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Fisheries Research 57 (2002) 51–62

FISHERIES RESEARCH

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Using otolith shape analysis to distinguish eastern Gulf of Mexico and Atlantic Ocean stocks of king mackerel

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Received 3 October 2000; received in revised form 18 April 2001; accepted 15 May 2001

Abstract

In winter, king mackerel from eastern Gulf of Mexico and Atlantic stocks mix off southeast Florida, where they support a large fishery. Neither tagging nor genetics has yielded a way to estimate mixing rates accurately. For management purposes, and based on tagging data from the mid-1970s, all of these fish have been considered to be from the Gulf stock. Our objectives were to examine the feasibility of using otolith shape data to distinguish the two stocks, and if the method proved feasible, to use it to estimate stock composition in the winter mixed-stock fishery.

In the feasibility phase of the study, we collected shape data from sagittae of 355 female king mackerel taken during summer spawning seasons, 1986–1993, outside the winter mixing area. Gulf fish were taken off the Florida panhandle and Atlantic fish from waters north of Cape Canaveral, FL. Shape data, obtained from the posterior half of the sagitta, included area, perimeter, and standardized Fourier amplitudes. Using a training set of 250 fish and a stepwise discriminant procedure, we selected a set of variables that correctly classified 80.4% of Atlantic and 85.7% of eastern Gulf fish of the remaining 105 individuals.

In the application phase of the study, we estimated mixed-stock composition in the 1996–1997 winter fishery. Shape data were extracted from sagittae of 363 females taken from distinct areas during the 1996 spawning season. A training subset of the data and a stepwise discriminant procedure were used to select a set of variables that correctly classified 71.1% of Atlantic and 77.5% of eastern Gulf fish in the remaining data (test set). We used that set of variables and a maximum likelihood method to estimate composition of the ensuing mixed-stock fishery from a sample of 463 females taken in that fishery. The resulting estimate was that 99.8% of individuals in the winter landings were from the Atlantic stock and only 0.2% were from the eastern Gulf stock, with a standard error of 3.4%.

Using otolith shape data, it is possible to distinguish individuals from eastern Gulf and Atlantic stocks of king mackerel and to estimate stock composition in the mixed-stock fishery. Our estimate of that stock composition is consistent with other recent studies, but is markedly different from the composition presently assumed in management. Because management can be ineffective if based on inaccurate estimates of stock composition, we recommend that such information be used regularly in management and that corresponding estimates be made in future years. Such continued analysis would serve both to confirm our results and to estimate year-to-year variability in stock composition of the mixed fishery. Published by Elsevier Science B.V.

Keywords: Shape analysis; Fourier; Otolith; *Scomberomorus*; Stock composition; Maximum likelihood

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0165-7836/02/$ – see front matter. Published by Elsevier Science B.V.
PII: S0165-7836(01)00332-0

1. Introduction

King mackerel, *Scomberomorus cavalla*, is a large scombrid that supports important commercial and recreational fisheries off the southeastern United States and Mexico. In the 1998–1999 fishing year, commercial and recreational landings were 1143 and 2071 mt from the southern US Atlantic coast and 1633 and 2824 mt from the US portion of the Gulf of Mexico (Anon., 1999). Commercial catches in Mexico during 1990–1991, the most recent data available, were 2676 mt (Anon., 1993).

King mackerel are jointly managed by the Gulf of Mexico and South Atlantic Fishery Management Councils under the Coastal Pelagics Management Plan, first implemented in February 1983 (Anon., 1983). Under the original plan, the species was managed as a single stock from North Carolina to Texas. In 1985, Amendment One of the plan recognized the existence of separate stocks, or "migratory groups", in the Atlantic and Gulf of Mexico (Anon., 1985). This division was based primarily on analyses of tag return data collected by the Florida Department of Environmental Protection (DEP) during 1975–1979 (Sutter et al., 1991), and on seasonal patterns of length-frequency, CPUE, and commercial landings data.

In 1990, the Mackerel Stock Assessment Panel (Anon., 1990), jointly appointed by the Gulf of Mexico and South Atlantic Fishery Management Councils, postulated the existence of east and west Gulf stocks of king mackerel based on enzymatic electrophoretic evidence (Johnson et al., 1994). Those studies, however, found no electrophoretic differences between eastern Gulf and Atlantic fish. Gold et al. (1997) also could not distinguish the two groups using electrophoresis, although they did find mtDNA evidence suggesting weak genetic differences between eastern Gulf and Atlantic fish; they also found, contrary to Johnson et al. (1994), that variation in PEPA-2 genotypes was not independent of sex or age. More recently, Gold[1] concluded that the evidence from allelic variation at seven microsatellites was "consistent with the hypothesis that there are two, very weakly differentiated 'genetic' stocks (subpopulations) of king mackerel" off Florida and separated by the peninsula. Analysis of 7 years of king mackerel size-at-age data by DeVries and Grimes (1997) revealed that fish (especially females) from the eastern Gulf persistently grew faster and to larger sizes than those from the Atlantic coast. Eastern Gulf females averaged about 15 cm larger at age than Atlantic females at ages above age 6. Age compositions also indicated distinct strong and weak year classes in all three groups (DeVries and Grimes, unpublished manuscript). Using stable nitrogen and carbon isotopes in dorsal fin spines, Roelke and Cifuentes (1997) suggested there were at least two groups in the Gulf of Mexico—one in Mexican waters and one in Florida waters—with possibly a third group in the northwestern Gulf. Thus, although the precise stock composition of *S. cavalla* within the Gulf of Mexico is still being studied, stock separation between fish in the eastern Gulf and the Atlantic is supported by scientific evidence.

