**Abstract.**—Stable nitrogen ($\delta^{15}N$) and carbon ($\delta^{13}C$) isotope measurements were used to differentiate groups of king mackerel, *Scomberomorus cavalla*, in the northwestern Gulf of Mexico and off the southeastern coast of Florida, as well as off the coast of Mexico. Northwestern (+13.1‰) and southeastern (Mexico=+10.8‰ and Florida=+10.8‰) groups, as well as the Atlantic group, had significantly different stable nitrogen isotope ratios. These were attributed to isotopic variations at the base of the food chain. Variability in $\delta^{13}C$ measurements was too large and did not corroborate the $\delta^{15}N$ results. The grouping suggested by the $\delta^{15}N$ data can be explained by the influence of the Mississippi River and the Gulf of Mexico Loop Current.

# Use of stable isotopes to assess groups of king mackerel, *Scomberomorus cavalla*, in the Gulf of Mexico and southeastern Florida

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King mackerel, *Scomberomorus cavalla*, is one of the most sought after migratory pelagic resources in waters of the contiguous United States (Dwinell and Futch, 1973; Manooch et al., 1978; Manooch, 1979; Finucane et al., 1986). This species is strongly exploited by both sport and commercial fisheries, and fishing pressure may exceed maximum sustainable yields of the Gulf resource (Gulf of Mexico and South Atlantic Fishery Management Councils[1]). In the United States, commercial catches of king mackerel were 2,013 metric tons (t) in 1994 (U.S. Dep. Commer., 1995). Recreational catches in the United States are thought to be larger than commercial landings (Deuel and Clark, 1968; Deuel, 1973; Manooch, 1979; U.S. Dep. Commer., 1985–1987). Recreational catches are reported as individuals rather than as weight; however, an estimated total weight of recreational catches for 1991 was 2,713 t (U.S. Dep. Commer., 1992).

Current management plans are based on a two-stock model, an Atlantic stock and a Gulf of Mexico stock (Gulf of Mexico and South Atlantic Fishery Management Councils[1]). However, general consensus among scientists is that two stocks of king mackerel exist within the Gulf of Mexico. Evidence for two stocks within the Gulf of Mexico includes fisherman observations of migration (Baughman, 1941), electrophoretic studies (Grimes et al., 1987; Johnson et al., 1994; May[2]), catch-per-unit-of-effort data from charter boats (Trent et al., 1987), and differences in spawning times (Grimes et al., 1990).

Stable isotopes (C, N) have been used to study trophic levels and feeding strategies of organisms (see Macko et al., 1984; Peterson and Fry, 1987; Koch et al., 1995). According to DeNiro and Epstein (1978), the carbon isotopic composition of a food source is not substantially altered during assimilation. DeNiro and Epstein (1981) found that animals also reflect the nitrogen isotopic composition of their diet; however, there is a trophic-level enrichment. Regardless of habitat, form of nitrogen excreted, and growth rate, an isotopic enrichment of +3.4

[1] Gulf of Mexico and South Atlantic Fishery Management Councils. 1992. Amendment 6 to the fishery management plan for coastal migratory pelagics in the Gulf of Mexico and South Atlantic includes environmental assessment regulatory impact review and initial regulatory flexibility analysis. Gulf Mex. S. Atl. Fish. Manage. Counc., Tampa, FL, var. pagin.

[2] May, B. 1983. Genetic variation in king mackerel (*Scomberomorus cavalla*). Final Rep. FL Dep. Nat. Resour. Contract C-1434, 20 p.

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Fishery Bulletin 95:540–551 (1997).

±1.1‰ occurs for nitrogen isotopes (Minagawa and Wada, 1984). Macko et al. (1984) also demonstrated that stepwise enrichment, which occurs from trophic level to trophic level, does not vary among locations. Finally, Minagawa and Wada (1984) suggested that individuals do not fractionate nitrogen isotopes differently at various ages.

Estep and Vigg (1985) observed that the carbon isotope discrimination between scale and muscle was consistent for a particular fish species, and stated that isotopic measurements in muscle and scales could be used to determine diet of fish. Studies that encompass time scales of months to years, however, may be compromised by fast turnover of muscle. Collagen, in contrast to muscle, has a slow turnover rate of carbon (Libby et al., 1964). Collagen amino acid composition varies only slightly among species (see Schoeninger and DeNiro, 1984); therefore, differences in collagen isotope ratios reflect isotopic changes in diet and not variations in chemical composition (Schoeninger and DeNiro, 1984). Additionally, we speculate that turnover of collagen may be slower in poikilotherms, such as fish, compared with homeotherms, such as mammals, owing to the lower metabolic rate of poikilotherms. The chemical uniformity and slow turnover time of collagen make it a suitable matrix for recording the dietary history of organisms that grow fin spines (fin spines consist of collagen fibers in a bony matrix) and live over periods of years.

In the Gulf of Mexico, Fry (1983) compared stable carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope ratios of several decapod crustaceans and two species of inshore fishes. The study revealed that groups feeding primarily in the eastern Gulf of Mexico have different $\delta^{15}N$ and $\delta^{13}C$ values from those feeding in the western Gulf of Mexico (Table 1). Macko et al. (1984) also reported geographical variations in isotopic ratios of sedimentary organic matter. From these studies, we hypothesized that stable carbon and nitrogen isotopes would aid in establishing group structure if 1) king mackerel feed in different regions of the Gulf of Mexico for extended periods of time, and 2) the carbon and nitrogen isotope composition of a food source is incorporated in a consistent manner into tissues of king mackerel. Dorsal fin spines were chosen for isotopic analyses because collagen has a slow turnover rate, and the isotopic ratio of the spine should reflect assimilated food at the time of formation. Therefore, the diet recorded within the spine is chiefly a record of early developmental years, when the majority of growth occurs. A previous study, however, showed a loss of the first annulus in fin spines of older swordfish (Tsimenides and Tserpes, 1989). We could find no such study of fin spine annulus of king mackerel to substantiate this loss in king mackerel. Loss of mass has not been investigated in swordfish research; therefore, we assumed that if any material is lost, it is minimal in comparison with the remaining material, because this phenomenon has been observed only in large individuals. Below, we report on the identification of two isotopically distinct groups of king mackerel in the Gulf of Mexico and compare our findings with previous studies conducted in order to determine location and number of king mackerel groups.

