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Discrimination Between Gulf of Mexico and Atlantic Ocean King Mackerel with Otolith Shape Analysis and Otolith Microchemistry: A Progress Report

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Abstract

Natural stock-specific tags were developed from otolith shape analysis and otolith microchemistry to discriminate between U.S. Gulf of Mexico (Gulf) and Atlantic Ocean (Atlantic) stocks of king mackerel. Fish were sampled from May through September in 2001 (n = 201) and 2002 (n = 231) from northwest Florida to Dauphin Island, Alabama in the Gulf and from Jacksonville, Florida to southeast North Carolina in the Atlantic. Age was estimated for all individuals by counting the number of opaque zones in whole or sectioned otoliths. One otolith from each fish then was digitized with an image analysis system and its shape characteristics were estimated with Fourier analysis. Linear discriminant function models were computed with shape data using a stepwise modelbuilding algorithm to distinguish samples from each stock. Jackknifed classification accuracies ranged from 65% to 81%, depending if sexes were modeled separately or iointly for each year. Following shape analysis, otoliths were cleaned and dissolved in ultra-pure nitric acid. Their chemical composition (Ba, Ca, Cd, K, Li, Mg, Mn, Na, and Sr) then was analyzed with sector field-inductively coupled plasma-mass spectrometry (SF-ICP-MS). (Note: Analysis of elemental signatures for 2001 samples has been completed but SF-ICP-MS analysis for 2002 samples is ongoing.) Linear discriminant function models were computed for 2001 samples with concentrations of five elements (Ba, Ca, Li, Mg, Mn, and Sr) using a stepwise model-building algorithm. Jackknifed classification accuracies ranged from 89% to 90%, depending if sexes were modeled separately or jointly. Sex-specific maximum likelihood stock mixing models then were parameterized with otolith shape data for each year and with otolith elemental signatures for 2001. Models were applied to shape and chemistry data of winter mixed stock landings sampled from three zones off south Florida to estimate the percentage Atlantic stock in each zone. In 2001, maximum likelihood estimates from otolith shape data indicated a gradient of distribution in both females and males from 80% to 90% Atlantic stock in SE Florida to approximately 60% Atlantic stock in SW Florida. Estimates from otolith elemental signatures ranged from 86% to 21% Atlantic stock across the same zones for females and from 83% to 40% for males. In 2002, winter mixing estimates computed with shape data were not consistent between sexes. Males in our samples were estimated to be 72% Atlantic stock off SE Florida to 46% Atlantic stock off SW Florida, while females were estimated to be 40% Atlantic stock off SE Florida to 15% Atlantic stock off SW Florida. Overall, these results indicate the current management practice of assigning all south Florida winter landings to the Gulf stock may greatly overestimate the contribution of the Gulf stock to winter landings.

King mackerel are large, piscivorus scombrids that occur in the western Atlantic from Massachusetts to Brazil, including the waters of the Gulf of Mexico (Gulf) and Caribbean Sea (Collette and Nauen 1983). Adults display sexual dimorphism with females attaining significantly larger sizes at age than males (DeVries and Grimes 1997). 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 Ocean (Atlantic) and Gulf; however, Gulf 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 Gulf and south Atlantic fish, mixing does occur between purported stocks. Tagging studies conducted in the 1970s and 1980s demonstrated king mackerel in the eastern Gulf and Atlantic migrate along the Florida peninsula in late fall and overwinter in south Florida where gillnet and troll commercial and hook-and-line recreational 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).

Throughout its range king mackerel supports important commercial and recreational fisheries. Concerns over fluctuations and declines in U.S. 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 U.S. waters (GMFMC and SAFMC 1983). Currently, king mackerel in U.S. waters are assumed to constitute two separate stocks (Gulf 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 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" or stocks existed (Powers and Eldridge 1983; Sutter et al. 1991). Subsequent genetic analyses have confirmed that Gulf and Atlantic fish are genetically distinct (Gold et al. 1997; Gold 2002).

The impetus for creating a federal management plan for king mackerel was the perception the species was subjected to overfishing in the 1970s. Regulations were implemented to decrease fishing mortality and increase spawning stock size beginning in the mid 1980s. The Atlantic stock experienced increased spawning stock size through the late 1990s and is estimated to be above its target biomass level (MSAP 2003). Routine overruns of total allowable catch (TAC) coupled with the absence of a clearly defined rebuilding strategy for the Gulf stock, however, resulted in it not recovering above an overfished threshold during the 1990s (MSAP 1999, 2000; Powers 1996)¹. Following the most recent full assessment of Gulf king mackerel, the Mackerel Stock Assessment Panel (MSAP) estimated the stock was not overfished (probability $B_{2002} < B_{MSY} = 24\%$) nor did it experience overfishing in the previous fishing year (probability $F_{2001/02} < F_{MSY} = 50\%$); however, the stock had yet to recover fully from being overfished (i.e., stock biomass remained below B_{MSY}) and fishing mortality remained high (Ortiz et al. 2002; MSAP 2002).