Exploitation histories of eastern Gulf and Atlantic stocks have been quite different. The Gulf group has been considered overfished for more than a decade, while that is not the case for Atlantic king mackerel. Currently, the convention adopted for management is that all king mackerel caught south of the Volusia–Flagler County border off northeast Florida during November–March, a period during which large gillnet and troll fisheries are prosecuted, are allocated to the Gulf migratory group[2] quota. During the rest of the year, the Monroe–Collier County border off southwest Florida is used as the dividing line between Gulf and Atlantic groups. This allocation is based primarily on the 1974–1979 Florida DEP mark–recapture study previously mentioned (Sutter et al., 1991) which suggested that more than half the fish along the Florida east coast in winter (November–March) were from the Gulf migratory group.

In contrast, more recent mark–recapture results estimate that a smaller percentage of king mackerel harvested off the Florida east coast in winter belongs to the Gulf migratory group. Approximately 12% of the 207 recoveries of 3901 king mackerel marked off

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[1] Gold, J.R., 2000. Genetic analysis to determine mixing proportions by season of western Atlantic and Gulf of Mexico stocks of king mackerel. Final Report of MARFIN Project NA57-FF-0295. National Marine Fisheries Service, Southeast Regional Office, St. Petersburg, FL.

[2] The terms stock and migratory group are used interchangeably by the Mackerel Stock Assessment Panel and herein, with the latter term used most often.

east Florida during the winters of 1988–1989 and 1989–1990 were recaptured in the Gulf of Mexico (Fable, 1993). Analysis of all mark–recapture results from 1985 to 1992 found that about 3% of fish tagged in the Atlantic Ocean were recaptured in the Gulf of Mexico (Cummings-Parrack, 1993).

The Mackerel Stock Assessment Panel (Anon., 1993) suggested several hypotheses that might explain the decreased proportion of Gulf Migratory Group fish along the Florida east coast, such as changing ocean environmental factors or variations in relative migratory group stock size and age structure, but only concluded that the mixing rates are dynamic. The Panel noted that future stock assessments could be based on estimated stock composition in the winter fishery along Florida's Atlantic coast. However, no means were available to estimate those proportions accurately or in a way that could account for interannual variation. Development of a method to accurately produce such estimates would significantly improve the biological basis of management.

Many recent studies have reported success in using shape analysis of scales and otoliths, and Fourier analysis in particular, to distinguish groups of fish. Cadrin and Friedland (1999) noted that image-processing techniques have significantly enhanced morphometric analysis, such as shape analysis of scales and otoliths, and can complement other methods of stock identification. Studies using scales have examined walleye (Jarvis et al., 1978; Riley and Carline, 1982), Atlantic salmon (de Pontual and Prouzet, 1987), and striped bass (Margraf and Riley, 1993; Richards and Esteves, 1997a,b). Studies involving otoliths have dealt with herring (Bird et al., 1986), Atlantic mackerel (Castonguay et al., 1991), deep slope red snapper (Smith, 1992), Atlantic cod (Campana and Casselman, 1993), Atlantic salmon (Friedland and Reddin, 1994), haddock (Begg and Brown, 2000), and silver hake (Bolles and Begg, 2000). Campana and Casselman (1993) analyzed otolith shape data from 2349 fish and concluded that "cod from stocks with clearly different growth rates can be reasonably well differentiated on the basis of otolith shape alone". Begg and Brown (2000) reported greater discriminatory success in year classes with greater differences in growth between regions. More recently, Finn et al. (1997) used discriminant analysis of Fourier amplitude data from otolith luminance profiles, rather than otolith shape, to successfully classify wild- and hatchery-reared salmon fry.

Growth differences between eastern Gulf and Atlantic king mackerel and encouraging results from preliminary shape analyses on otoliths (DeVries and Grimes, 1993) suggest that Fourier analysis could allow estimation of stock composition in the mixed-stock winter fishery. In addition, Johnson (1995), using a truss system of measurements on king mackerel otoliths and stepwise discriminant analysis, correctly classified the geographic origin (North Carolina, northwest Florida, or Yucatan, Mexico) of 58–78% of his 105 specimens, a significant improvement from the expectation under a random distribution hypothesis.

Our first objective was to determine the feasibility of developing mathematical models based on otolith shape measurements, particularly Fourier coefficients, that could distinguish Atlantic from eastern Gulf king mackerel. The second objective, contingent on success of the first, was to estimate recent stock composition of the winter king mackerel fishery off eastern Florida in 1996–1997.