**Table 1**

Mean stable isotope (C and N) values of sediment, particulate organic matter, zooplankton, shrimp, and mackerel for Florida, Northwestern Gulf of Mexico, and Mexico. Standard error is presented when available. GOM = Gulf of Mexico. nd = no data. Florida king mackerel data comprise collection sites Panama City, FL, and Fort Pierce-Palm Beach, FL. Northwestern king mackerel data comprise collection sites Port Aransas, TX; Galveston, TX; Grand Isle, LA; and Gulf Port, MS. Mexico king mackerel data comprise collection sites Dzilam DeBravo, Celestun, and Veracruz.

| | $\delta^{13}C$ | | | $\delta^{15}N$ | | |
|---|---|---|---|---|---|---|
| Sample type | Florida | Northwestern GOM | Mexico | Florida | Northwestern GOM | Mexico |
| Sediment[1] | −18.5 ±0.7 | −20.6 ±0.6 | nd | 3.6 ±0.1 | 6.5 ±0.2 | nd |
| Particulate organic matter[1] | −19.4 ±1.2 | −21.0 ±1.4 | nd | −0.9 ±1.4 | 7.5 ±0.8 | nd |
| Zooplankton[1] | −18.4 ±1.1 | −19.2 ±0.7 | nd | 5.9 ±0.7 | 8.9 ±0.9 | nd |
| *Penaeus* shrimp[1] | −14.8 ±0.5 | −15.6 ±1.1 | nd | 8.4 ±0.9 | 12.9 ±1.1 | nd |
| *Penaeus* shrimp[2] | −14.6 | −15.9 | nd | 8.3 | 12.6 | nd |
| King mackerel (this study) | −18.9 ±1.1 | −18.1 ±0.9 | −17.7 ±1.5 | 10.8 ±1.1 | 13.1 ±1.3 | 10.8 ±1.0 |

[1] Data, excluding the king mackerel data, were compiled from Fry (1983) and Macko et al. (1984).
[2] Data are based on estimated values from Figure 7 in Fry (1983).

## Methods and materials

King mackerel were obtained from the Southeast Fisheries Center, National Marine Fisheries Service, Panama City, FL, and laboratory of John R. Gold, Department of Wildlife and Fisheries Sciences, Texas A&M University. These samples were collected within the Gulf of Mexico and Atlantic Ocean (Fig. 1) during November and December 1991; February, May, and July 1992; and March, May, and June 1993 (Table 2). Two to twenty fish were analyzed per site (average of seven per locality). Locality, date collected, fork length (standard measure of size), weight and sex of the fish specimens were recorded for most samples. According to the length-at-age study of DeVries and Grimes,[3] all fish were between 1 and 19 years of age.

Stable carbon and nitrogen isotope measurements were performed on dorsal fin spines. Dorsal fin spines were extracted and frozen prior to laboratory processing. After thawing, fin spines were cleaned of epidermal and dermal tissue, soaked in a dilute solution of $HClO_3^-$ (bleach) to remove excess tissue, and then washed thoroughly with double-distilled water (no significant difference was observed with the dilute bleach method of cleaning and simply scraping the spine clean). Collagen was extracted according to the method of Tuross et al. (1988), who found that collagen extractions obtained with ethylenediaminetetraacetic acid (EDTA) yielded higher demineralization than those obtained with hydrochloric acid. Contamination of EDTA had been detected at less than 1 ng EDTA per mg of dry protein (Tuross et al., 1988). Spines of each individual were soaked separately in 50 mL of 0.5M EDTA, pH 7.2, at 4°C and shaken on a laboratory shaker for five days to remove mineralized bone. Mineralized bone was considered removed by evidence of a translucent, pale yellow appearance (Tuross et al., 1988). The remaining collagen was washed with dilute NaOH, rinsed thoroughly with double distilled water, and freeze-dried.

An investigation of sample preparation techniques was conducted to ensure accurate data collection. Incomplete removal of the mineral phase of the dorsal fin spine would cause erroneous $^{13}C$-enriched values. In turn, poor conversion of collagen carbon to $CO_2$ would result in CO production and inaccurate $^{15}N$-enriched values owing to $^{13}C^{16}O$, which interferes with the $^{15}N^{14}N$ signal on the mass spectrometer. These sources of contamination were most likely to occur in large samples, reflecting a relation between sample size and isotope value.

Owing to the large size of these dorsal fin spines, multiple sections were taken from all samples to ensure that the whole spine was measured isotopically. Spines were divided into approximately 3-mg sections; therefore, spines from larger mackerel had more sections than did spines from smaller mackerel. Each section of the dorsal fin spines was placed in a separate quartz tube with elemental copper and cupric oxide and sealed under vacuum. These sections were converted to $CO_2$ and $N_2$ gas with modified Dumas combustion (850°C for two hours ) (Macko, 1981). The $CO_2$ and $N_2$ were then isolated cryogenically and analyzed on Finnigan MAT 251 and Nuclide 3-60-RMS isotope ratio mass spectrometers. The reproducibility of the measurements for $\delta^{13}C$ was ±0.2‰ and ±0.3‰ for $N_2$. Minimum sample size was 50 µg for both $\delta^{13}C$ and $\delta^{15}N$.

Stable carbon and nitrogen isotope measurements were performed on 65 and 64 dorsal fin spines, respectively. Stable isotope ratios, denoted in parts per mil, were calculated in terms of δ as follows:

[3] DeVries, D. A., and C. B. Grimes. 1991. Spatial and temporal variation in age composition and growth of king mackerel *Scomberomorus cavalla* from the southeastern U.S., 1986–1989; implications for stock structure and recruitment variability. U.S. Dep. Commer., NOAA, NMFS, 3500 Delwood Beach Rd., Panama City, FL 32408-7403. Unpubl. manuscript, 41 p.

