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FEATURE ARTICLE

Age, growth, and mortality of King Mackerel in the western Gulf of Mexico

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Abstract

Objective: Temporal and spatial variation in growth can have significant implications for the assessment and management of exploited populations. Therefore, the age and growth of King Mackerel *Scomberomorus cavalla* were estimated for the western Gulf of Mexico, where there are large gaps in the available data.

Methods: A total of 727 sagittal otoliths from 411 females, 248 males, and 68 individuals of unknown sex were collected from headboats, private recreational anglers, tournaments, and fishery-independent sampling and aged.

Result: Ages ranged from 0 to 17 years with lengths ranging from 13 to 147 cm fork length. The distribution of lengths and ages differed marginally for fishing sector (i.e., tournament vs. headboat vs. private). The fish that were collected from tournaments were larger than those collected from headboats and private anglers. The distribution of lengths and ages did vary by sex, with females obtaining larger sizes than males. However, there was no difference in mean age by sex. Using the multimodel approach, the Richards model improved the fit for both the youngest and oldest fish in the sample relative to the other growth models that were evaluated. Sex-specific differences in the Richards model were detected, with females growing larger than males but more slowly. Although peak catch was observed at age 5, King Mackerel were not fully recruited to the recreational fishery until age 6. The Chapman-Robson Peak Plus estimate of Z was 0.37.

Conclusion: These data provide a contemporary snapshot of size structure, age, growth, and mortality for King Mackerel from an undersampled region of the Gulf of Mexico and highlight several key considerations for upcoming stock assessments.

KEYWORDS

age and growth, fisheries, marine nearshore, marine offshore

INTRODUCTION

King Mackerel *Scomberomorus cavalla* are large coastal migratory pelagic fish that occur in the western Atlantic, including the Gulf of Mexico (GOM) and Caribbean Sea (Collette and Nauen 1983). This species is economically and ecologically important, supporting both commercial and recreational fisheries in the northwestern Atlantic

Ocean and GOM. Under the Coastal Migratory Pelagic Resources Fishery Management Plan, this fishery is managed as two different stocks: the GOM stock, which extends from west coast of Florida to the Texas–Mexico border, and the Atlantic stock, which ranges from the New England region to the southeast coast of Florida (Palmer et al. 2014). Historically, the GOM population has been exploited at a higher rate than the Atlantic population. The GOM population routinely exceeded catch limits (Southeast Data, Assessment, and Review [SEDAR] 2004), and assignment of the winter landings in the mixing zone off Florida to the GOM allocation led the GOM population to be classified as overfished in 1998 (Gulf of Mexico Fishery Management Council and the South Atlantic Fishery Management Council 1998). In 2001, after estimating the composition of the landings in the winter mixing zone, the population was reclassified as not overfished (SEDAR 2004).

Although the GOM stock is managed as a single stock, fishery management councils recognize that there are two groups—an east and west that are roughly divided by the Mississippi River (Grimes et al. 1987; Johnson et al. 1994). Genetic evidence does not support two distinct populations in the GOM (Gold et al. 1997, 2002), but tagging and landings data support the existence of at least two migratory groups. In the 1970s and 1980s, tagging studies found that larger individuals were reported to remain resident off Louisiana in both summer and winter months, whereas younger individuals that were tagged in the northern GOM were recaptured off south Florida or in Mexican waters (Fable et al. 1987). Subsequently, fished that were tagged off Veracruz, Mexico, were reported recaptured off Texas, indicating that winter mixing may also be occurring between fish in western U.S. GOM waters and fish in Mexican waters. This pattern was supported by the landings data, which showed a seasonal component to the Mexican fishery. Although fish were present throughout the year in Mexico, a clear north–south migration is apparent in late fall and a south–north migration in late winter (Arreguín-Sánchez et al. 1995; Chavez and Arreguin Sanchez 1995). This finding supports the hypothesis that some King Mackerel make seasonal migrations from U.S. waters to Mexico, comprising the western GOM migratory group. Further evidence for distinct migratory groups included regional spawning seasonality with King Mackerel that were caught in the southwestern GOM having a longer spawning season (January–September) than those in the northern GOM (May–October; Collins et al. 1989; Grimes et al. 1990; Johnson et al. 1994). The King Mackerel otoliths from Mexico and south Texas are also typically much more difficult to age (i.e., had very diffuse annuli) than those from the northern and eastern GOM, likely due to the western GOM group spending more time in the warmer waters of the southwestern GOM, where there are less-pronounced seasonal differences and further supporting the hypothesis of multiple migratory groups in the GOM. The lack of large seasonal temperature differences increases the potential for diffuse annuli to form in the otolith (SEDAR 2009, C. Palmer, National Marine Fisheries Service [NMFS], personal communication). In addition, DeVries and Grimes (1997) reported interregional differences in growth rates, with fish belonging to the eastern GOM migratory group having a higher growth rate than those from the western GOM migratory group.