2. Methods

For the feasibility phase of the study, shape data were taken primarily from the left sagittae of 355 female king mackerel, 181 from the Atlantic Ocean and 174 from the eastern Gulf of Mexico, collected between 1986 and 1993 in support of stock assessments. Females were used because growth differences between Atlantic and eastern Gulf females are greater than those for males (DeVries and Grimes, 1997). Eastern Gulf specimens were collected off the panhandle of Florida near Panama City and Pensacola; Atlantic fish were taken off Virginia ($n = 5$), South Carolina ($n = 88$), Georgia ($n = 77$), and northeast Florida ($n = 11$) (Fig. 1). To ensure stock-specific samples for model development, we only used fish collected during spawning seasons (May–September), when mixing of stocks should be minimal, and only from sites outside the winter mixing area. The size range was restricted to 80–104 cm FL to limit any variability related to fish size or age and to develop a model based on, and thus applicable to, commonly caught sizes. We used all available eastern Gulf fish

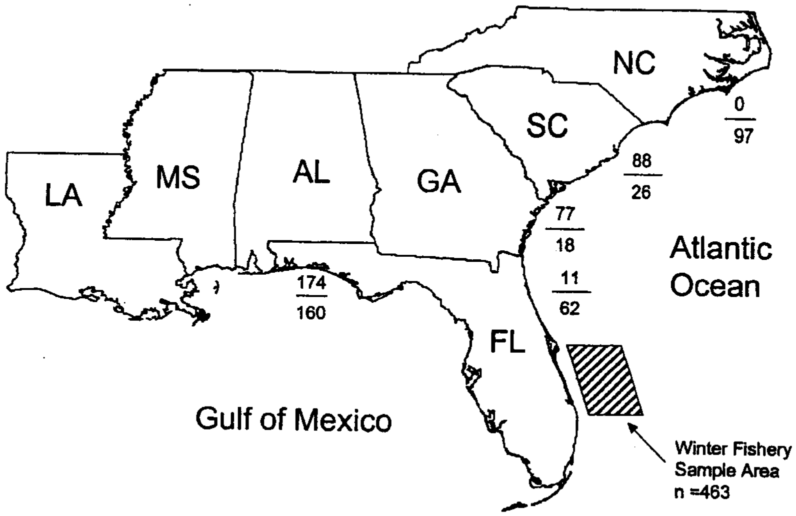

Fig. 1. Geographical distribution and sample sizes of otolith samples used in feasibility (upper number) and application (lower number) studies.

meeting those criteria. Having more Atlantic than eastern Gulf fish, we used stratified random sampling by 5 cm interval (without replacement) to generate an Atlantic sample of the same size and size distribution. We randomly selected 250 of the 355 specimens, 125 from the east Gulf and 125 from the Atlantic, as a training set for developing a classification model. The remaining 105 observations (56 Atlantic and 49 east Gulf) were used as an independent test set for evaluating the model.

To estimate stock composition in the 1996–1997 winter fishery while controlling for any interannual variation in otolith shape, we collected additional otoliths from spawning areas during 1996. The size range, 80–96 cm FL, was smaller than that in the feasibility study and more closely matched the size range in the winter mixed-stock fishery. Shape data were collected from sagittae of 363 females, 160 from northwest Florida (primarily off Panama City and Destin) and 203 from Atlantic waters: 97 off North Carolina, 26 off South Carolina, 18 off Georgia, and 62 off Florida north of Cape Canaveral (Fig. 1). Samples were taken from May to October, 1996. We randomly selected 240 of the 363 specimens, 120 from the eastern Gulf and 120 from the Atlantic, as a training set, with the remaining 83 Atlantic and 40 eastern Gulf fish forming an independent test set.

Estimates of stock composition in the subsequent mixed-stock fishery were based on data from sagittae of 463 females, 80–96 cm FL, caught by commercial trollers between Cape Canaveral and West Palm Beach, FL (Fig. 1) from 3 December 1996 to 6 February 1997. These dates bracketed the peak of that winter's king mackerel season. Samples were collected at commercial fish houses from large vats containing pooled catches taken within the previous 24 h. Fish were removed haphazardly from the vats, and otoliths were collected from all females within the specified size range. The temporal distribution of sampling was highly dependent on fishery activity, which was closely correlated with weather and sea conditions, as well as market factors.