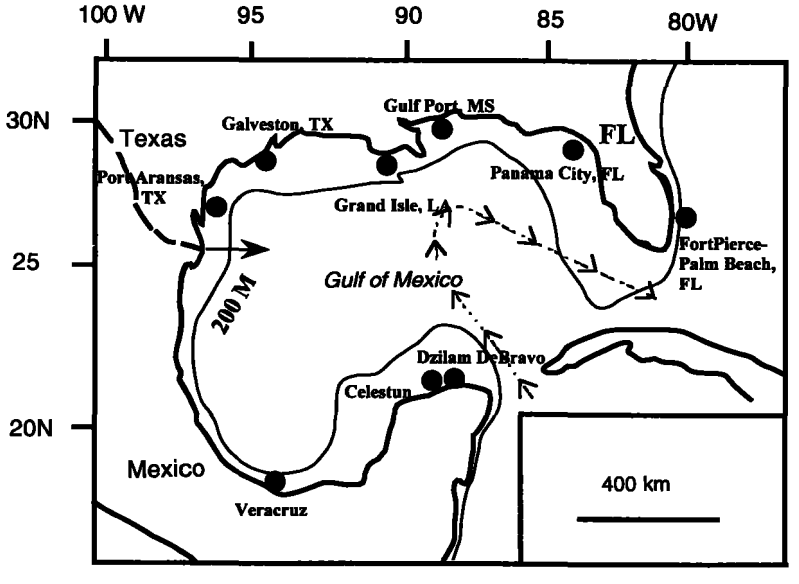


**Figure 1**

King mackerel study sites. Dotted line is mean position of the Loop Current. Arrow heads on the dotted line denote direction of flow. Solid arrow indicates convergence zone at Brownsville, TX.

**Table 2**

Mackerel collection data and range of stable isotope (C and N) values for each dorsal spine analyzed. nd = no data.

| Collection site | Sex | Fork length (cm) | Month of collection | Range of $\delta^{13}C$ (‰) for each spine | Range of $\delta^{15}N$ (‰) for each spine |
|---|---|---|---|---|---|
| Celestun, Mexico | male | 91 | 12 | 4.1 | 0.9 |
| Celestun, Mexico | female | 81 | 12 | 1.5 | 0.8 |
| Celestun, Mexico | male | 78 | 12 | 2.5 | 0.7 |
| Celestun, Mexico | female | 76 | 12 | 3.3 | 4.3 |
| Gulf Port, Mississippi | male | 126 | 7 | 3.0 | 0.2 |
| Gulf Port, Mississippi | female | 120 | 7 | 2.1 | 0.9 |
| Gulf Port, Mississippi | male | 100 | 7 | 2.6 | 0.5 |
| Gulf Port, Mississippi | male | 117 | 7 | 2.3 | 0.2 |
| Gulf Port, Mississippi | male | 85 | 7 | 2.9 | 0.5 |
| Gulf Port, Mississippi | female | 113 | 7 | 2.5 | 1.1 |
| Veracruz, Mexico | male | 71 | 5 | 1.7 | 0.7 |
| Veracruz, Mexico | male | 68 | 2 | 3.1 | 0.3 |
| Dzilam DeBravo, Mexico | unknown | 73 | 11 | 3.3 | 0.9 |
| Dzilam DeBravo, Mexico | unknown | 51 | 11 | 0.7 | 1.0 |
| Dzilam DeBravo, Mexico | unknown | 54 | 11 | 1.8 | 0.5 |
| Dzilam DeBravo, Mexico | unknown | 71 | 11 | 2.3 | 0.2 |
| Dzilam DeBravo, Mexico | unknown | 78 | 11 | 1.8 | 1.4 |
| Dzilam DeBravo, Mexico | unknown | 70 | 11 | 1.4 | 3.5 |
| Dzilam DeBravo, Mexico | unknown | 64 | 11 | 0.7 | nd |
| Dzilam DeBravo, Mexico | unknown | 79 | 11 | 3.5 | 0.2 |
| Dzilam DeBravo, Mexico | unknown | 65 | 11 | 1.4 | 0.2 |
| Dzilam DeBravo, Mexico | unknown | 93 | 11 | 1.3 | 0.3 |
| Dzilam DeBravo, Mexico | unknown | 80 | 11 | 1.2 | 0.4 |
| Dzilam DeBravo, Mexico | unknown | 73 | 11 | 2.4 | 1.1 |
| Dzilam DeBravo, Mexico | unknown | 69 | 11 | 1.3 | 0.2 |
| Dzilam DeBravo, Mexico | unknown | 65 | 11 | 0.9 | 4.1 |
| Dzilam DeBravo, Mexico | unknown | 73 | 11 | 3.8 | 0.5 |
| Dzilam DeBravo, Mexico | unknown | 80 | 11 | 3.1 | 3.0 |
| Dzilam DeBravo, Mexico | unknown | 65 | 11 | 3.6 | 2.8 |
| Dzilam DeBravo, Mexico | unknown | 89 | 11 | 2.4 | 3.2 |
| Dzilam DeBravo, Mexico | unknown | 69 | 11 | 1.2 | 1.8 |
| Dzilam DeBravo, Mexico | unknown | 79 | 11 | nd | 0.9 |
| Galveston, Texas | unknown | 86 | 7 | 2.7 | 0.6 |
| Galveston, Texas | unknown | 70 | 7 | 2.3 | 0.7 |
| Galveston, Texas | unknown | 67 | 7 | 2.9 | 0.3 |
| Port Aransas, Texas | unknown | 81 | 7 | 3.9 | 0.2 |
| Port Aransas, Texas | unknown | 81 | 7 | 0.4 | 0.8 |
| Port Aransas, Texas | unknown | 113 | 7 | 4.3 | 0.5 |
| Port Aransas, Texas | unknown | 94 | 7 | 3.0 | 2.9 |
| Port Aransas, Texas | unknown | 75 | 7 | 3.0 | 1.1 |
| Port Aransas, Texas | unknown | 97 | 7 | 3.4 | 0.7 |
| Port Aransas, Texas | unknown | 88 | 7 | 2.2 | 0.6 |
| Port Aransas, Texas | unknown | 91 | 7 | 1.6 | 0.1 |
| Port Aransas, Texas | unknown | 121 | 7 | 5.4 | 1.0 |
| Grand Isle, Louisiana | unknown | 88 | 7 | 2.6 | 0.1 |
| Grand Isle, Louisiana | unknown | 99 | 7 | 2.5 | 0.9 |
| Grand Isle, Louisiana | unknown | 49 | 7 | 2.4 | 1.1 |
| Grand Isle, Louisiana | unknown | 74 | 7 | 1.1 | 0.3 |
| Grand Isle, Louisiana | unknown | 58 | 7 | 0.4 | 0.1 |
| Grand Isle, Louisiana | unknown | 73 | 7 | 2.7 | 0.2 |
| Grand Isle, Louisiana | unknown | 75 | 7 | 2.4 | 0.2 |
| Grand Isle, Louisiana | unknown | 96 | 7 | 4.2 | 0.2 |
| Grand Isle, Louisiana | unknown | 61 | 7 | 1.9 | 0.9 |
| Grand Isle, Louisiana | unknown | 80 | 7 | 3.1 | 0.4 |
| Panama City, Florida | female | 85 | 6 | 2.6 | 0.3 |
| Panama City, Florida | female | 80 | 6 | 2.9 | 0.2 |