¹Prior to the 2000 MSAP report, overfished was defined for Gulf king mackerel as having a transitional spawning potential ratio (SPR) less than 30%. Currently, overfished is defined as biomass having a greater than 50% probability of being less than the minimum stock size threshold (MSST), which is equal to (1-M)*(B_{MSY}) or 0.8B_{30%SPR}.

As a conservation measure to aid recovery of the overfished Gulf stock, a winter mixing zone in southern 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 (Fig. 2). Although stock mixing was not well understood at the time of its creation, all fish harvested in this area from November through March have since been attributed to the Gulf stock such that management regulations can limit winter mixing zone landings as added protection for that stock. Results of simulation modeling demonstrated, however, that estimates of Gulf stock biomass and health (relative to a benchmark SPR of 30%) actually were overestimated when the Atlantic stock was assumed not to contribute to winter mixing zone landings (Legault 1998). Legault (1998) estimated increasing the percentage of fish in the winter mixing area attributed to the Atlantic stock had no effect on the status of the Atlantic stock (i.e., no effect on transitional SPR), but both its estimated population size and allowable biological catch (ABC) increased as the percentage of fish in the mixing area assigned to it increased. Conversely, the estimated Gulf stock population size and ABC decreased as Atlantic stock contribution to the mixed fishery increased. Worse yet, estimated SPR for the Gulf stock decreased as the percentage of fish assigned to the Atlantic stock increased. The implication of these results for management is that if the Atlantic stock contributes to winter landings off southeast Florida, an ABC recommended for the Gulf stock assuming the present mixing scenario likely would lead to overfishing (Legault 1998). Additionally, an amendment to the CPMP proposed by the SAMFC (Draft Amendment 13, SAMFC 2001) calls for separate management of Gulf and Atlantic king mackerel stocks that would require readdressing current seasonally varying stock boundaries.

To address these issues, several recent studies have examined differences between Gulf and Atlantic king mackerel genetics, otolith shape, and otolith elemental signatures, with the common goal of developing natural markers that could be used to estimate stock identity of mixing zone fish. Gold et al. (2002) reported patterns of genetic variability found in nuclear-encoded microsatellites indicated weakly divergent genetic stocks; however, less than 0.2% of the total genetic variance occurred between stocks. The authors estimated the stock composition of landings from several regions around the southern tip of Florida based on stock-specific microsatellite signatures. They reported roughly half of fish sampled in each region had a Gulf or Atlantic genetic signature regardless of the month samples were taken. These results may indicate the stock composition of winter mixed stock fisheries in all regions around south Florida is evenly split between the two stocks, or, alternatively, microsatellite markers were such weak discriminators that results did not deviate from expectation under random assignment (i.e., a 1:1 ratio of outcomes).

While genetic differences may be insufficient to estimate stock identity of mixing zone landings, recent studies employing otoliths as natural stock markers have shown great promise (DeVries et al. 2002; Patterson et al. unpub. MS). Reasons why otoliths are ideal natural makers of fish populations or stocks are straightforward. Otoliths are calcium carbonate and protein matrices that are deposited in the vestibular system of bony fishes as they grow (Casselman 1987). Otoliths grow or accrete relative to somatic growth and form concentric opaque and translucent zones with which the age of the fish may be estimated; increments in otoliths are deposited sub-daily, daily, and annually. Otoliths are metabolically inert once formed and are never resorbed under natural

conditions (Campana and Neilson 1985; Casselman 1987). Therefore, otolith characteristics that are unique to individual species or stocks have proven to serve as ideal, permanent natural tags.

