Abstract.—Evidence supporting a two stock hypothesis for king mackerel, *Scomberomorus cavalla*, in the Gulf of Mexico was developed principally from the results of electrophoretic patterns of one polymorphic dipeptidase locus and supporting evidence from mark-recapture, charterboat catch, and spawning studies.

There are two identifiable stocks of king mackerel in the Gulf of Mexico: a western stock and an eastern stock. The western stock migrates northward along the Mexico-Texas coast during the spring and early summer from its winter grounds in Mexico (Yucatan Peninsula). This stock has a high frequency of the dipeptidase *PEPA-2*a* allele. The eastern stock migrates at the same time northward along the eastern coast of the Gulf of Mexico from its winter grounds in south Florida (Gulf of Mexico and Atlantic coast). This stock has a high frequency of the dipeptidase *PEPA-2*b* allele. Both stocks migrate simultaneously into the northern Gulf of Mexico and mix at varying degrees in the northern summering grounds (Texas to northwest Florida).

Manuscript accepted 17 August 1993
Fishery Bulletin 92:91–101 (1994)

Evidence for distinct stocks of king mackerel, *Scomberomorus cavalla*, in the Gulf of Mexico

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The king mackerel, *Scomberomorus cavalla,* is a widely distributed, coastal pelagic species in the western Atlantic Ocean. This scombrid is found from the Gulf of Maine to Rio de Janiero, Brazil, including the Gulf of Mexico and Caribbean Sea (Rivas, 1951; Collette and Nauen, 1983). It is a valuable resource that supports fisheries throughout most of its range (Manooch et al., 1978).

The U.S. and Mexico have been major exploiters of king mackerel resources. U.S. commercial landings have been reported since 1888. Landings have ranged from 2,213 metric tons (t) (1972) to 4,746 t (1974). U.S. recreational catches are estimated to be two to ten times larger than the commercial catches (Deuel and Clark, 1968; Deuel, 1973; Manooch, 1979; U.S. Dep. Commer., 1984, 1986, 1987). In Mexican waters, commercial landings for king mackerel from 1968 to 1988 have ranged from 784 t (1968) to 6,133 t (Collins and Trent, 1982[1]).

Because king mackerel are presently managed in the southeastern U.S. (represented by more than eight states and two regional fishery management council jurisdictions) and support both recreational and mixed gear commercial fisheries, the identities of component stocks are important. Current management of king mackerel fisheries assumes two migratory stocks with overlapping ranges, one in the U.S. Atlantic Ocean and one in the Gulf of Mexico (Gulf of Mexico and South Atlantic Fishery Management Councils, 1985). This separation is based on mark-recapture results (Sutherland and Fable, 1980; Williams and Godcharles, 1984[2]; Sutter et al., 1991).

The concept of a stock is one of the most fundamental to fishery management. A stock is variously defined, ranging from the strict definition of a single interbreeding population to a unit capable of in-

[1] L. A. Collins and L. Trent, Natl. Mar. Fish. Serv., Panama City, FL, pers. commun. 1992.

[2] Williams, R. O., and M. F. Godcharles. 1984. Completion report, king mackerel tagging and stock assessment. Project 2–341–R. Fla. Dep. Natl. Resour. Unpubl. Rep., 45 p.

dependent exploitation or management and containing as much of an interbreeding unit or as few reproductively isolated units as possible (Royce, 1972). An additional term that has been used to define the stock concept used in fishery management is "unit stock" which was referred to by Kutkuhn (1981) as "one consisting of randomly interbreeding members whose genetic integrity persists whether they remain spatially and temporally isolated as a group, or whether they alternately segregate for breeding and otherwise mix freely with members of other unit stocks of the same species." This term is more functional for application to many marine resources which have identifiable components but for which reproductive isolation has not been demonstrated. We consider stock and unit stock to be identical with regard to king mackerel resources at the present time.

Using Kutkuhn's (1981) definition, this report presents evidence of two stocks of king mackerel existing in the Gulf of Mexico (the Gulf), an eastern and a western stock which winter off south Florida and off the Yucatan peninsula (Mexico), respectively. In the spring these fish migrate along their respective coasts to summer areas in the northern Gulf. The concept of two Gulf of Mexico stocks was first presented by Baughman (1941). He based his hypothesis on observations by fishermen of simultaneous migrations along the eastern and western sides of the Gulf. More recently, May (1983)[3] reported electrophoretic differences in king mackerel between the eastern and western Gulf. Using more recent tagging data and electrophoretic information, Grimes et al. (1987) reintroduced the hypothesis.

Additional evidence for a two-stock hypothesis is the following:

1 Fish movements along the coast, as indicated by mark-recapture studies (Fable et al., 1990[4]).
2 The simultaneous migration along the eastern and western coasts of the Gulf in spring and early summer as detected by analysis of charterboat CPU data (Trent et al., 1987b).
3 The difference in spawning times of king mackerel in the northern and southern areas of the Gulf (Grimes et al., 1990).