**Table 2 (continued)**

| Collection site | Sex | Fork length (cm) | Month of collection | Range of $\delta^{13}C$ (‰) for each spine | Range of $\delta^{15}N$ (‰) for each spine |
|---|---|---|---|---|---|
| Panama City, Florida | female | 84 | 6 | 1.5 | 0.6 |
| Panama City, Florida | female | 81 | 6 | 3.0 | 0.6 |
| Panama City, Florida | female | 80 | 6 | 2.2 | 0.3 |
| Panama City, Florida | female | 90 | 6 | 2.0 | 0.4 |
| Fort Pierce-Palm Beach, FL | female | 102 | 5 | 2.2 | 0.5 |
| Fort Pierce-Palm Beach, FL | male | 100 | 5 | 3.5 | 0.3 |
| Fort Pierce-Palm Beach, FL | male | 87 | 5 | 3.5 | 0.7 |
| Fort Pierce-Palm Beach, FL | male | 71 | 3 | 1.3 | nd |
| Fort Pierce-Palm Beach, FL | male | 75 | 3 | 2.1 | 0.4 |
| Fort Pierce-Palm Beach, FL | male | 70 | 3 | 1.7 | 0.2 |

$$\delta X\,[‰] = (R_{sample}/R_{standard} - 1) \times 10^3, \quad (1)$$

where $X$ = the heavier isotope (either $^{13}C$ or $^{15}N$); and
$R$ = the ratio (either $^{13}C$:$^{12}C$ or $^{15}N$:$^{14}N$).

The working standard for carbon was tank $CO_2$ which was identified as $\delta^{13}C_{PDB} = -1.85‰$, and the standard for nitrogen was $N_2$ from air, which is 0‰ by definition (see Eq. 1).

Because spines were too large to measure whole, they were divided into segments that were analyzed separately, and the weighted average was calculated as

$$\frac{\sum_{n=1}^{x}(W_n)(\delta_n)}{\sum_{n=1}^{x}W_n} \quad (2)$$

where $W_n$ = weight of the segment in milligrams; and
$\delta_n$ = isotopic value for the segment.

Multivariate analysis of covariance (MANCOVA) was used to determine which independent variables had significant effects in the general linear models (GLM) (Eqs. 3 and 4) (SAS, 1990).

$$\delta^{15}N \text{ or } \delta^{13}C = collection\ site + season + sex; \quad [\text{length was used as a covariate.}] \quad (3)$$

$$\delta^{15}N \text{ or } \delta^{13}C = region + season + sex; \quad [\text{length was used as a covariate.}] \quad (4)$$

If an independent variable did not have a significant effect on the model, the variable was eliminated and the GLM was conducted again. Least squared means (LSmeans) and a pairwise comparison, with a 95% confidence interval ($P$=0.05), were performed to determine significant differences in nitrogen and carbon isotope data between sample collection sites and regions. As king mackerel increased in fork length, an increase in $^{15}N$ was observed (Fig. 2B); therefore, analysis of covariance was used to control for differences in fish size. Fork length was used as the covariate.

## Results

No significant correlation between weight of the fin spine sample segment and $\delta^{15}N$ ($r^2$=0.03) or $\delta^{13}C$ ($r^2$=0.06) was detected for any of the samples, suggesting that the mineral phase had been completely removed, and 100% collagen carbon and nitrogen as $CO_2$ and $N_2$ had been recovered, respectively.

Isotopic variations within individual spines were examined to try to determine the life history of individuals. Spines were delineated into three portions (tip, mid, and base) (Fig. 3). The base of the spine is believed to contain more recently acquired material. Isotopic trends in carbon, along the length of the spine, were observed for many sites. Isotopic values for carbon became lighter as the fish aged (from tip to base); however, few trends existed for nitrogen. In general, the isotopic difference within the spine was generally less for nitrogen compared with carbon.

Nitrogen and carbon isotopic differences were observed between various sites and regions (Table 1; Fig. 4). In the pairwise comparison, more significant differences were found between individual sites for nitrogen isotope ratios than for carbon isotopic ratios (Fig. 4). Nitrogen isotopic data displayed a geographical pattern (Fig. 5). In general, king mackerel from Mississippi, Louisiana, and Texas were $^{15}N$-enriched in contrast with those from the Mexican

and Florida sites. Spines of individuals from Florida were typically $^{13}C$-depleted in contrast with those from the Mexico, Mississippi, Louisiana, and Texas sites.