Differences in otolith morphology have been reported among closely related species (Johnson 1995) and among stocks of single species (Bird et al. 1996; Begg and Brown 2000), and are thought to reflect genotypic variability as well as differential environmental histories and growth rates (Campana and Casselman 1993). These differences have been used as stock-specific natural tags in many species (e.g., Begg and Brown 2000; Bird et al. 1996; Campana and Casselman 1993) and otolith shape analysis recently has been used to discriminate among Gulf and Atlantic king mackerel. DeVries et al. (2002) reported differences in sagittal otolith shape parameters were significant between Atlantic and Gulf females in summer 1996 (when stocks were separate), and developed a quadratic discriminant function (with otolith perimeter, area, and 10 harmonics of Fournier amplitude as independent variables) that classified 71% of Atlantic fish and 78% of Gulf fish accurately. The authors then parameterized a maximum likelihood stock mixing model with the same set of variables to estimate the stock composition of 463 fish sampled during winter 1996/97 off southeast Florida. They estimated 99.8% (SE = 3.4%) of winter samples belonged to the Atlantic stock. Futhermore, the authors concluded results from otolith shape analysis suggested that for management purposes the stocks did not mix off southeast Florida in winter 1996/97.

An equally promising otolith-based approach to estimate movement patterns or stock mixing of adult fishes involves using elemental and isotopic signatures as natural biogeochemical tags of fish from different water bodies, geographic areas, or stocks (Begg et al. 1998; Kennedy et al. 2000; Patterson et al. 1998, 2002; Thorrold et al. 1998, 2001). As otoliths grow minor and trace metals are incorporated into their matrices from the water in which the fish lives (Bath et al. 2000; Hoff and Fuiman 1995; Kalish 1989). Because otoliths are metabolically inert once formed and the chemistry and environmental parameters of seawater vary geographically, analysis of otolith microchemistry reveals the environmental history of fish and can be used as natural biogeochemical tags of fish populations or stocks (Campana et al. 1999; Patterson et al. 1998, 2002; Thorrold et al. 1998, 2001). Patterson et al. (unpub. MS) demonstrated Gulf and Atlantic king mackerel collected on their summer spawning grounds in 1995 had otolith elemental signatures that were stock specific. Classification accuracies computed from linear discriminant function analysis (LDFA) with elemental concentrations (Ba, Mn, Mg, and Sr) as dependent variables were 85.3% for females and 76.8%% for males.

The purpose of this study was to continue lines of research aimed at developing natural tags derived from otolith shape analysis and otolith elemental signatures of Gulf and Atlantic king mackerel. Our objectives were to test if otolith shape or elemental signatures provided accurate stock-specific tags; to test if shape parameters or elemental signatures were significantly different between stocks, sexes, and sampling years; to use shape parameters or elemental signatures to estimate the percentage of winter landings in south Florida contributed by the Atlantic stock; and, to estimate if stock composition estimates from winter samples differed between sexes.

Methods

Otolith Shape Analysis:

King mackerel were sampled from recreational landings caught in the U.S. south Atlantic and eastern Gulf during summer 2001 and 2002 when stocks were separate (Figure 2). Fish were measured to the nearest mm fork length (FL) and sex was determined by macroscopic examination of gonads. We attempted to extract both sagittal otoliths from each fish; however, at least one otolith was extracted from each fish, cleansed of adhering tissue, and placed in plastic vials for storage.

Fish age was estimated following the methods of DeVries and Grimes (1997). Opaque zones generally could be counted in whole otoliths of females less than 900 mm FL and males less than 800 mm. Otoliths of fish larger than these sizes generally had to be sectioned to estimate age; therefore, we only were able to conduct otolith shape and otolith microchemistry analyses on otoliths of large individuals from which both sagittae were collected.

After age estimation, otolith shape analysis was conducted following the methods established by DeVries et al. (2002). The proximal lateral surface of otoliths was digitized with an Image-Pro® image analysis system. The left otolith was digitized when available; otherwise, the right otolith was digitized and inverted to approximate the left otolith (DeVries et al. 2002). Otolith perimeter was traced by the software prior to estimation of shape parameters. The rostrum of king mackerel otoliths is fragile and often broken during extraction. Therefore, the anterior portion of otolith perimeter was estimated around the tip of the antirostrum and then from its ventral posterior terminus across the posterior portion of the rostrum in a line perpendicular to the transverse axis of the otolith (DeVries et al. 2002).