Identical laboratory procedures were used for data extraction from known-stock and mixed-stock samples. Fourier coefficients (Bird et al., 1986) and otolith area and perimeter were obtained from a digitized image (magnified approximately ×27) of the posterior distal lateral surface of the left sagitta using Optimas software, an image analysis system from Bioscan. If the left sagitta was not available, we used the software to generate a mirror image of the right sagitta. Campana and Casselman (1993) found that coefficients of variation for Fourier amplitudes were 1.5–4.0 times higher among cod of a given sample than between left and right otoliths of the same fish. Begg and Brown (2000) reported that in haddock "overall otolith shape was not significantly different between left and right otoliths for samples from the same region, age group, and year class". We used only the posterior portion because the rather delicate rostrum was often broken off, and had we restricted ourselves to whole otoliths, sample size would have been much smaller. Because only the posterior portion of the otolith was used, digitization of the perimeter was done manually, as we were unable to use the software's edge-following routine. The actual portion digitized differed slightly between feasibility and application phases of the study. In the feasibility phase, digitization of the perimeter always began at the axis of the anti-rostrum and rostrum and proceeded counterclockwise; in the application phase, digitization began at the anterior tip of the anti-rostrum and went immediately across the rostrum to the ventral edge, then continued along the edge counterclockwise (Fig. 2). The change was made because the axis of the anti-rostrum and rostrum was not always clear and was therefore a potential source of variability, whereas the tip of the anti-rostrum was a very clear landmark. Because the entire application phase of the study used the improved procedure, this small change in the area digitized caused no inconsistency in the analysis; it did, however, preclude us from using discriminant rules from one phase of the study to classify samples from the other phase to examine the temporal variability of classification success.

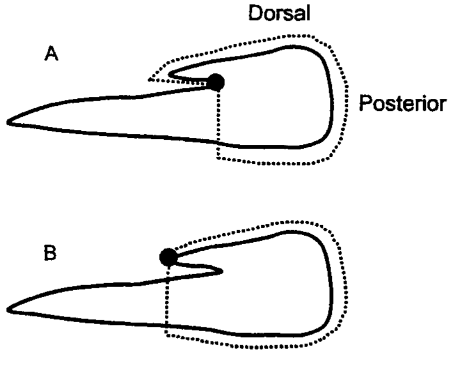

Fig. 2. Portion of the sagitta used in the shape analysis (indicated by the dotted line). Digitization always began at the point marked by the dot and proceeded counterclockwise. (A) Area digitized in the feasibility study; (B) area digitized in the application study.

Fourier coefficients (amplitude and phase angle) were calculated by the software using the mathematical centroid as the otolith center; the first 20 harmonics were included in the analysis. The 20 amplitude harmonics plus perimeter and area gave 22 variables for analysis. Amplitudes were standardized to minimize effects of fish length, and this was done by dividing each by the mean radius (=zero amplitude divided by 64). The Optimas software stores the mean radius as the mean times n in the zero amplitude, where n is the number of boundary radials sampled. Campana and Casselman (1993) found no clear advantage in (1) using ANCOVA to remove effects of fish or otolith length over the standardized amplitudes automatically generated by the software, or (2) using the nucleus instead of the centroid as the otolith center. Perimeter and area were standardized to a common fish size ($\overline{\mathrm{FL}}$) by removing the common, pooled-group slope (b) of fish length on the appropriate variable (Campana and Casselman, 1993); in the application phase $\overline{\mathrm{FL}} = 87.7$ cm, perimeter $b = 0.23$, and area $b = 0.42$.

Variables used in the analysis were tested for normality using a Shapiro-Wilkes statistic, W (SAS Institute, 1988a), and transformed if necessary. Fourier amplitude harmonics 1, 3, 4, 5, 7, 11, 13, and 19 in the feasibility phase and harmonics 6, 14, 15, 16, 17, 18, and 20 in the application phase were normalized with a square-root transformation. In the application phase, area was normalized through a natural-log transformation. Campana and Casselman (1993) discussed the problems associated with trying to transform frequently bimodal Fourier phase angle data and decided to give relatively little weight to them in their analyses. Following their reasoning, we excluded phase angles from our analyses.

Many shape variables were significantly correlated, but all were kept in the analysis because those correlations were at best moderate and most were very weak. Standardized perimeter and standardized area (or ln standardized area) were most highly correlated, with $r^2 = 0.55$ in the feasibility phase and $r^2 = 0.45$ in the application phase of the study, and only nine other variable pairs in this latter phase had r^2's as high as 0.20–0.28.

Discriminant analysis was performed with the PROC DISCRIM procedure in SAS (SAS Institute, 1988b). Because covariance matrices were not homogeneous between stocks, we used quadratic, rather than linear, discriminant functions. Performance of discriminant functions was evaluated using Cohen's kappa, a statistic which provides an objective means of calculating the chance-corrected percentage of agreement between actual and predicted group memberships; values of kappa range from 0 to 1, with 0 indicating the discriminant analysis yielded no improvement over chance, and 1 indicating perfect agreement (Titus et al., 1984).

Both forward selection and backward elimination techniques (Huberty, 1984) were used to choose which suite of variables to include in the discriminant function, and the results of the two were compared. Discriminant functions were evaluated using cross-validation and independent test data. Cross-validation, also called the *U*-method (Dillon and Goldstein, 1984), uses the same data set to generate and evaluate the discriminant function by calculating the function with $n - 1$ observations, classifying the one observation left out, and then repeating this procedure for all n observations. This method is nearly unbiased but has a relatively large variance (Dillon and Goldstein, 1984; SAS Institute, 1988b). Using an independent set of test data produces an unbiased estimate but, with small sample size, can have a large variance (SAS Institute, 1988b). In the application study, when using the cross-validation method, we used just the training set of data ($n = 240$) first, then repeated the analysis using all 160 Gulf fish and a random sample of 160 of the 203 Atlantic fish (total $n = 320$). Prior probability of classification was assumed to be equal for all analyses.