[3] May, B. 1983. Genetic variation in king mackerel (*Scomberomorus cavalla*). Final Rep. Fla. Dep. Natl. Resour. Contract C-14–34, 20 p.

[4] Fable, Jr., W.A., J. Vasconcelos P., K. M. Burns, H. R. Osburn, L. Schultz R., and S. Sanchez G. (1990). King mackerel, *Scomberomorus cavalla*, movements and migrations in the Gulf of Mexico. Natl. Mar. Fish. Serv., Panama City Lab., Panama City, FL (unpubl. ms.).

We report the results from electrophoretic investigations and summarize current information from tagging, migration, and spawning time studies. We also propose a possible mechanism to explain the observed results with regard to the water circulation of the area.

Methods and materials

Samples of muscle tissue, along with fork length (mm) and sex, were collected during 1985 through 1990 from fish obtained in recreational and commercial fisheries from North Carolina to Yucatan (Table 1). The samples were frozen as soon as possible in the field and then shipped frozen to the National Marine Fisheries Service's Panama City Laboratory. Muscle tissue (about 10 grams) was excised from each sample and stored in a freezer (in 1985 at –5° to –10°C and from 1986 through 1990 at –100°C).

Tissue extracts were prepared by mixing equal volumes of muscle tissue and distilled water and grinding with glass rods to uniform pastes. Extracts were centrifuged at 3,400 rpm (1,000 × G) for five minutes, then supernatants were drawn onto 4 mm × 8 mm filter paper inserts (Whatman 1).

Starch gel electrophoretic separation of the extracts was performed following the methods of Kristjansson (1963). Electrophoretic buffers were those of A) Markert and Faulhaber (1965), and B) N-(3–aminopropyl)-morpholine-citrate (pH 6.1) buffer of Clayton and Tretiak (1972). The gel consisted of 35 g of starch (Sigma Chemical Co. lots 123F-0591, 35K-0383, and 94F-0536) plus 250 mL of buffer. Amperage during electrophoresis was kept below 50 MA, and voltage varied between 100 and 400 V, depending on the buffer. Temperature was maintained at 2°C by using a refrigerated cooling system (see Aebersold et al., 1987, for description). After electrophoresis, the gels were sliced into four horizontal sections and stained for dipeptidase (EN 3.4.-.-). In 1985 (1,223 fish) and 1988 (879 fish), 27 additional enzymes were examined. Methods followed May (1983)[3] and Aebersold et al. (1987).

We conducted statistical analyses using Biosys-1 (Swofford and Selander, 1981) to test for conformance to Hardy-Weinberg expectations and spatially related differences in allele frequencies compared to distance and physical feature subdivisions. The Kolmogorov-Smirnov goodness-of-fit test was used for comparing allele distributions by size of fish (100–mm-FL intervals), while the chi-square contingency test was used for comparing allele distributions by sex (see Sokol and Rohlf (1981) for procedures).

Table 1

King mackerel (*Scomberomorus cavalla*) *dipeptidase*-2^*a allele frequencies by state for each month and year.

State and year	Month[1]												
	1	2	3	4	5	6	7	8	9	10	11	12	Total
Gulf of Mexico													
Florida[2]													
1985		0.050(26)				0.012(83)	0.132(32)		0.034(29)				0.041(170)*
1986							0.107(28)		0.93(43)				0.099(71)
1987				0.000(8)	0.000(24)	0.257(191)*		0.000(31)	0.085(106)				0.161(360)*
1988				0.000(8)		0.138(40)*	0.017(64)		0.033(75)	0.167(21)			0.072(208)*
1989	0.174(23)				0.160(53)		0.026(39)	0.100(115)*	0.159(148)*	0.159(148)*			0.128(378)*
1990	0.677(12)		0.167(9)	0.000(4)	0.042(24)*	0.125(88)	0.402(61)*	0.182(22)					0.227(220)*
Alabama													
1986							0.186(35)		0.038(26)				0.123(61)
1987					0.159(44)*	0.179(14)	0.468(77)		0.380(83)*				0.353(218)*
1988							0.920(88)						0.920(88)
1989								0.688(8)					0.688(8)
1990							0.306(18)						0.306(18)
Mississippi													
1986							0.684(38)	0.147(17)	0.,788(14)				0.551(69)*
1987						0.579(19)			0.564(47)				0.568(66)
1988						0.935(23)	0.750(32)		0.206(17)				0.671(72)*
1989									0.833(3)				0.833(3)
1990						0.500(9)*	0.333(13)	0.000(13)					0.250(34)*
Louisiana													
1985									0.040(25)	0.940(25)	0.477(22)	0.615(52)	0.536(124)*
1986							0.455(44)*	0.520(25)*				0.382(17)	0.459(86)*
1987	0.612(58)						0.541(148)	0.606(109)	0.633(64)				0.586(379)
1988							0.750(60)	0.306(18)					0.647(78)
1989							0.534(29)						0.534(29)
Texas (east)[3]													
1986							0.851(104)*	0.575(100)*					0.716(204)*
1987								0.606(113)					0.606(113)
1988							0.911(225)*						0.911(225)*
1989							0.814(110)*	0.902(132)					0.806(242)*
1990					0.000(1)	0.657(35)							0.639(36)
Texas (south)[3]													
1985					0.000(1)	0.657(35)							0.463(353)
1986					0.929(7)	0.515(67)	0.434(234)	0.353(17)	0.536(28)				0.777(146)
1987					0.457(47)	0.735(34)	0.655(103)	0.725(302)		0.810(42)			0.695(528)