After the nonsignificant variable (sex) was eliminated from the GLM (Eq. 3), the season of sample collection ($P$=0.0001), fork length ($P$=0.031), and collection site ($P$=0.0001) influenced the variation in nitrogen isotope data ($F$=9.27; $P$=0.0001 for the overall model). Only collection site ($P$=0.028) significantly influenced the revised GLM (Eq. 3) for $\delta^{13}C$ ($F$=2.38; $P$=0.0281 for the overall model). A GLM was also constructed for the three regions in this study: Florida, Mexico, and northwestern Gulf of Mexico (Eq. 4). These regions were determined on the basis of previous king mackerel stock structure studies (Baughman, 1941; Trent et al., 1987; Johnson et al., 1994; May[2]) and isotopic patterns observed in previous studies (Fry, 1983; Macko et al., 1984) as well as in this study. The GLM (Eq. 4) for $\delta^{15}N$ ($F$=26.42; $P$=0.0001) showed that collection site ($P$=0.0001) and fork length ($P$=0.0023) were statistically significant regionally. Collection site ($P$=0.023) and fork length ($P$=0.047) also had a significant regional influence on $\delta^{13}C$ ($F$=4.04; $P$=0.011) (Eq. 4).

## Discussion

Although the dorsal fin spines were divided into multiple sections, and isotopic trends were observed along a spine (Fig. 3, A and B), life history could not be determined from isotopic data because it was not possible to assign accurately an age to a particular portion of the spine. The length-at-age relation varies regionally and shows large individual variation (DeVries and Grimes[3]). For example, male king mackerel from the eastern Gulf of Mexico, with a fork length of 105–110 cm, ranged from 4 to 22 years of age (DeVries and Grimes[3]). Additionally, female king mackerel are larger than males at a given age (Beaumariage, 1973; Johnson et al., 1983; DeVries and Grimes[3]) and sex was not known for the majority of the fish analyzed (Table 2).

Isotopic differences within individual dorsal spines were studied. One would generally expect the king mackerel with the greater fork length to have a larger range of isotopic values within its dorsal spine owing to variation in trophic-level feeding with size; however, no clear trends were found (Table 2). For example one 113-cm-FL female king mackerel from Gulf Port, MS, exhibited little variation among the segments analyzed. The $\delta^{15}N$ varied by only 1.1 and

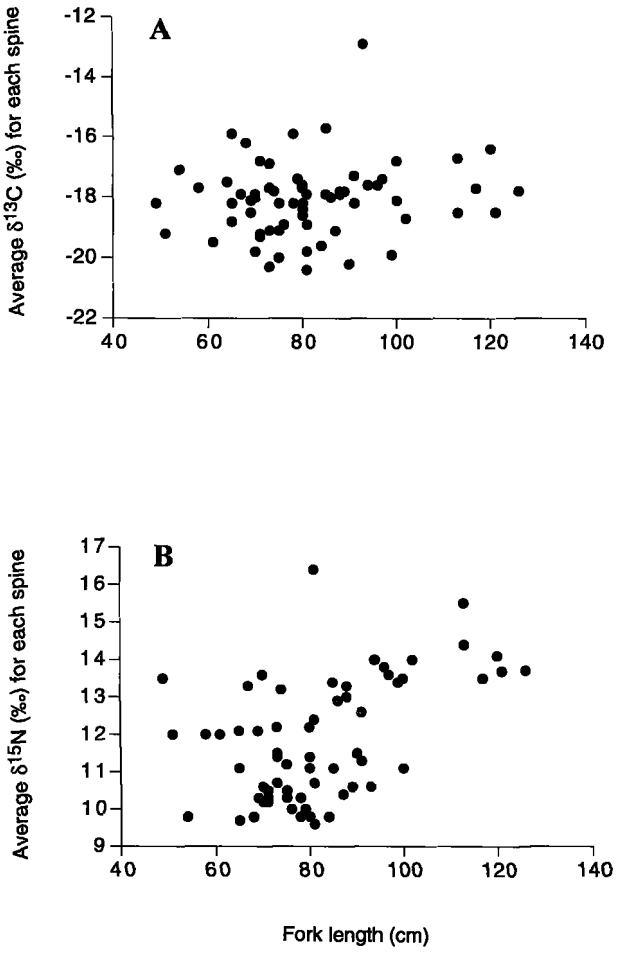


**Figure 2**

King mackerel fork length versus (**A**) stable carbon and (**B**) nitrogen isotopes. King mackerel fork length showed a positive relation to nitrogen isotopic values, but not to carbon isotopic values.

the isotopic ratio of carbon varied by only 2.5‰. Conversely, a 76-cm-FL female from Celestun, Mexico differed by 4.3‰ in nitrogen and 3.3‰ in carbon among the spine segments analyzed.

Additionally, an isotopic trend of an individual spine becoming heavier over time (from tip to base) would be expected because of an increase in trophic level feeding; however, this trend was not generally observed in the sites or regions for either carbon or nitrogen (Fig. 3). A greater enrichment in nitrogen, compared with carbon, would be expected for an increase in trophic level feeding (DeNiro and Epstein, 1978; DeNiro and Epstein, 1981); however this tendency was not observed. In fact, carbon isotopic trends were contradictory to this assumption, and no clear nitrogen isotopic trends could be detected