To estimate composition of the mixed-stock fishery, we used a maximum likelihood (ML) estimation procedure based on finite-mixture distributions (Wolfe, 1970; Everitt and Hand, 1981). Similar methods have been used and studied in fishery science by Fournier et al. (1984), Pella and Robertson (1978), Millar (1987, 1990b), and Wood et al. (1987). These methods differ from discriminant analyses in estimating stock composition directly, rather than attempting to classify individuals. Because finite-mixture methods do not require prior estimates of stock composition, as does discriminant analysis, they are usually more appropriate for estimating composition in mixed-stock fisheries. The results of composition estimates made with discriminant analysis are sensitive to the prior probabilities chosen; since these are in essence, the unknown mixing proportions (stock composition), discriminant analysis is difficult to apply optimally for this purpose. The method used here overcomes this difficulty.

Composition estimates were obtained from a short program, written in the S-Plus statistical software (Mathsoft, 1999), that iteratively estimated mixing proportions using an EM algorithm (Dempster et al., 1977; McLachlan and Krishnan, 1997). The program's method is similar to that used previously in fisheries, e.g., by the HISEA software of Millar (1990a). However, our procedure differed from that of Millar (1990a) in being able to accommodate unequal covariance matrices between groups. Standard errors and approximate 90% confidence intervals on estimated proportions were obtained through bootstrapping (Efron, 1982) with 500 replications.

3. Results

The size and age distributions of the training and test data sets for each stock in both the feasibility and application phases of the study are shown in Figs. 3 and 4. Among the winter fishery samples, the size distribution was weighted more towards the lower end of the size range than the application phase training sample, with 54% of the fish ≤85 cm FL; the age distribution was even more skewed and was dominated by 2-year old fish (Fig. 5). The temporal distribution of samples in the feasibility study was somewhat dissimilar between stocks, with most Gulf samples collected in 1989, 1991, and 1992, and most Atlantic fish in 1989, 1990, and 1992 (Fig. 6). Samples collected from the winter fishery for estimating stock composition were collected between 3 December 1996 and 6 February 1997, with about 90% taken by 7 January 1997 (Fig. 7).

Our highest classification success rate in the feasibility study for a given suite of variables was 80.4% of Atlantic and 85.7% of east Gulf king mackerel, while the highest in the application study was 71.1% of Atlantic and 77.5% of Gulf fish (Table 1). The quadratic discriminant functions which yielded these results were generated using an independent test data set, and in both cases, the successful classification rate was far better than one would expect by chance. There were 15 variables in the suite used in the feasibility

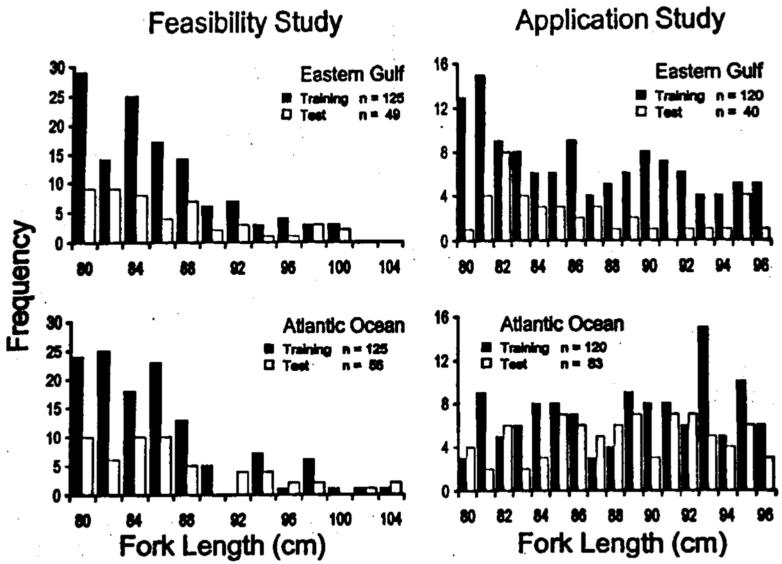

Fig. 3. Length-frequency distributions of the king mackerel training and test data sets used in the feasibility and application studies to construct and evaluate the quadratic discriminant functions.

study—standardized perimeter and area and 13 amplitude harmonics, while there were 12 variables in the suite used in the application study—standardized perimeter and area, and 10 amplitude harmonics (Table 1). Overall, classification success was similar for Gulf and Atlantic fish in the feasibility study, while in the application study, in most cases, it was a little higher for Gulf (65.0–80.0%) than Atlantic (65.8–72.3%), depending on the evaluation method (cross-validation or independent test data) and variable selection method used (Table 1). In the application study, there was no obvious improvement in the classification rates of the discriminant functions evaluated with cross-validation using the larger data set ($n = 320$)