Table 1 (Continued)

State and year	Month[1] 1	2	3	4	5	6	7	8	9	10	11	12	Total
Texas (south)[3] Continued													
1988					0.921(101)*	0.978(93)*	0.750(138)*	0.799(127)					0.847(459)*
1989				0.967(15)	0.911(84)*	0.963(41)	0.953(109)	0.833(24)	0.922(53)				0.934(324)*
1990				0.935(46)	0.667(3)	0.766(64)	0.836(61)						0.833(174)*
Veracruz, MX													
1985				0.031(16)									0.31(16)
1986				0.910(100)*		0.896(91)		0.600(70)					0.822(261)
1987				0.801(187)									0.801(187)
1988				0.810(77)									0.810(77)
1989			0.883(192)*										0.883(192)*
1990			0.969(128)*										0.969(128)*
Yucatan, MX													
1986		0.447(76)						0.778(18)					0.511(94)*
1987				0.716(76)									0.716(76)
1988			0.670(100)*										0.670(100)*
1990			0.846(159)*										0.846(159)*
Atlantic Coast: Florida													
1985		0.017(60)				0.010(50)	0.040(161)						0.037(271)*
1986						0.000(15)	0.034(104)	0.067(15)					0.034(134)
1987				0.031(16)	0.063(16)								0.047(32)
1988					0.67(45)	0.158(19)		0.079(19)				0.125(20)	0.097(103)
1989		0.077(13)											0.077(13)
1990	0.150(30)					0.667(3)							0.197(33)
Georgia													
1986					0.032(31)	0.015(66)							0.021(97)
1988					0.105(19)	0.154(13)	0.118(5)						0.106(47)
1989				0.42(36)			0.100)90)		0.188(16)				0.102(142)
1990					0.035(43)	0.000(3)	0.197(60)						0.123(106)
South Carolina													
1985							0.048(31)*	0.013(78)					0.023(109)*
1986						0.000(19)	0.022(113)*						0.019(132)*
1988				0.111(9)	0.180(50)*	0.100(75)		0.231(130					0.139(147)*
1989				0.083(18)	0.237(17)	0.021(29)	0.056(45)						0.064(109)
1990					0.000(26)	0.060(29)							0.036(55)*
North Carolina and Virginia													
1985							0.000(17)		0.063(8)	0.047(95)	0.000(5)		0.040(125)
1986						0.023(132)							0.034(132)
1987					0.011(45)	0.060(50)	0.000(17)						0.031(112)
1988						0.188(8)	0.083(30)						0.105)38)
1989					0.024(21)	0.000(18)							0.013(39)

[1] *PEPA-2*a* allele frequencies by month. In parenthesis ( ) is number of fish. Asterisk (*) means sample phenotypic distribution deviated from Hardy-Weinberg expectations ($P<0.05$).
[2] Key West to Pensacola, FL. Months 1–4 from Ft. Meyers to Key West, FL. Months 5–12 from Panama City to Pensacola, FL.
[3] Texas (east) is Galveston, TX. Texas (south) is Port Aransas to Brownsville.

Results

Of the 50 loci surveyed in 1985, 30% were variable. In 1988, the 50 loci were again surveyed (879 fish from 10 locations) and 24% of the loci were found to have variants. Variations other than dipeptidase (EN 3.4.-.-) *PEPA-2** were found in low frequency (uncommon allele 0.000 to 0.063) in 18 polymorphic systems. Occurrence of these variants differed between locations and years. Electrophoretic variants were found for loci including aspartate aminotransferase (EN 2.6.1.1) *sAAT**, acid phosphatase (EN 3.1.3.2) *ACP-2**, adenosine deaminase (EN 3.5.4.4) *ADA**, adenylate kinase (EN 2.7.4.3) *AK-1** and *AK-2**, alanine aminotransferase (EN 2.6.1.2) *ALAT-1** and *ALAT-2**, esterase-D (EN 3.1.-.-) *ESTD-2** and *ESTD-3**, fructose-bis-phosphate aldolase (EN 4.1.2.13) *FBALD-2**, glucose-6–phosphate isomerase (EN 5.3.1.9) *GPI-1** and *GPI-2**, isocitrate dehydrogenase (NADP+) (EN 1.1.1.42) *sIDHP**, malic enzyme (NADP+) (EN 1.1.1.38) *ME-2**, mannose-6–phosphate isomerase (EN 5.3.1.8) *MPI**, dipeptidase (EN 3.4.-.-) *PEPA-1**, phosphogluconate dehydrogenase (EN 1.1.1.44) *PGDH**, and phosphoglucomutase (EN5.4.2.2) *PGM-2**.