Otolith shape parameters were computed for each sample using an algorithm in Image-Pro®. The software was used to compute otolith perimeter, area, roundness, circularity, and rectangularity, as well as amplitudes of the first twenty Fourier harmonics. All 25 shape parameters were standardized by removing the common pooledgroup slope of the linear relationship between each parameter and fish length. Variables were tested for normality with Shapiro-Wilkes' test and for homogeneity of variances with an F_{max} test, and were transformed when necessary to meet parametric assumptions (Sokal and Rohlf 1981). Differences between stocks, collection years, and sexes were tested with multivariate analysis of variance (MANOVA) of shape data to determine if significant differences in otoliths shape existed (SAS, Inc. 1996). A stepwise discriminant model building procedure in SAS then was used to compute discriminant functions to distinguish Atlantic and Gulf stocks (PROC STEPDISC; SAS, Inc., 1996). Models were computed for separately for each sex in each year. In the model building procedure, the significance level to enter or retain a given parameter was set to 0.15 and maximum tolerance was set to 0.80 to avoid potential problems with collinearity among shape parameters. Classification success of discriminant function models was computed with the jackknife crossvalidation option in SAS (PROC DISC; SAS, Inc. 1996).

King mackerel were sampled from three zones around south Florida in winter 2001/02 and 2002/03 to estimate the contribution of the Atlantic stock to landings in each zone (Figure 3). Otolith shape analysis was conducted as above. Sex- and year-specific maximum likelihood models were parameterized with shape parameters resulting from

discriminant function analysis of summer-sampled fish to estimate the stock composition of winter mixed stock samples (DeVries et al. 2002). Models were computed to estimate the percentage of samples from each zone that were Atlantic stock fish and 95% confidence intervals were bootstrapped (n = 500) about each estimate in S-Plus.

Otolith Elemental Signatures:

The elemental composition of otoliths was analyzed once shape analyses were completed. Samples were prepared for analysis in a class-100 clean room at the Department of Geological Sciences, Louisiana State University. Otoliths were cleaned of any remaining tissue by rinsing with ultrapure water (18.3 megaohm polished water) and scrubbing their surface with an acid-leached synthetic bristle brush. Otolith surfaces then were flooded with 1% ultrapure nitric acid and repeatedly rinsed with ultrapure distilled water. Cleaned samples were air-dried in a laminar flow class-10 clean hood and then weighed.

Otoliths were dissolved in 1% ultra-pure nitric acid at a near constant ratio of acid volume to otolith weight. Solutions were spiked with Indium as an internal standard and then analyzed with a Finnigan MAT Element II sector field-inductively coupled plasmamass spectrometer (SF-ICP-MS) at the Department of Chemistry and Biochemistry, Old Dominion University. Precision and accuracy of sample analyses were determined by the method of standard addition and by periodic running of an otolith certified reference material.

Otolith elemental data obtained from SF-ICP-MS analysis were analyzed statistically to determine stock-specific elemental signatures following the same methods applied to shape data. Likewise, elemental signatures resulting from discriminant function analysis were used to parameterize maximum likelihood stock mixing models and applied to otolith microchemistry data from winter samples to estimate the percentage of winter samples derived from the Atlantic stock.

Results

Otolith Shape Analysis:

Otolith shape analysis was performed for 201 samples collected in summer 2001 and 231 samples collected in summer 2002 (Figure 4). The ratio of females to males for summer samples of both stocks was approximately 1:1 during both years except for Atlantic samples in summer 2002 (1.49:1). Fork length and age distributions were similar within year between stocks for both males and females (Figures 4 & 5).

Standardized perimeter data were log-transformed and standardized amplitudes of harmonics 13 through 16 were square root-transformed to meet parametric assumptions of normality and homogeneity of variances. Multivariate analysis of variance (MANOVA) computed with shape parameters as dependent variables indicated there were significant differences in otolith shape between sexes (Pillai's Trace $F_{d.f.=30:401}$ = 2.93; p < 0.001) and stocks (Pillai's Trace $F_{d.f.=30;175} = 2.18$; p < 0.001) but not years (Pillai's Trace $F_{d.f.=30;401} = 0.763$; p = 0.813). Linear discriminant function analysis of otolith shape parameters yielded jackknifed classification accuracies ranging from 65.8 to 76.4% when sexes and years were modeled separately (Table 1).

Otolith shape analysis was performed for 350 king mackerel sampled from three zones in south Florida in winter 2001/02 and for 389 fish sampled in winter 2002/03 (Figures 6 & 7). Sex- and year-specific maximum likelihood models were parameterized with shape data from summer-sampled fish to estimate the percentage of Atlantic stock fish among those sampled from each zone in each winter. Resulting estimates indicated a high percentage of samples from each zone in each year of the study were Atlantic stock fish; however, 95% confidence intervals about the estimates were wide (Table 2).