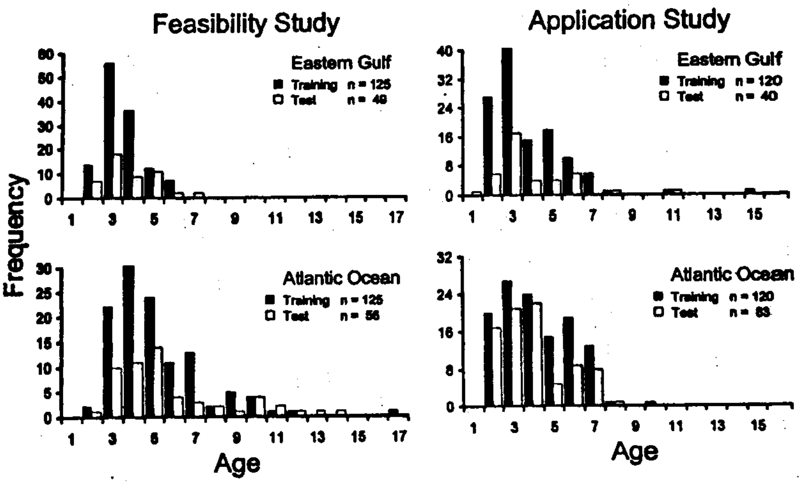

Fig. 4. Age-frequency distributions of the king mackerel training and test data sets used in the feasibility and application studies to construct and evaluate the quadratic discriminant functions.

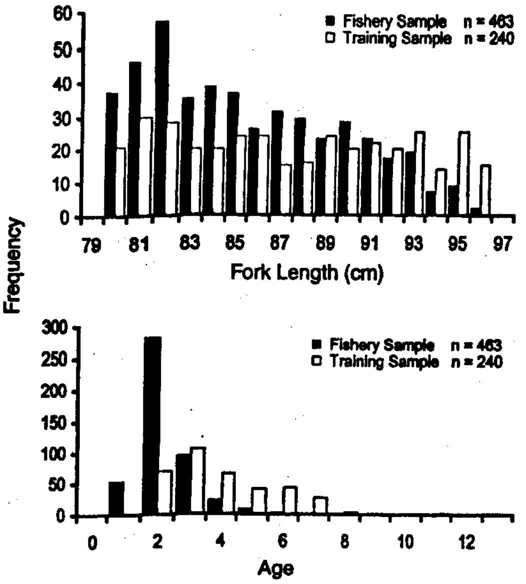

Fig. 5. Length- and age-frequency distributions of the king mackerel sampled from the east Florida, 1996–1997 winter fishery, and of those collected for the application study in the summer of 1996 to use for constructing the quadratic discriminant functions (the training data set).

over the smaller data set ($n = 240$). Estimates of Cohen's kappa indicated that the improvement over chance for all the discriminant functions shown in Table 1 ranged from 57 to 66% (with 95% confidence limits ranging from 40 to 81%) in the feasibility study and 32–44% (95% confidence limit: 24–61%) in the application study.

The estimated percentage of Atlantic stock in the landings from the 1996–1997 winter fishery was $\hat{P} = 99.8\%$ with the remainder (0.2%) from the Gulf stock. These estimates were based on the same variable suite which yielded the highest classification success in the application study and are highlighted in Table 1. The associated standard error of $\hat{P}$, derived from a bootstrap with 500 replications, was 3.4%; the estimated empirical 90% confidence interval on the proportion from the Atlantic was 89.4–99.9%; a bias-corrected (BC) 90% confidence interval (Efron, 1982) on the same proportion was 99.9–100.0%. Because BC intervals can be estimated imprecisely, it is not clear which interval is more likely to be correct here.

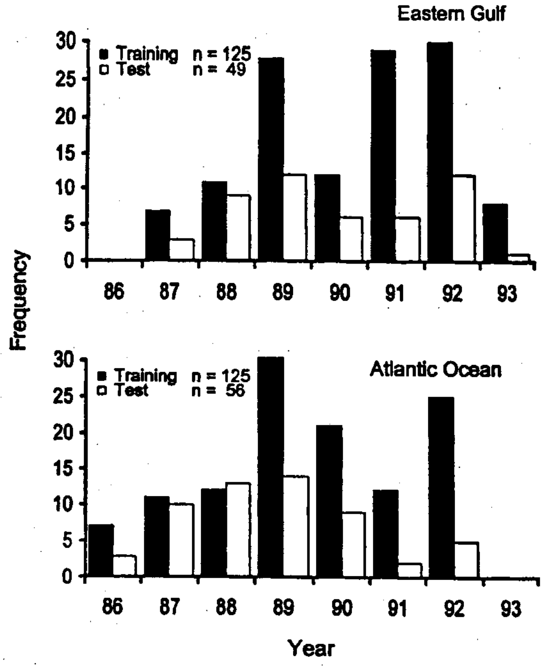

Fig. 6. Temporal distributions of king mackerel training and test data sets used in the feasibility study to construct and evaluate the quadratic discriminant functions.