Use of very low-frequency variations for stock identification of king mackerel was impractical, because sufficient sample sizes (numbers of fish) for detection during short time periods (one month or less) were unavailable. Tagging studies (Fable et al., 1990[4]) indicated that discrete geographic population units were not available during the time intervals required to obtain sufficient samples. Only dipeptidase (glycyl-leucine substrate)[5] consistently varied between locations. In 1985 (1,223 fish), 1986 (1,537 fish), 1987 (2,120 fish), 1988 (1,631 fish), 1989 (1,502 fish), and 1990 (963 fish), muscle tissues were examined for the dipeptidase variation. This enzyme developed on electropherograms as two zones of activity, and showed the pattern of a two allele (**a* and **b*) polymorphism in the most anodal zone (*PEPA-2**, in most collections, as described by May [1983]). We refer to May's 1 and 2 alleles (electromorphs) as **a* and **b*, respectively (Fig. 1). A third allele (**c*) which is anodal of the **a* allele was found in 1988 and 1989 collections from Veracruz, Mexico to Alabama.[6] Only one homozygote (**c***c*) and 20 heterozygotes (**c***a*) were found from 3,487 fish.

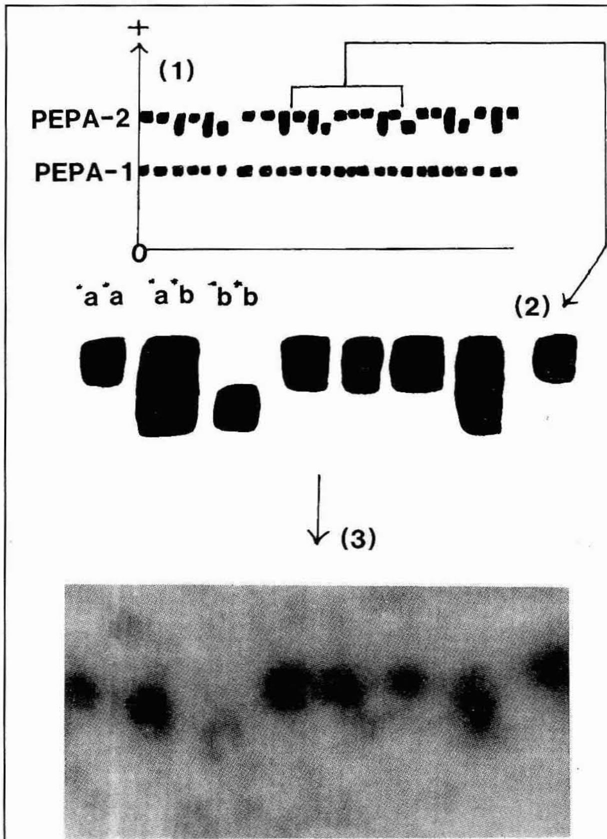

Figure 1

King mackerel (*Scomberomorus cavalla*) dipeptidase (*PEPA-1** and *PEPA-2**): (1) schematic of gel with 25 samples (*PEPA-2***a* is 0.700), (2) schematic of enlargement of section of *PEPA-2** on gel showing three phenotypes (**a***a*, **a***b*, **b***b*), and (3) photograph of actual gel section used for schematic (2).

Because of the rareness of this allele (**c*), it was combined with allele **a* for analysis.

Allele frequencies and phenotypic distributions varied extensively within and between areas from 1985 to 1990 (Table 1). The majority of monthly collections conformed to the Hardy-Weinberg expectation; however, many of the yearly collections did not conform. In general, higher **a* allele frequencies were found west of Florida than in Florida and along the Atlantic coast.

The phenotypic distributions of the dipeptidase polymorphism were not significantly correlated with body length, with few exceptions. When the phenotypic distribution was compared by 100–mm-FL size intervals for five geographic locations (Atlantic coast, Alabama-Mississippi, Louisiana, east Texas, and south Texas) by year, only seven of the 78 comparisons were significantly different (Kolmogorov-Smirnov goodness-of-fit test, $P<0.05$). Four of these

[5] Enzyme is also active with valyl-leucine and leucyl-tyrosine as substrates.