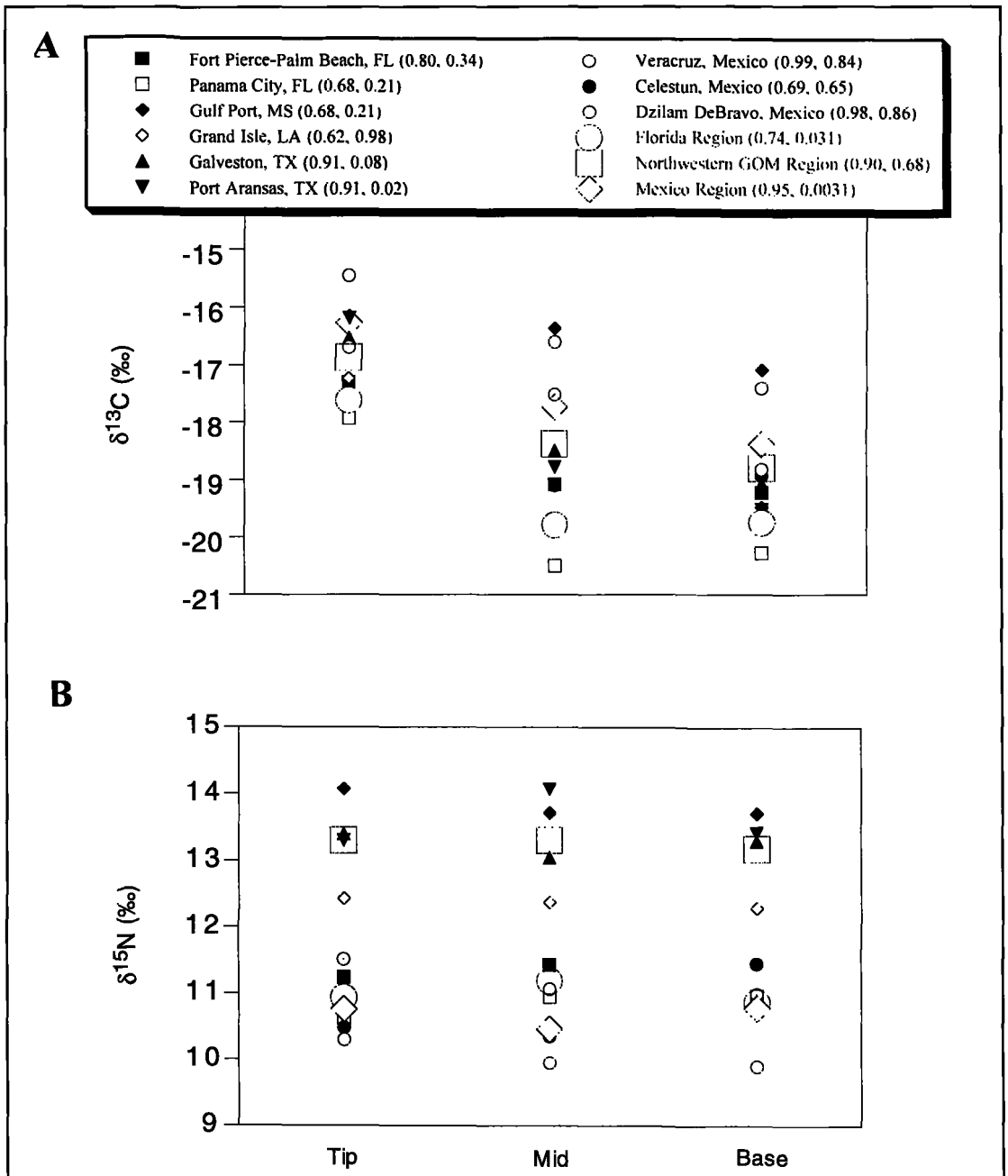


**Figure 3**

(**A**) Stable carbon and (**B**) nitrogen isotopic results along the length of a spine for each king mackerel site and region. Legend contains $r^2$ values or carbon and nitrogen isotopes respectively. Whole spines were delineated into three sections each (tip, mid, and base). If the spines had more than three divisions for analysis, the middle sections were averaged together to create one value. If the spine was divided into two sections for analysis, the middle section was excluded for the figure.

along the individual spines for the sites or regions. The data suggest a factor other than change in trophic level determines isotopic values found within the spines. Numerous factors could influence the range and trend of isotopic values found within a dorsal spine, such as feeding region, trophic-level status of the individual, and the manner in which the spine was segmented.

Stable carbon and nitrogen isotopic values at the base of the food chain vary within the Gulf of Mexico (Table 1), particularly among waters off southern Florida and the northwestern Gulf of Mexico. We

observed similar differences for mean $\delta^{15}N$ values of king mackerel spines collected in these regions. The $\delta^{15}N$ data of Macko et al. (1984), Fry (1983), and this study all showed an $^{15}N$-enriched in the northwestern Gulf of Mexico relative to samples collected in Florida and Mexico. Enriched nitrogen values are often observed off the mouths of estuaries (e.g. Cifuentes et al., 1989). This enrichment often reflects the assimilation of isotopically altered inorganic nitrogen from riverine sources by algae. The influence of the Mississippi River could account for the more positive $\delta^{15}N$ values (Lopez-Veneroni[4]) detected in the northwestern Gulf of Mexico.

In contrast to the $\delta^{15}N$ data for the king mackerel, $\delta^{13}C$ measurements were not as discriminating between sites (Fig. 4) or regions (Table 1). Although not significant, the king mackerel $\delta^{13}C$ values for the northwestern Gulf of Mexico region were more negative than those for the Mexico region. More negative $\delta^{13}C$ values were also detected at the base of the food chain in the northwestern Gulf of Mexico region in comparison with those for Florida (Table 1). The influence of the Mississippi River on the northwestern Gulf of Mexico area is most likely the primary reason for $\delta^{13}C$ values being more negative. Although $CO_2$ depletion resulting from enhanced primary production can increase $\delta^{13}C$ values (Raven et al., 1993), the primary impact of the Mississippi River is the large terrestrial input of particulate organic matter (Trefry et al., 1994) leading to more negative $\delta^{13}C$ values.

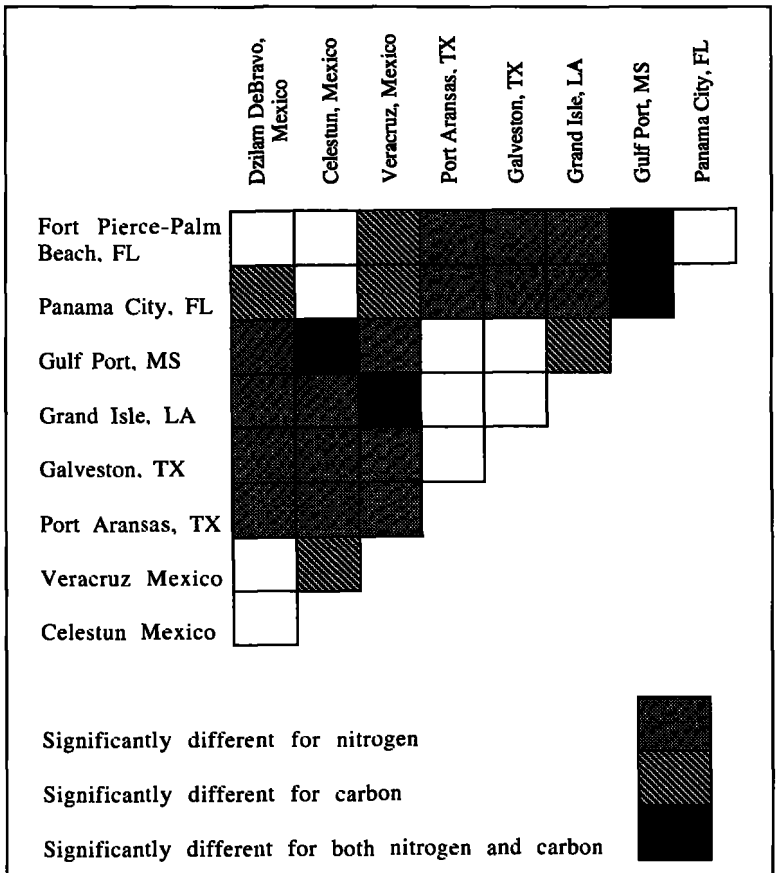


**Figure 4**

Results of MANCOVA, LSmeans, and pairwise comparison for all mackerel sites. Fork length is a covariate.