Otolith Elemental Signatures:

Analysis of otoliths collected in 2002/03 with HR-ICP-MS is ongoing; thus, only results for samples collected in fishing year 2001/02 will be presented here. Of the 201 otoliths collected in 2001, only 176 were judged to be suitable for chemical analysis (n = 52 females and 49 males from the Atlantic and 38 females and 37 males from the Gulf). Unsuitable otoliths either were stored with excessive amounts of tissue on their surface or were broken following shape analysis. Removing these samples did not alter the FL or age distributions relative to samples used for otolith shape analysis.

Nine elements were quantified in king mackerel otolith solutions: Ba, Ca, Cd, K, Li, Mg, Mn, Na, and Sr (Figure 8). Cadmium concentrations were low and were below the detection limit in 18 samples; therefore, Cd was not used to derive stock-specific elemental signatures. Sodium and K also were not used, but they were omitted because their concentration in otoliths is thought to be under physiologic control; therefore, their suitability as stock markers is suspect. Of the remaining elements, Li, Mg, and Sr were log-transformed to meet parametric assumptions of normality (all three) and homogeneity of variances (Mg). Multivariate analysis of variance (MANOVA) computed with element concentrations as dependent variables indicated there were significant differences in otolith elemental signatures between stocks (Pillai's Trace $F_{d.f.=4;176} = 66.7$; p < 0.001) but not between sexes (Pillai's Trace $F_{d.f.=4;176} = 1.598$; p = 0.178). Linear discriminant function analysis of otolith elemental signatures yielded jackknifed classification accuracies ranging from 89.0 to 89.8% (Table 3).

Otolith shape analysis was performed for 323 of the 350 king mackerel sampled from three zones in south Florida in winter 2001/02. Sample sizes were 140 for zone1 (female = 77; male = 63), 49 for zone2 (female = 44; male = 5), and 134 for zone3 (female = 65; male = 69). Maximum likelihood models were parameterized with otolith elemental signatures derived from summer-sampled fish to estimate the percentage of Atlantic stock fish among those sampled from each zone in each winter. Results indicated nearly all fish sampled in zone3 off southeastern Florida were estimated to be Atlantic stock fish, while most fish sampled in zone1 off southwestern Florida were not (Table 4).

Discussion

Preliminary results from this study indicate both otolith shape analysis and analysis of otolith elemental signatures provided effective natural tags of king mackerel stocks. Otolith shape analysis has several advantages over analyzing otolith elemental signatures in that is less costly, less time consuming, and nondestructive. However,

otolith elemental signatures provided higher classification success which was not affected by modeling sexes jointly or separately.

Otolith shape discriminant function classification accuracies were similar to those reported by DeVries et al. (2002) for female king mackerel sampled in summer 1996 despite lower sample sizes in our study. Otolith shape classification accuracies were slightly lower for males than females in this study, which might be expected given greater differences in female growth between stocks (DeVries and Grimes 1997). One also might expect differences between sexes in shape parameters included in discriminant function given that otolith shape was estimated to be significantly different between sexes. The fact that such different models resulted within sex between years is difficult to explain, however, because year was not a significant year effect in the MANOVA model and there was significant overlap in year classes from 2001/02 to 2002/03 in the dataset.

Our results indicate stock markers derived from otolith elemental signatures were more effective than those based on otolith shape analysis in distinguishing king mackerel stocks in 2001/02. We are further encouraged that no difference in elemental signatures existed between sexes and that our stepwise discriminant function algorithm retained the same suite of elements in all models. Together, these results indicate elemental signatures reflected environmental differences experienced by each stock and that males and females likely shared migration pathways. Data from 2002 summer-collected fish will allow us to test if elemental signatures are temporally stable between years, which may provide greater evidence of the utility of using otolith elemental signatures as stock-specific markers.

Despite differences in discriminant function classification success between otolith shape analysis and otolith microchemistry methods, maximum likelihood estimates of percent Atlantic stock contribution to 2001 winter samples were somewhat similar between methods for both males and females. Both methods estimated the majority of zone3 landings were contributed by the Atlantic stock. However, maximum likelihood models based on otolith shape data estimated over half the fish sampled in zone1 off southwestern Florida also were Atlantic stock fish, while estimates based on otolith elemental signatures indicated the majority of zone1 samples were not Atlantic fish. Without corroborating evidence of stock composition it is difficult to assess which estimates were closer to true mixing conditions. Perhaps more weight should be given to the elemental signature estimates given the greater classification success with summer samples, but it is difficult to have much confidence in point estimates derived from either method given the wide confidence intervals estimated with each.