[6] The genetic nomenclature for this polymorphic system according to the recommendations of Shaklee, et al. (1990), is dipeptidase 3.4.-.-(*PEPA-2**) with three variant alleles **110*, **105*, and **100*. These alleles are represented in this report as **c*, **a*, and **b*, respectively.

deviant collections occurred in the northern Gulf (east Texas and Alabama-Mississippi). The other three (1988–*a*a phenotype on Atlantic coast; 1989–*b*b, and 1990–*a*a phenotypes in northwest Florida) are believed to have resulted from sampling inadequacies (in 1988, only 9 *a*a were collected on the Atlantic coast, and in 1989 northwest Florida had 136 of the 275 *b*b in the <600–mm-FL cell, which represented 167 of the 344 fish; and in 1990, northwest Florida had 12 *a*a of the 17 *a*a in the 900, 1,000, and >1,100 mm cells).

When allele distributions were compared by sex at seven locations for each year in which sufficient data were available, eight of the 23 allele comparisons deviated significantly (chi-square contingency test, $P<0.05$). Six deviant collections occurred in the northern Gulf (Texas-Mississippi 1985–1989) and were from collections that did not conform to Hardy-Weinberg expectations with regard to their phenotypic distributions. Two others occurred in Veracruz, Mexico (1988 and 1990). The total allele-sex (1985–90) comparisons for the seven locations did not deviate significantly, except for Veracruz, Mexico. Veracruz collections were dominated by small fish (<600 mm FL) of which sex determination was difficult, especially early in the year (Jan.–July) because of undeveloped gonads. Sex could only be determined for 68% of the fish tested from this area.

The geographic pattern of dipeptidase (*PEPA-2**) (1985–90) indicated that western Gulf differed from eastern Gulf and Atlantic coast king mackerel. In all years except 1985, comparison of allele counts (Table 1) of the various geographic groupings of the Gulf varied significantly ($P<0.05$) both within the Gulf and between the Gulf and the Atlantic coast. On the Atlantic coast (north of Florida vs. Florida), the variation was found not significant (except in 1990). The trend in these comparisons was for excess *a allele in the western Gulf and for excess *b allele in the eastern Gulf and the Atlantic coast.

Discussion

Comparisons of subdivisions (Table 2) show a consistently higher level of *PEPA-2*a* in western Gulf king mackerel and a deficit of this allele in king mackerel in the eastern Gulf and along the Atlantic coast.

Electrophoretic data (ours and that of May (1983)[3] indicating high dipeptidase *PEPA-2*a* frequency in the western Gulf and low *a frequency in the eastern Gulf and along the Atlantic coast supports a two stock hypothesis for king mackerel in the Gulf. Supporting information can be obtained from other investigations: mark-recapture (Fable et al., 1990[4]), charterboat catches (Trent et al., 1987b) and spawning date analysis (Grimes et al., 1990). Fish movements indicated by mark-recapture are consistent with the two stock hypothesis. The charterboat information provides evidence of simultaneous northward migration on both sides of the Gulf, while the spawning date information offers evidence for reproductive isolation.

The king mackerel dipeptidase (*PEPA-2**) variation found in 1985–90 was similar to the variation first reported by May (1983)[3]. His data showed higher dipeptidase *a allele frequencies for Louisiana (0.618) and Texas (0.736) than were found eastward.

Temporal variations in the *PEPA-2** allele frequencies are difficult to interpret without taking into consideration the migratory behavior. The variation was extreme at some locations, giving the impression that the samples were collected from different or mixed schools from different origins. For example, in east Texas (Galveston-Freeport area) (1986), five discrete collections (5 July–28 August) of 27 to 56 fish each (204 total) were sampled. The *PEPA-2*a* frequencies were 0.933, 0.769, 0.202, 0.839, and 0.037 (in collection order). In other collection periods, variations in frequencies indicated that we had sampled the same school of fish. For example, in Louisiana (1987) three collections 7 days apart (21 Aug.–4 Sept.) were obtained. Their *PEPA-2*a* frequencies were 0.590 (50 fish), 0.580 (50 fish), and 0.594 (48 fish). In view of the extreme variability of *PEPA-2** frequencies, numerous deviations from Hardy-Weinberg expectations, and sampling difficulties (one or more schools per collection), proper spatial subdivision and grouping of collections for testing specific hypotheses is arduous. The expanse of the sampling area (Virginia to Yucatan) can be divided into various subdivisions representing distance or physical features (Table 2). Examples of subdivisions by distance are the following: Mississippi westward vs. Alabama eastward, Alabama to Florida Keys, Florida vs. Atlantic coast, and Florida east vs. Georgia northward. Examples of physical subdivisions are the following: Florida peninsula (Florida east coast versus Florida west coast), eastern Gulf and Atlantic coast (Alabama to Florida Keys versus Atlantic coast), and northern and western Gulf (Louisiana-Mississippi versus Texas versus Mexican sector of the Gulf) (See also Collard and Ogren, 1990).