Commonly, less variability is observed in carbon isotopes than with nitrogen. This trend was not observed in this study. Our results, however, are consistent with some previous studies that reported that $\delta^{15}N$ data could be more discriminating than $\delta^{13}C$ data. For example, Sholto-Douglas et al. (1991) used carbon and nitrogen isotopes to study food web relations among plankton and pelagic fish and found greater variability in $\delta^{13}C$ data than in $\delta^{15}N$ measurements. Perhaps these systems have numerous carbon sources that create greater than expected variation in stable carbon isotope values, thereby rendering them ineffective.

Numerous studies have observed seasonal migrations of king mackerel. King mackerel migrate along the eastern coast of the Gulf of Mexico and into the northern Gulf of Mexico from southeastern Florida (wintering grounds) in the summer (Trent et al., 1987; Sutter et al., 1991; see also Johnson et al., 1994). Migrations may extend as far as Galveston and Port Aransas, TX (Williams and Sutherland, 1978). A return migration from the northern Gulf of Mexico into southeast Florida occurs in late summer and early fall (Williams and Sutherland, 1978). While the king mackerel that winter in southeast Florida are migrating into the northern Gulf of Mexico, a simultaneous migration from the Yucatan area (wintering grounds) occurs along the western coast of the Gulf of Mexico into the northern Gulf of Mexico (Trent et al., 1987; see also Johnson et al., 1994).

Wind circulation along the Mexican and south Texas coast during the late spring and early summer may cause upwelling off the Texas-Mexico border (Dagg et al., 1991). Consequently, coastal bound-

[4] Lopez-Veneroni, D. 1997. Oceanography Department, Texas A&M University, College Station, TX 77843. Manuscript in prep.

ary water masses off Mexico and south Texas may collide and form a convergence zone that directs low-salinity waters offshore, near Brownsville, TX (Vastano[5]) (Fig. 1). This convergence zone may act as a temporary boundary between northwestern Gulf of Mexico fish and Mexico fish.

The innate migratory patterns of the king mackerel can influence the isotopic values observed in their dorsal spines. The location in which food is assimilated should directly influence the isotopic value recorded in the spine. Consequently, the area in which the individual fed, rather than collection site of the individual, would be detected in the spine. Therefore, determination of groups of king mackerel from collection site alone, may be inappropriate. In addition, regional groupings of the mackerel that were based upon isotopic data and on previous king mackerel studies may be more suitable for drawing conclusions.

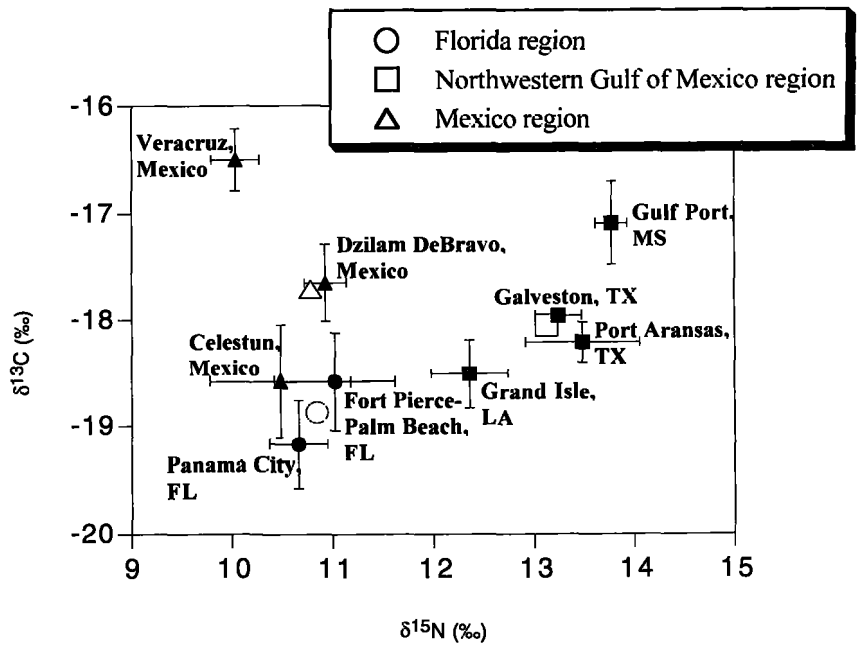


**Figure 5**

Weighted mean $\delta^{15}N$ versus $\delta^{13}C$ values for all king mackerel sample collection sites and regions. Number of samples per site can be seen in Table 2. Standard error bars are shown for sites. Regions were defined according to stable isotopic data and stock structure studies (Baughman, 1941; Fry, 1983; Macko et al., 1984; Trent et al., 1987; Fable et al., 1990; Johnson et al., 1994; May[2]).

Likewise, the migratory nature of king mackerel complicates the use of season of collection as a variable (Table 2). For example, the GLM (Eq. 3) indicated that the season in which the specimens were collected, fork length, and collection site influenced the nitrogen isotope results. However, when the data were divided into regions, fork length and region were the only variables that had a significant effect on the GLM (Eq. 4). Again, consideration of the data by region, as opposed to individual site, may be more appropriate, particularly because, in the former case, time of collection did not bias the isotopic findings.