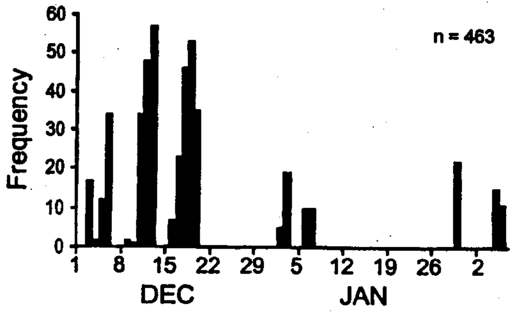

Fig. 7. Temporal distribution of the king mackerel samples from the east Florida, 1996–1997 winter fishery.

4. Discussion

The results of our feasibility study, i.e., the ability to correctly classify 80% of Atlantic and 86% of east Gulf stock king mackerel with a model based on otolith shape, convinced us that shape data can be used to estimate stock composition in the mixed-stock fishery. The estimate of Cohen's kappa indicated that

Table 1

Summary of percent correct classifications of Atlantic and East Gulf king mackerel using the quadratic discriminant function, comparing evaluation and variable selection methods for the feasibility and application studies (the two studies were based on otoliths collected during 1986–1993 and 1996, respectively)[a]

Evaluation method	Variable selection method	Correctly classified (%)		Cohen's kappa/95% CI	No. of variables	Variables included[b]
		Atlantic	Gulf			
Feasibility study						
CV[c]	F[d]	77.6	80.8	0.58/0.48–0.69	6	Perimeter, 6, 8, 9, 13, 19
	F	80.8	76.8	0.58/0.47–0.68	8	Area, 6, 7, 8, 9, 13, 17, 18
	B[e]	77.6	79.2	0.57/0.46–0.67	13	Perimeter, 2, 4, 6, 7, 8, 9, 10, 13, 14, 15, 17, 20
	B	76.0	81.6	0.58/0.47–0.68	12	Perimeter, 2, 3, 4, 6, 7, 8, 9, 10, 13, 14, 15
ITD[f]	F	75.0	81.6	0.56/0.40–0.73	5	11, 12, 14, 16, 19
	F	78.6	79.6	0.58/0.42–0.74	6	10, 11, 12, 14, 16, 19
	B	80.4	85.7	0.66/0.51–0.81	15	Perimeter, area, 1, 5, 6, 9, 10, 11, 13, 14, 15, 16, 19, 20
Application study						
CV ($n = 240$)	F	65.8	71.7	0.38/0.26–0.50	7	Perimeter, 3, 6, 10, 13, 14, 17
	B	65.8	75.0	0.41/0.29–0.53	11	Perimeter, area, 1, 6, 8, 10, 13, 14, 15, 17, 20
CV($n = 320$)	F	66.9	65.0	0.32/0.24–0.40	4	Perimeter, 10, 12, 16
	B	68.1	74.4	0.43/0.32–0.53	12	Perimeter, area, 1, 3, 6, 7, 10, 11, 13, 15, 18, 19
ITD	F	72.3	67.5	0.37/0.20–0.55	3	Perimeter, 5, 8
	B	*71.1*	*77.5*	*0.44/0.28–0.61*	*12*	*Perimeter, area, 3, 4, 6, 8, 9, 11, 13, 16, 17, 18*
	B	67.5	80.0	0.42/0.26–0.59	12	Perimeter, area, 3, 4, 6, 7, 8, 10, 11, 16, 17, 18

[a] The row in italics is the variable suite used to estimate stock composition of the 1996–1997 winter fishery.

[b] Numbers indicate Fourier harmonic number.

[c] Cross-validation.

[d] Forward.

[e] Backward.

[f] Independent test data.

these success rates were significantly better than the 50% expected by chance alone. We believe stock composition can best be estimated by developing a model with data collected during a spawning season and using that model to estimate stock composition in the ensuing mixed-stock fishery the following winter. In such a procedure, any growth anomalies present in the current cohorts might serve to accentuate differences in otolith shape and improve the quality of estimation.

The high, and similar, classification success in both phases of the study (71–86%) strengthened our confidence in using shape data to estimate stock mixing proportions. That the single-year (1996) data set did not produce a discriminant function with a classification success rate higher than that obtained in the feasibility study from 8 years of pooled data was not surprising, and does not invalidate our hypothesis about the possible advantage of using recently collected shape data. Only if there was a strong year class dominating the samples of one of the stocks, or a different one in each stock, or if growth rates had changed markedly, one would expect an improved discrimination ability.

Ehrllich et al. (1983) argued that Fourier coefficients of lower harmonics are interpretable and relate to the general shape of the otolith; however, most of the harmonics used in our maximum likelihood estimation procedure were higher level ones that defined the finer details of the otolith perimeter, making it difficult to relate them to actual shape differences between the two stocks. The senior author, with over 13 years experience examining over 20 000 specimens, has seen considerable variation in shape within stocks but has not noticed, just by eye, any obvious, consistent shape differences between them. Although it is somewhat unsatisfying that there is not a clear relationship between many of the Fourier harmonics

and morphological characteristics of the otoliths, the important fact is that these harmonics do provide a repeatable, statistically valid way to distinguish the two stocks. As Cadrin and Friedland (1999) noted, "Fourier analysis is apparently an efficient method for describing outline shapes, but understanding the reason for subtle, but statistically significant, shape differences is abstract".