Caution should be applied to interpreting electrophoretic results in which variation has not been proven to be of genetic origin by the use of breeding analysis (i.e., crossing of phenotypes and analysis of offspring). Deviation from Hardy-Weinberg expectations can result from stock mixing, natural selection, or drift in small populations (Smith, 1990). While we favor the interpretation that these king mackerel data suggest stock mixing, consideration should be given to natural selection as the ultimate maintenance factor of *PEPA-2** frequencies as suggested for dipeptidase (*PEPA-LT**) and other variations found in *Menidia beryllina* (Johnson, 1974).

Electrophoretic data suggest that two stocks of king mackerel occur in the Gulf, a western stock with high frequency of the **a* allele and an eastern stock with a low frequency of the **a* allele. The northern Gulf appears to be a zone of mixing of these two stocks during the summer. Our electrophoretic information does not distinguish the eastern Gulf fish from those along the Atlantic coast.

Historical tagging data showed migration between south Florida and the north and northwest Gulf. Williams and Godcharles (1984)[2] (and Sutter et al.'s later analysis (1991) of Williams and Godcharles' data) can be examined in light of the two stock hypothesis. Williams and Godcharles tagged approximately 12,000 king mackerel off south and southeast Florida, primarily in winter months. Forty-nine tags were recovered in the northeast Gulf and another 49 tags were returned from the northwest Gulf. Almost all tagged fish were recaptured in the warmer months of the year, supporting the hypothesis of migration from wintering grounds in southeast Florida waters to northern Gulf of Mexico waters

Table 2

Comparisions of geographic groupings of allele counts of dipeptidase (*PEPA-2**) in king mackerel. (*Scomberomorus cavalla*), 1985–90.

Location[1]	Year	Alleles	χ^2	df	*P*	Remarks
MS westward vs. AL eastward (distance)[2]						
	1985	1,620	297.3417	1	<0.001	Deficient **b* in MS westward
	1986	1,676	340.9499	1	<0.001	Devidient **b* in MS westward
	1986	3,976	283.7311	1	<0.001	Deficient **b* in MS westward
	1988	2,468	812.6335	1	<0.001	Excess **b* east of Al Deficient **a* east of AL
	1990	1,926	793.5280	1	<0.001	Excess **b* east of AL Deficient **a* east of AL
Key West, FL westward vs. Atlantic coast (physical)						
	1985	2,630	329.0983	1	<0.001	Excess **a* in Gulf
	1986	2,662	879.2843	1	<0.001	Excess **a* in Gulf
	1987	3,865	271.3356	1	<0.001	Excess **a* in Gulf
	1988	3,084	643.4390	1	<0.001	Excess **b* in Atl. coast Deficient **a* in Gulf
	1989	3,004	657.913	1	<0.000	Excess **b* in Atl. Coast Deficient **a* in Atl. Coast
	1990	1,926	339.2062	1	<0.001	Excess **b* in Atl. coast Deficient **a* in Atl. coast
AL to Key West, FL vs. Atlantic coast (distance)						
	1985	1,518	0.0040	1	>0.90	
	1986	1,258	33.1770	1	<0.001	Excess **a* in Gulf
	1987	1,550	64.6325	1	<0.001	Deficient **a* in Atl. coast
	1988	1,022	10.4639	1	<0.001	Excess **a* in Atl. coast Deficient **a* in Gulf
	1989	1,406	6,2033	1	>0.01	Excess **a* in Gulf Deficient **a* in Atl. Coast
	1990	864	22.0855	1	<0.001	Excess **a* in AL to Key West, FL Deficient **a* in Atl. coast
Within northern and western Gulf (LA-MS, TX, MX) (physical)						
	1985	1,110	7.9835	2	>0.01	
	1986	1,410	135.5281	3	<0.001	Excess **b* in LA-MS Excess **a* in MX
	1987	2,416	71.5602	2	<0.001	Excess **b* in LA-MS Excess **a* in MX
	1988	2,062	40.1994	2	<0.001	Excess **b* in LA-MS Deficient **b* in TX
	1989	1,598	70.2421	2	<0.001	Excess **b* in LA-MS Deficient **a* in LA-MS
	1990	1,062	120.9159	2	<0.001	Excess **b* in LA-MS Deficient in **a* in LA-MS Deficient in **b* in MS
Within Atlantic coast (N of FL vs. FL) (distance)						
	1985	1,008	0.0738	1	>0.70	
	1986	992	1.8493	1	>0.10	
	1987	336	0.1133	1	>0.70	
	1988	616	0.9336	1	>0.30	
	1990	388	6.0278	1	>0.01	Excess **a* in FL

[1] Abbreviations are used for states: AL=Alabama; FL=Florida; LA=Louisiana; MS=Mississippi; TX=Texas; MX=Mexico

[2] In parentheses ( ) general classification of range subdivisions. See text.

in the summer. These authors also tagged fish off North and South Carolina, but none were recovered in the Gulf.