Our method of using stable isotopes is a new approach in trying to determine the number and location of king mackerel groups. An advantage of isotopic analysis over that of genetics is that stable isotopes enable researchers to view significant changes in an individual, whereas genetic methods require generations to see significant variations. The disadvantage to stable isotopes is that the signal is acquired only from areas in which food is assimilated, which may or may not represent the location and number of king mackerel groups. Although the number and location of king mackerel stocks have been researched previously by using genetic techniques (see below), several scenarios exist. Research by DeVries and Grimes (1991) has suggested the possibility of three stocks: a western Gulf of Mexico, an eastern Gulf of Mexico, and an Atlantic stock. From mitochondrial DNA data, Gold et al. (in press) found weak genetic differences between Atlantic and Gulf of Mexico king mackerel that implied more than one stock. Additionally, Johnson et al. (1994), using electrophoretic data, suggested the existence of two stocks, eastern and western, within the Gulf of Mexico. The idea of separate eastern and western stocks of king mackerel within the Gulf of Mexico has also been supported by Baughman (1941), May,[2] and Trent et al. (1987) with observational, electrophoretic, and catch results, respectively.

Our $\delta^{15}N$ data showed significant differences between king mackerel caught in Mexican and Florida waters in contrast to those collected in the northwestern Gulf of Mexico. Thus, our isotopic results suggest that at least two distinct groups exist within

[5] Vastano, D. 1995. Oceanography Department, Texas A&M Univ., College Station, TX 77843.

the Gulf of Mexico (Fig. 5). Statistically, the Mexico and Florida regions are significantly different in carbon isotopes; however, neither region differs significantly from the northwestern Gulf of Mexico. It is conceivable that a separate Mexico and Florida group of king mackerel exists. Possibly neither site differed significantly from the northwestern Gulf of Mexico owing to individuals from both the Mexico and Florida regions being contained in the catch from the northwestern Gulf of Mexico. Recall, the northwestern Gulf of Mexico individuals were collected in the summer when migrations to the northwestern Gulf of Mexico from Florida and Mexico have been documented (Trent et al. 1987; Sutter et al. 1991). However, the similarity in nitrogen isotopic composition indicates that the Florida and Mexico regions are related.

A year-round sustained population in the northwest Gulf of Mexico would contribute to their isotopically different nitrogen values compared with Mexican and Florida fish. Other studies have surmised that Louisiana may have a resident population (Fisher, 1980; Fable et al., 1987) along a broad area from the Mississippi delta westward to regions off Texas, which are adjacent to oil rigs (Trent et al., 1983). These artificial structures may attract bait fish (Wickham et al., 1973). Northwestern Gulf of Mexico fish, being significantly $^{15}N$-enriched, might be a nonmigrating or a separate group of king mackerel that feed on an isotopically enriched food source compared with king mackerel from Mexico and Florida. Alternatively, it is conceivable that the individuals are migratory and that the isotopic signal is due to assimilation of material from the northwestern Gulf of Mexico region although they are not permanent inhabitants of the region.

Physical dynamics within the Gulf of Mexico may influence mixing between sites and therefore the isotopic values in mackerel found at different sites. The primary current in the Gulf of Mexico is the Loop Current, which enters the Gulf of Mexico through the Yucatan Channel and exits through the Florida Straits (Leipper, 1970; Cooper et al., 1990) (Fig. 1). This current is formed by waters from the western, north, and south Atlantic and the Mediterranean Sea that flow into the Caribbean Sea (Koch et al., 1991). It has a mean position of 88° and 89°W and 27°N (Auer, 1987). Although the Loop Current reaches into the northern Gulf of Mexico, its influence is to the east of the Mississippi Delta. Thus, Mexican and Florida fish could be linked by the Loop Current to the extent that they consume isotopically similar food sources. In contrast, fish in the northwestern Gulf of Mexico are most likely minimally affected by the Loop Current.

Northwestern Gulf of Mexico fish may also be strongly influenced by runoff from the Mississippi River system (Dagg et al., 1991). The majority of this runoff (two thirds) is westward and contains high concentrations of dissolved nutrients in relation to the open Gulf of Mexico (Dagg et al., 1991). Dagg et al. (1991) also suggested that the Mississippi River system is the ultimate source of much of the biological productivity on the Louisiana and Texas shelf. The flow of the Mississippi River into the northwestern area influences the isotopic differences within these Gulf of Mexico sites (Lopez-Veneroni[4]). Although Gulf Port, MS, is east of the Mississippi river, specimens collected from this area could conceivably be feeding in or near the Mississippi River Plume region. Discharge from the Mississippi River is transported west along the shore (Dagg et al., 1991), and consumption of prey from this region would be heavily influenced by the Mississippi River leading to $^{15}N$-enriched values found in this study. Furthermore, Dagg et al. (1991) stated that king mackerel from the northern Gulf of Mexico generally consumed prey that were estuarine dependent and are, therefore, most likely influenced by runoff.

## Conclusions

Stable nitrogen isotope values of spines of king mackerel varied geographically. The northwestern Gulf of Mexico (+13.1‰) was isotopically distinct from the Mexican and Florida (+10.8‰ and +10.8‰) regions. We interpret these results to mean that there are, at least, two distinct groups of king mackerel within the Gulf of Mexico. Our results contrast with certain previous stock-structure assessments that distinguish only between Gulf of Mexico and Atlantic stocks. Stable carbon isotopes were able to distinguish between Mexico and Florida regions, although, not the northwestern Gulf of Mexico region. Although carbon isotopes were expected to be less variable than nitrogen, owing to the enrichment from trophic level to trophic level, they were found to be more variable within individual spines. The variability and perplexing isotopic trends within individual spines create difficulties in drawing conclusions from the data for stable carbon isotopes. In addition, fewer significant differences were detected between sites for stable carbon isotopes than for nitrogen isotopes. Stable carbon isotopes may be more useful when the isotopic discrimination among food resources is greater, which may be found when individuals also feed in coastal habitats. King mackerel, being of great commercial and recreational value, need to be managed with a clearer understanding of the number of groups

that exist. The isotopic data we have generated in conjunction with genetic research and tagging studies may be able to answer questions pertaining to location and number of king mackerel groups.

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