Otolith shape maximum likelihood estimates of percent Atlantic stock contribution to sampled landings were very different between sexes among zones in winter 2002/03. Estimates for males followed an east-west gradient similar to that estimated with otolith microchemistry data in 2001/02, while the Atlantic stock was estimated to have contributed less than 50% of female samples in all three zones. Completion of 2002/03 winter stock composition estimates based on otolith elemental signatures may provide greater evidence that the majority of winter landings in southeast Florida are contributed by the Atlantic stock.

Despite some uncertainty in our stock mixing estimates off south Florida from both the 2001/02 and 2002/03 winters, this study adds to a growing body of evidence that

the current management strategy of assigning all winter mixing zone landings to the Gulf stock does not reflect real mixing conditions (DeVries et al. 2002; Gold et al. 2002). Preliminary results from this study indicate both otolith shape analysis and analysis of otolith elemental signatures hold some promise as effective tools to estimate stock composition of winter landings off south Florida. It appears stock discrimination is greater with otolith elemental signatures than with shape analysis but this should be evaluated further once 2002/03 otolith microchemistry analyses are completed. For now, however, it appears there is sufficient evidence to compute stock assessment models assuming at least half and perhaps more of king mackerel caught in the winter mixing zone are contributed by the Atlantic stock.

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Table 1. Resultant linear discriminant function models computed with otolith shape variables to distinguish king mackerel sampled from the Atlantic and Gulf stocks in summer 2001 and 2002. Classification success was computed with the jackknife crossvalidation option in PROC DISC

	Parameters Included		Classification %			
Model			Atl.	Total		
2001 Females	Harmonics 3,5,6, 8, 9, and 10		71.1	76.4		
2001 Males	Roundness, Rectangularity, and Harmonic 3,7, and 20	69.7	67.6	68.7		
2002 Females	Perimeter, Roundness, and Harmonics 2, 9, 13, 15, and 16	67.9	70.8	69.4		
2002 Males	2 Males Perimeter, Rectangularity, and Harmonics 2, 8, 11, and 13		70.4	65.8		

Table 2. Results of maximum likelihood models computed with otolith shape data to estimate the percentage of Atlantic stock in king mackerel samples collected from three zones around the southern tip of Florida in winter 2001/02 and 2002/03. Models were parameterized with variables listed in Table 1 for each sex/year combination.

Year	Zone	Model	% Atlantic	95% CI	Model	% Atlantic	95% CI
2001/02	1	Females	60.1	40.2-73.9	Males	61.0	32.2-82.7
	2	Females	48.6	20.1-67.2	Males	99.9	60.9-100.0
	3	Females	76.0	57.0-97.7	Males	83.8	62.9-99.8
2001/03	1	Females	14.5	0-29	Males	45.5	21-70
	2	Females	41.3	21-69	Males	83.1	49-100
	3	Females	40.4	24-60	Males	71.9	52-99

Table 3. Resultant linear discriminant function models computed with otolith elemental concentrations to distinguish king mackerel sampled from the Atlantic and Gulf stocks in summer 2001. Classification success was computed with the jackknife crossvalidation option in PROC DISC.

Model	Parameters Included	Classification %		
		Gulf	Atl.	Total
2001 Females	Ba, Mg, Mn, and Sr	98.1	81.6	89.8
2001 Males	Ba, Mg, Mn, and Sr	91.8	86.5	89.2
2001 All Data	All Data Ba, Mg, Mn, and Sr		88.0	89.0

Table 4. Results of maximum likelihood models computed with otolith elemental signatures to estimate the percentage of Atlantic stock in king mackerel samples collected from three zones around the southern tip of Florida in winter 2001/02. Models were parameterized with elements listed in Table 1 for each sex/year combination.

Year	Zone	Model	% Atlantic	95% CI	Model	% Atlantic	95% CI
2001/02	1	Females	21.1	7-35	Males	39.7	19-62
	2	Females	38.7	21-59	Males	73.8	16-99
	3	Females	85.6	68-99	Males	83.1	66-99

Figure 1. Map depicting boundaries of the winter mixing area off south Florida. All landings from this area made during November through March are attributed to the Gulf stock. During all other months mixing zone landings are attributed to the Atlantic stock. The seaward boundary of the mixing zone is the edge of U.S. exclusive economic zone; however, most king mackerel are caught over the continental shelf which is represented by the 200 m isobath.