According to Fable et al. (1990),[4] king mackerel tagged in northwest Florida have been recovered in south Florida. Typically, these are the smallest and youngest tagged in the southeast United States. Sutherland and Fable (1980) showed that northeast Gulf fish migrated to south Florida. However, additional tagging (Fable et al., 1990[4]) showed that northeast Gulf fish eventually moved westward to Louisiana, Texas, and Mexico waters when they had been free for a sufficient time and grown to a larger size.

Tagging off Louisiana from 1983 to 1985 (Fable et al., 1987) indicated that the northwest Gulf may have year round residental large king mackerel that mix in the warm months with smaller migrants from south Florida and Mexico. Recent tagging data (Fable et al., 1990[4]) from this region have provided additional recoveries from both south Florida and Mexico, strengthening this interpretation. Additional support is provided by the occurrence in Louisiana of a year-round king mackerel fishery, whereas elsewhere the fishery is seasonal.

In contrast to historical reports, recent tagging (Fable et al., 1990[4]) showed movements between Texas and Mexico. Fish tagged in Texas waters migrate to both Florida and Mexico. Additionally, fish movements between Texas and eastward (as far as Panama City, FL) were documented.

Mark-recapture data (Fable et al., 1990[4]) from tagging in Mexican waters suggest that the states of Campeche and Yucatan are wintering areas for king mackerel in the western Gulf. Fish tagged in warmer months (April–July) in Texas, Tamaulipas, and Veracruz were found in Campeche and Yucatan in the winter. Tagging efforts (Fable et al., 1990[4]) in Veracruz have provided evidence of northward migrations to Tamaulipas and Texas in spring and summer, and movement to the Yucatan peninsula in winter.

Additional evidence supporting two Gulf stocks can be found in catch-effort data of king mackerel. Although the data are complicated by different fishing strategies depending on the type of fishery (recreational or commercial) and regulatory closures, detailed analysis of catch data from the southeastern United States charterboat fishery indicated that in spring and early summer some stocks of fish simultaneously migrated northward along the western and eastern coasts of the Gulf (Trent et al., 1987b). They also developed the "... idea that part of the population of large fish remains in the Louisiana area year-round and that the abundance of these fish is greatest during cold months."

The fishery for king mackerel in Louisiana is unique among the fisheries in the northern Gulf of Mexico in that it is year-round; elsewhere it takes place mainly from late spring to late fall. The winter fishery (commercial hook-and-line) in Louisiana began in 1981–82. Distinctive differences characterized winter and spring-fall seasons: 1) the smallest fish (both males and females) were caught April to October whereas the largest fish were caught between November and March; 2) females were more abundant in the winter fishery than at other times of the year (Trent et al., 1987a).

For two or more populations to maintain separate identities they must be isolated, either physically or reproductively (Hartl, 1980). In the case of Gulf king mackerel, there is evidence for reproductive isolation. Grimes et al. (1990) presented a detailed examination of the distribution and occurrence of larval and juvenile king mackerel in the Gulf (based on published reports, neuston sampling, and Mexican trap net and trawl collections). The spawning season in the northern Gulf (U.S. waters), as indicated by the seasonal occurrence of larvae, is May to October. Larval collections off Mexico were sparse and offered little information on spawning seasonality.

The summer spawning period in the northern Gulf was also indicated by seasonal gonadal development of king mackerel (Finucane et al., 1986). They reported that reproductive activity occurred from May through September; a few fish were reproductively active as early as April and as late as October. However, spawning dates of January through August for Mexican juveniles estimated from otolith data showed a bimodal distribution, which suggests that spawning seasons in Mexican waters are different from those in the northern Gulf (Grimes et al., 1990).

Two of the four collections of juvenile king mackerel in Mexico used by Grimes et al. (1990) had tissue samples (Tampico, July 1986, and Playa Norte, Sept. 1986), and we analyzed these samples for *PEPA-2** variation. Spawning dates of fish in the Tampico collection ranged from mid-February to mid-April and *PEPA-2*a* frequency was 0.896. The Playa Norte collection's spawning dates ranged from mid-April to mid-July, and *PEPA-2*a* frequency was 0.600 (Table 1).

Water circulation data for the Gulf of Mexico (Salsman and Tolbert, 1963[7]) and information from Trent et al. (1987b), Grimes et al. (1990), Fable et al. 1990,[4] along with our data on king mackerel, sug-

[7] Salsman, G. G., and W. H. Tolbert. 1963. Surface currents in the northeastern Gulf of Mexico. U.S. Navy Mine Defense Laboratory, Panama City, FL, Res. and Dev. Rep. 209, 43 p.

gest one plausible scenario with regard to king mackerel stocks in the Gulf of Mexico. A western population exists that winters and spawns in the Gulf of Campeche. The Mexican Current serves as an entrainment system for its young. As these young become older and larger, they are able to cross the region of offshore advection and utilize the northern Gulf area (Texas to Florida) for summer feeding. This stock of fish has a high *PEPA-2*a* frequency and spawns earlier in the year than fish in the northern and eastern Gulf of Mexico. No information (tagging, electrophoretic, or reproductive) is available on fish of the Yucatan Straits area and the Caribbean Sea to evaluate their relation to the western Gulf of Mexico fish. An eastern population of king mackerel uses the eastern and northern Gulf of Mexico area as entrainment systems for its young and the northern Gulf (Florida-Texas) as summer feeding grounds. The spawning area extends from Texas to northwest Florida between April and October; the majority of spawning probably occurs in the northwest Florida-Louisiana area. Tagging studies suggest that this stock uses south Florida and the southeast coast of Florida as its wintering grounds.

