sizes than Atlantic fish. Both of those findings are consistent with the older growth models. The Atlantic male  $L_{\infty}$  estimate being

greater than that for GOM males likely is a function of small sample size rather a difference in growth between populations, but additional samples are required to address that issue.

Otolith shape discriminant function classification success rates that we report (mean 66.0%) are similar but slightly lower than those reported by DeVries *et al.* (2002) (average 74.5%) and Patterson *et al.* (2004) (average 68.5%). This low classification success indicates otolith shape may not be a robust natural tag of king mackerel stocks. Furthermore, this imprecision was manifested in wide bootstrapped confidence intervals around point estimates of Atlantic stock contribution to mixed-stock landings among south Florida winter sampling zones. While otolith shape analysis may not be the most robust technique for estimating the composition of winter landings (Patterson *et al.* 2004), certain advantages do make it a valuable tool nonetheless. Shape analysis is significantly less expensive and time consuming than methods involving chemical analysis or artificial tagging. Contamination also is not a concern as it is with otolith chemistry applications. Otolith shape can only be altered by breakage, but broken otoliths are easily identified and removed from the sample.

The pattern of spatial variation we report in estimated Atlantic stock contribution to landings across the latitudinal gradient of winter sample zones is consistent with previous estimates based on otolith shape analysis. DeVries *et al.* (2002) estimated that 99.8% of females sampled off southeastern Florida in winter 1996/97 were derived from the Atlantic stock. Patterson *et al.* (2004) sampled the same three winter sampling zones as in the current study, with zone 3 corresponding to the sampling area of DeVries *et al.* (2002). They reported that estimated Atlantic stock contribution to winter landings increased from west to east across south Florida, which was consis-

tent between sexes and years. In both years of their study, zone 3 Atlantic contribution estimates were substantially lower than the 99.8% reported by Devries *et al.* (2002). From the 2006/2007 mixed winter fishery, we report there also was a general increase in the percentage of Atlantic stock landings from west to east across the sampling zones. That pattern is most evident in estimates from the model of combined male and female data.

The fact that confidence intervals around point estimates of Atlantic stock contribution were affected by the classification accuracy of stock-specific shape parameters and by sample size also is evident in results from winter sampling zones. For example, although jackknifed classification accuracies were lowest for the combined sex model, narrower confidence intervals relative to the female model likely resulted from increased sample size. Additionally, females sampled from zone 3 in February 2007 had a low sample size ( $n = 25$ ) and the summer 2006 female shape data did a relatively poor job of distinguishing Atlantic from GOM fish. The result was a point estimate of 50% Atlantic stock contribution and a confidence interval from zero to 100.

Monthly sampling in zone 3 during winter 2006/2007 allowed us to examine temporal variability in estimated Atlantic stock contribution to king mackerel landings across the months when all mixing zone landings are attributed to the GOM stock. In general, and as expected *a priori*, zone 3 had the highest estimated Atlantic stock contribution among the three zones. Unfortunately, samples sizes in December were too small to analyze that month separately. Otherwise, the trend among months was a general increase in Atlantic stock contribution from December/January through March. Point estimates among models ranged from 35 - 59% Atlantic fish in December/January to 43 - 75% Atlantic fish in March samples. One inference that might be drawn from that result is that as waters warm at the end of winter and fish begin to move north to summer areas, a lower percentage of GOM fish are located in waters off southeast Florida. However, it should be reiterated that wide confidence intervals preclude definitive conclusions about the percentage of Atlantic fish in landings sampled in any of the zones in any of the sampling months. Therefore, any trends in point estimates should be interpreted cautiously.

Increased sample sizes and exploration of other techniques may enable more definitive conclusions to be made about king mackerel stock mixing and growth. Data presented here are results from the first year of a two-year study. Additional samples were collected from the GOM and Atlantic king mackerel stocks during summer 2007, and samples also will be collected from the 2007/2008 winter fishery. Age and length data from fish sampled in summer 2006 and 2007 will be combined to compute more robust growth functions for each population, and the time series of shape-based mixing estimates will be continued in 2007/2008 for all winter sampling zones. In addition, the

elemental and stable isotope composition of otoliths from both years will be analyzed to derive natural stock-specific markers based on otolith chemistry. Patterson *et al.* (2004) reported cross-validated classification success was, on average, 9% higher for otolith elemental signature versus otolith shape discriminant function models computed for king mackerel sampled during summer 2001 and 2002. Likewise, they reported confidence intervals around estimates of Atlantic stock contribution to winter landings were narrower for otolith chemistry than for otolith shape models, although trends in Atlantic stock contribution to winter sampling zones were similar between the two approaches. Preliminary data on  $\delta^{18}\text{O}$  and  $\delta^{13}\text{C}$  delta values in king mackerel otoliths suggest classification accuracies might be increased as much as 10% with their inclusion in otolith chemistry signatures (W.F.P, unpublished data). Therefore, we are optimistic that greater accuracy in stock-specific natural tags derived from otolith chemistry will provide greater precision in estimates of Atlantic stock contribution to winter sampling zones in future analyses.