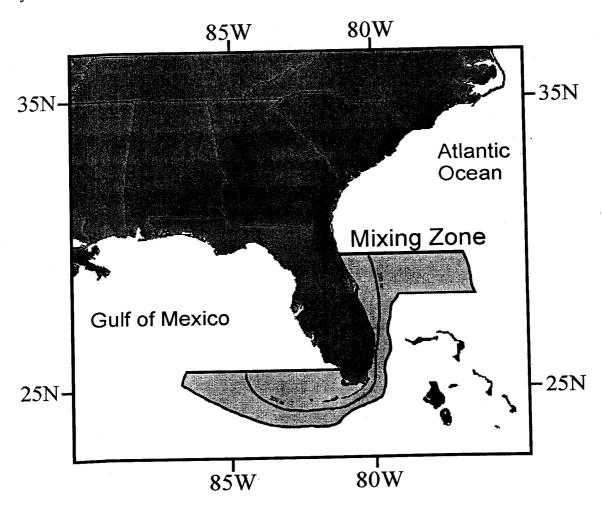


Figure 2. Map of sampling locations for king mackerel sampled in summer 2001 and 2002. In the Gulf of Mexico, sample locations from east to west were Dauphin Island, Alabama, Destin, Florida and Panama City, Florida. Sample locations from north to south in the Atlantic Ocean were southeastern North Carolina, Charleston, South Carolina, and Jacksonville, Florida.

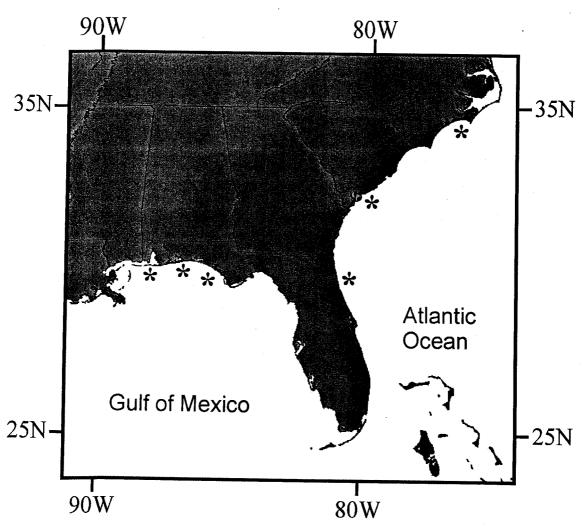


Figure 3. Map of three zones in south Florida where king mackerel were sampled in winter 2001/02 and 2002/03.

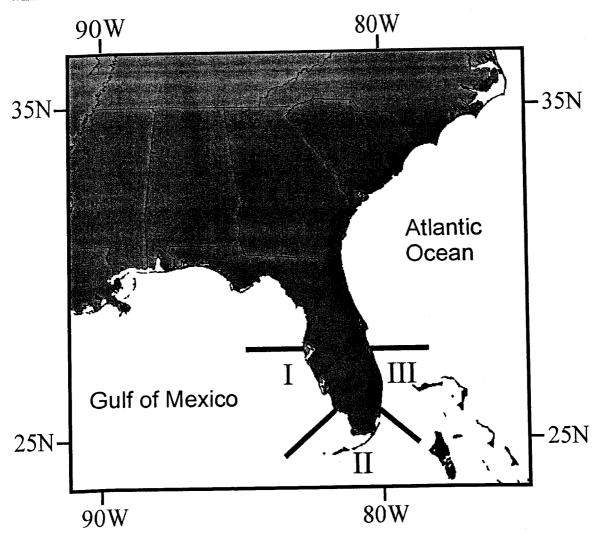


Figure 4. Fork length distributions and sample sizes of king mackerel sampled in the Gulf of Mexico and U.S. south Atlantic Ocean in summer 2001 and 2002.

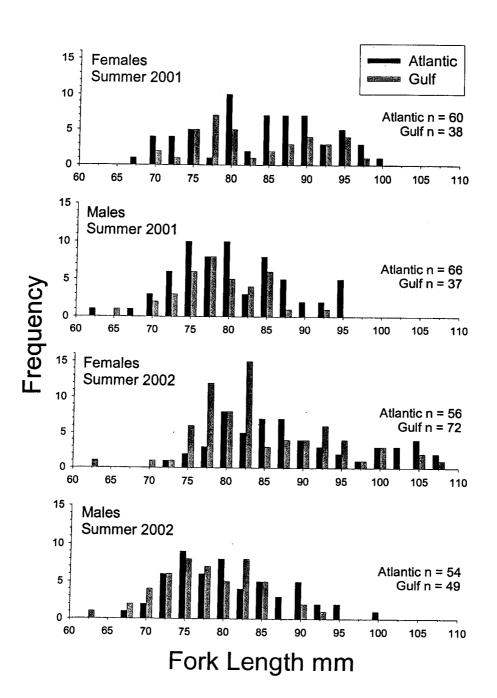


Figure 5. Age distributions of king mackerel sampled in the Gulf of Mexico and U.S. south Atlantic Ocean in summer 2001 and 2002.