The Louisiana area is somewhat of an enigma. Tagging studies indicate that the area is used by fish from both sides of the Gulf, fish are in the area year-round, *PEPA-2*a* frequencies are between the extremes of the east and west Gulf, and tag recoveries from winter tagging in Louisiana have been from Louisiana and westward, whereas recoveries from summer tagging were both east and west of Louisiana. Additionally, Finucane et al. (1986) suggested an earlier distinct peak in gonadal development (May) for Louisiana-Mississippi than in northwest Florida (August) and in Texas (August). The question still remains: Does the Louisiana area have an independent spawning population that utilizes the northern Gulf currents for its life cycle? The existing evidence (especially tagging) suggests the area is not independent; however, information comes from larger fish. Thus, the area may be occupied by individuals from both sides of the Gulf which may or may not reproduce in the area. Further investigation especially on the younger life stages using other methods of analyses may answer this question.

Another group (stock) of king mackerel that impinges upon the Gulf of Mexico resources (officially recognized by Fishery Management Councils) is the Atlantic Migratory Group. This group has a varying range from Virginia to southwest Florida depending on the time of the year (Gulf of Mexico and South Atlantic Fishery Management Councils, 1985). The stock is considered to winter in South Florida and ranges along the Atlantic coast to North Carolina and South Carolina during the summer. The fish probably spawn from May to October with a peak in July (Finucane et al., 1986). These fish are currently regulated as a group with seasonal southern boundaries of lat. 25°48'N (the Collier/Monroe County line, FL) from 1 April to 31 October and lat. 29° 25'N (the Volusia/Flagler County line, FL) from 1 November to 31 March. Tagging information supports this separation (Gulf of Mexico and South Atlantic Fishery Management Councils, 1985).

*PEPA-2*a* allele frequencies are generally low (0.00–0.10) along the Atlantic coast as in the eastern Gulf of Mexico. The higher *PEPA-2*a* values (>0.10) occasionally encountered may be the result of fish entrapped in water masses coming up the coast from outside the east coast of Florida. This possibility is suggested by the recovery along this coast of drift bottles that were released in the Yucatan Straits area (Salsman and Tolbert, 1963[7]).

All these stocks need to be further investigated in order to be elevated to the status of genetic stocks (i.e., completely isolated reproductive populations of the same species).

Conclusion

Four lines of evidence for a two stock hypothesis for the Gulf of Mexico king mackerel have been presented. The two stock hypothesis states that the Gulf contains a western stock of king mackerel, which winters in Mexico and migrates in spring and early summer to the northern Gulf (Texas-Alabama), and an eastern Gulf stock which winters in south Florida and migrates in spring and early summer to the northern Gulf. The two stocks mix in the northern Gulf during the summer.

The four lines of evidence are the following:

1 Dipeptidase (*PEPA-2**) data showing western Gulf fish high in **a* allele and eastern fish low in **a* allele.
2 Mark-recapture data showing movement along both sides of the Gulf from south to north.
3 Catch data indicating simultaneous migrations northward on each side of the Gulf in early spring and summer.
4 Estimates of spawning dates suggesting possible temporal and spatial differences between the northern and southern Gulf.

Acknowledgments

Especially helpful in collecting specimens and data were staff members of the following organizations:

Florida Department of Natural Resources (Tallahassee, FL); Gulf Coast Research Laboratory (Ocean Springs, MS); Instituto Nacional de la Pesca (Mexico City, Mexico); Louisiana State University (Baton Rouge, LA); Mote Marine Laboratory (Sarasota, FL); North Carolina Division of Marine Fisheries (Morehead City, NC); Savannah State College (Savannah, GA); Texas Parks and Wildlife (Austin, TX); Virginia Institute of Marine Sciences (Gloucester Point, VA); and the various laboratories of the National Marine Fisheries Service, Southeast Fisheries Center (Miami, FL). Special thanks go to B. May, Cornell University (Ithaca, NY) for sharing his experience with king mackerel with us, to K. M. Burns, Mote Marine Laboratory (Sarasota, FL) for coordinating field work and obtaining specimens in Mexico, and to P. Ramsey, Louisiana Technical University (Ruston, LA), and to J. Shaklee, Washington State Department of Fisheries (Olympia, WA) for their helpful suggestions and efforts on our behalf.

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