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#### LITERATURE CITED

- Anonymous. 2004. SEDAR5 Stock assessment report South Atlantic and Gulf of Mexico king mackerel. SEDAR5 Assessment Workshop Panel, NOAA, NMFS, SEFSC, Miami Laboratory. Technical Report. 104 pp.
- Bird, J.L., D.T. Eppler, and D.M. Checkley, Jr. 1986. Comparisons of herring otoliths using Fourier series shape analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **43**:1228-1234.
- Campana, S.E., and J.M. Casselman. 1993. Stock discrimination using otolith shape analysis. *Canadian Journal of Fisheries and Aquatic Science*. **50**:1062-1083.
- Conover, D.O. and S.B. Munch. 2002. Sustaining fisheries yields over evolutionary time scales. *Science* **297**:94-96.
- Devries, D.A., and C.B. Grimes. 1997. Spatial and temporal variation in age and growth of king mackerel, *Scomberomorus cavalla*, 1977-1992. *Fishery Bulletin* **95**:694-708.
- Devries, D.A., C.B. Grimes, and M.H. Prager. 2002. Using otolith shape analysis to distinguish eastern Gulf of Mexico and Atlantic Ocean stocks of king mackerel. *Fisheries Research* **57**:51-61.
- Fable, W.A., Jr. 1990. King mackerel, *Scomberomorus cavalla*, mark-recapture studies off Florida's east coast. *Marine Fisheries Review* **56**:13-23.
- Fischer, A.J., M.S. Baker, Jr., and C.A. Wilson. 2004. Red snapper (*Lutjanus campechanus*) demographic structure in the northern Gulf of Mexico based on spatial patterns and morphometrics. *Fishery Bulletin* **102**:593-603.
- Friedland, K.D., and D.G. Reddin. 1994. Use of otolith morphology in stock discriminations of Atlantic salmon (*Salmo salar*). *Canadian Journal of Fisheries and Aquatic Sciences* **51**:91-98.

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- Gold, J.R., A.Y. Kristmundsdottir, and L.R. Richardson. 1997. Mitochondrial DNA variation in king mackerel (*Scomberomorus cavalla*) from the western Atlantic Ocean and Gulf of Mexico. *Marine Biology* **129**:221-232.
- Gold, J.R., E. Pak, and D.A. Devries. 2002. Population structure of king mackerel (*Scomberomorus cavalla*) around peninsular Florida, as revealed by microsatellite DNA. *Fishery Bulletin* **100**:491-510.
- GMFMC and SAFMC. 1983. Fishery management plan, final environmental impact statement, regulatory impact review, final regulations for coastal pelagic resources (mackerels) in the Gulf of Mexico and South Atlantic region. GMFMC, Tampa, Florida and SAFMC, Charleston, South Carolina USA.
- GMFMC and SAFMC. 1985. Final admendment 1, fishery management plan and environmental impact statement for coastal migratory pelagic resources (mackerels) in the Gulf of Mexico and South Atlantic region. GMFMC, Tampa, Florida and SAFMC, Charleston, South Carolina USA.
- Legault, C.M. 1998. What if mixing area fish are assigned to the Atlantic migratory group instead of the Gulf of Mexico group? NMFS SEFC Sustainable Fisheries Division Contribution SFD-97/98-12. Mackerel Stock Assessment Panel Report MSAP/98/08.
- Patterson III, W.F., R.L. Ship, T.R. Clardy, and Z. Chen. 2004. Discrimination among US South Atlantic and Gulf of Mexico king mackerel stocks with otolith shape analysis and otolith microchemistry. Final Report: NOAA MaRFIN NA17FF2013. 33 pp.
- Powers, J.E. 1996. Benchmark requirements for recovering fish stocks. *North American Journal of Fisheries Management* **16**:495-504.
- Smith, M.K. 1992. Regional differences in otolith morphology of the deep slope red snapper *Etelis carbunculus*. *Canadian Journal of Fisheries and Aquatic Sciences* **49**:795-804.
- Sutter, III, F.C., R.O. Williams, and M.F. Godcharles. 1991. Movement patterns and stock affinities of king mackerel in the Southeastern United States. *Fishery Bulletin* **89**:315-324.