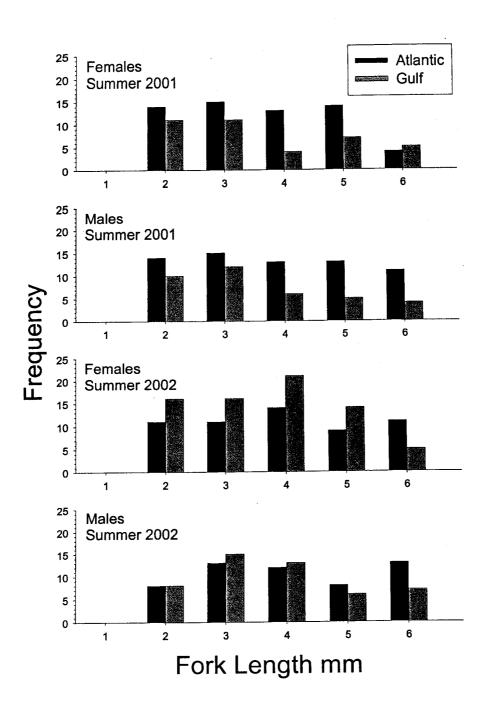


Figure 6. Fork length distributions and sample sizes of king mackerel sampled from three zones around south Florida in winter 2001/02 and 2002/03.

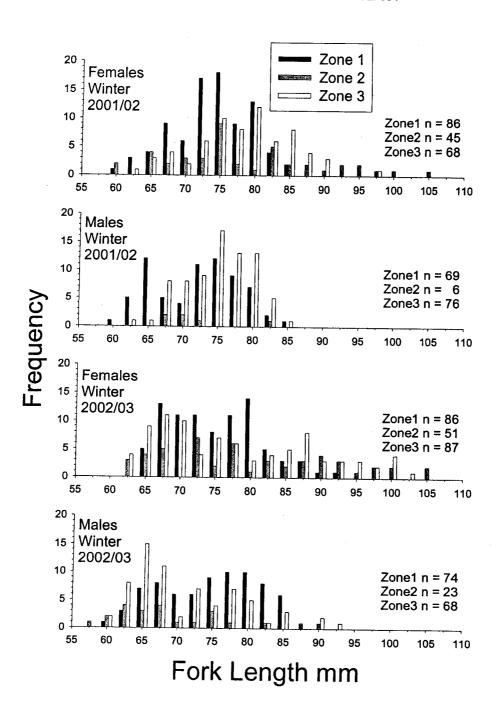


Figure 7. Age distributions of king mackerel sampled from three zones around south Florida in winter 2001/02 and 2002/03.

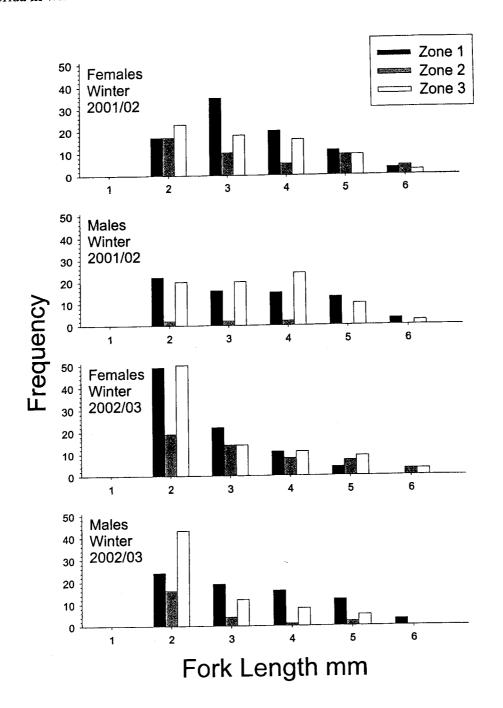


Figure 8. Boxplots of otolith elemental concentrations for eight elements quantified in king mackerel otoliths. Upper and lower sides of plots are the 75th and 25th percentiles of the concentration range and extended bars are the 5th and 95th percentiles. Horizontal bars are sample medians. Along the x-axis, labels A, G, Z1, Z2, and Z3 are for summer Atlantic and Gulf and winter zone1, zone2, and zone3 samples, respectively.