By using a finite-mixture method for the final estimate of stock composition, we avoided a pitfall in the use of discriminant analysis: the need to provide estimates of the priors. Because classification success of discriminant analysis depends on having correct priors,[3] we recommend that fishery scientists not use discriminant analysis to estimate mixture compositions and instead use more appropriate methods, such as those of Fournier et al. (1984), Millar (1990b), and Pella and Robertson (1978). Work remains to be done to determine specific algorithms that will serve fishery science best.

The BC confidence intervals computed are somewhat questionable. Such intervals assume the quantity on which the interval is constructed can be transformed to normality. Because our intervals are on proportions, and because the distributions of bootstrap estimates were highly asymmetric, validity of the intervals is unknown. Nonetheless, the small standard errors on the estimates suggest the estimates are precise. More extensive simulation trials—beyond the scope of this paper—would be needed to gather detailed information on the properties of the estimates used here.

Some assumptions were necessary in estimating stock composition. Our models were based only on female fish, thus we had to assume sex ratios of the two stocks were similar, and males mixed at the same rates as females; both of these assumptions seem reasonable. The higher the proportion of females in each stock, the less is the potential for problems resulting from the use of only females. Trent et al. (1981) found that among fish >70 cm, females dominated commercial catches in south and southeast Florida in the late 1960s and mid-late 1970s. Because shape data were collected only from fish 80–96 cm long, we also had to assume mixing rates of fish outside this range were no different, or that most of the fishery was composed of fish within this size range (as was the case in this study). Finally, we assumed the samples collected from the mixed-stock fishery adequately represented the total catch. King mackerel are schooling fish that may school by stock, and schools may remain in an area for more than 1 day; thus, we sampled throughout the fishing season, collecting otoliths on 21 days between 3 December and 6 February. We also sampled at four different sites between Cape Canaveral and Palm Beach County to account for possible latitudinal segregation of stocks within the fishing grounds.

Our estimate of stock composition—that the vast majority of the fish in the 1996–1997 mixed-stock fishery were from Atlantic stock—is virtually opposite to the composition the Fishery Management Councils have assumed since the mid-1980s and have incorporated in their assessments and management, i.e., 0% Atlantic and 100% Gulf. Likewise, Gold[1] found no genetic evidence, using microsatellites, that stock boundaries varied seasonally in the manner currently assumed for stock assessments. However, he did report that his data suggest continual (versus seasonal) high levels of genetic mixing, with most samples from either coast containing roughly equal numbers of Gulf and Atlantic fish. Although his findings seem to contradict ours, it could very well be that there is enough gene flow to produce considerable genetic mixing, but the management units we identified using a phenotypic character, for all practical purposes, do not mix off southeast Florida during winter.

Our findings have serious implications, and if used by the Councils, will have a significant impact on the assessment and management of the species. For example, Legault (1998) calculated that assigning all fish from the mixing area to the Atlantic group would increase the 1998/1999 allowable biological catch (ABC) for that group, assuming an $F_{30\%\ \mathrm{SPR}}$ management strategy, between about 400 and 2000 mt, depending on the level of bycatch used; under this scenario, he projected that the Gulf ABC would decrease approximately 550 mt. Estimates of fishing mortality remained about the same for both groups

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[3] An appropriate application of discriminant analysis would be estimating the probabilities of class (stock) membership of an individual, conditional on knowing the overall probabilities of class membership (the priors). For example, classifying an individual to species, based on certain characteristics, when the relative abundance of the several species is already known.

when all mixing area fish were assigned to the Atlantic group (Legault, 1998).

Regularly estimating the proportions of each migratory group in the winter fishery along the Florida east coast could markedly enhance future stock assessments. Available mark–recapture data suggesting over half of the fish along the Florida east coast in winter were Gulf Migratory Group fish may have never adequately supported allocation of all king mackerel caught south of the Volusia/Flagler county border in northeast Florida during November–March to the Gulf Migratory Group. Furthermore, the recent mark–recapture analyses indicate that an even smaller percentage of king mackerel (3–12%) harvested along the Florida east coast in winter may belong to the Gulf Migratory Group. Inclusion of estimates of actual proportions of each migratory group present in the winter fishery would directly address this problem.

Because of differing recruitment and mortality in the two stocks over time, mixing rates are likely to be dynamic. If stock composition is estimated in the winter fishery by using otolith shape data, or any other technique, estimates should be made annually (or at least every few years) in order to follow the dynamics and accurately assess the status of the stocks.

Acknowledgements

David Libby of the Maine Department of Marine Resources and Andrew David provided valuable assistance on using Optimas to obtain Fourier coefficients. Many NMFS and cooperating state port samplers provided otolith samples, and we would especially like to thank Bill Walling, Charles Schaefer, and Claudia Dennis for their extra effort in obtaining samples from the winter fishery. Chris Palmer and Tracy Schall handled the tedious task of digitizing the otoliths. Enric Cortes, Andrew David, and Gerry Scott provided constructive comments on an earlier version of the manuscript.

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