Impact statement

Overall, this study characterized the growth and mortality of the western Gulf of Mexico King Mackerel stock, which is largely underrepresented in the stock assessment. We suggest the Richards growth model rather than the typical von Bertalanffy growth model may be better suited for estimating King Mackerel growth and should be explored for future stock assessments.

Knowledge of age and growth is an important life history component that is essential for proper management, and these data can be used to evaluate the effects of fishing pressure and fishing gear on population dynamics. The resulting age–length keys and estimated growth parameters are also needed for stock assessment models, which allow for comparisons of different stocks and, indirectly, the identification of population structure (Sutter et al. 1991). Age data for King Mackerel from Texas are limited, and as noted by the most recent stock assessment, they constrain the age structure estimates in the western GOM (SEDAR 2014). For example, between 1986 and 2013, only 9.1% ($n = 2513$) of the King Mackerel that were aged from the GOM were from Texas, with only 225 fish from Texas having been aged since 1996 (Palmer et al. 2014). Past studies of age and growth of King Mackerel have suggested that there are consistent differences between migratory groups and sexes, with females growing faster and larger than males and the eastern GOM group growing faster than the western GOM or Atlantic migratory groups (DeVries and Grimes 1997). More recent age and growth studies have demonstrated potential density-dependent responses to changes in the population size. For example, within the Atlantic King Mackerel stock, which experienced an estimated 45% decline in spawning stock biomass from the 1980s to 2000s (SEDAR 2009), Shepard et al. (2010) observed increases in size at age for more-recently collected Atlantic King Mackerel (2006–2007) than for fish from historical periods (1977–1979 and 1986–1992). Conversely, they demonstrated decreases in size at age between fish from recent versus historical periods for the eastern GOM migratory group, which experienced a 2.5-fold increase in stock biomass during that same period.

Collectively, most age and growth studies of King Mackerel have focused on the Atlantic and eastern GOM migratory groups, with little attention given to the western GOM group. Furthermore, age data that are used in stock assessments comprise mostly samples that are taken from the commercial handline fishery (SEDAR 2020). Given the potential for temporal changes in age and growth (e.g., Shepard et al. 2010) and the limited available data for the western GOM migratory group, the goal of our study was to describe the age, growth, and mortality of King Mackerel from Texas. We included samples from multiple sectors of the fishery to improve growth and mortality parameter estimates and compare our estimates with those from previous studies in other regions of the GOM.

METHODS

Sample collection

King Mackerel were collected from both fishery-dependent and fishery-independent sources between May 2017 and August 2018 along the Texas coast from Sabine Pass to Port Isabel (Figure 1). Fishery-dependent samples were collected weekly from the for-hire fleet and from private anglers at boat ramps and fish-cleaning stations during randomly selected creel surveys, during which all the King Mackerel that were encountered were sampled, provided that the angler granted permission. Additional King Mackerel were collected opportunistically during co-operating fishing tournaments. The fishery-independent

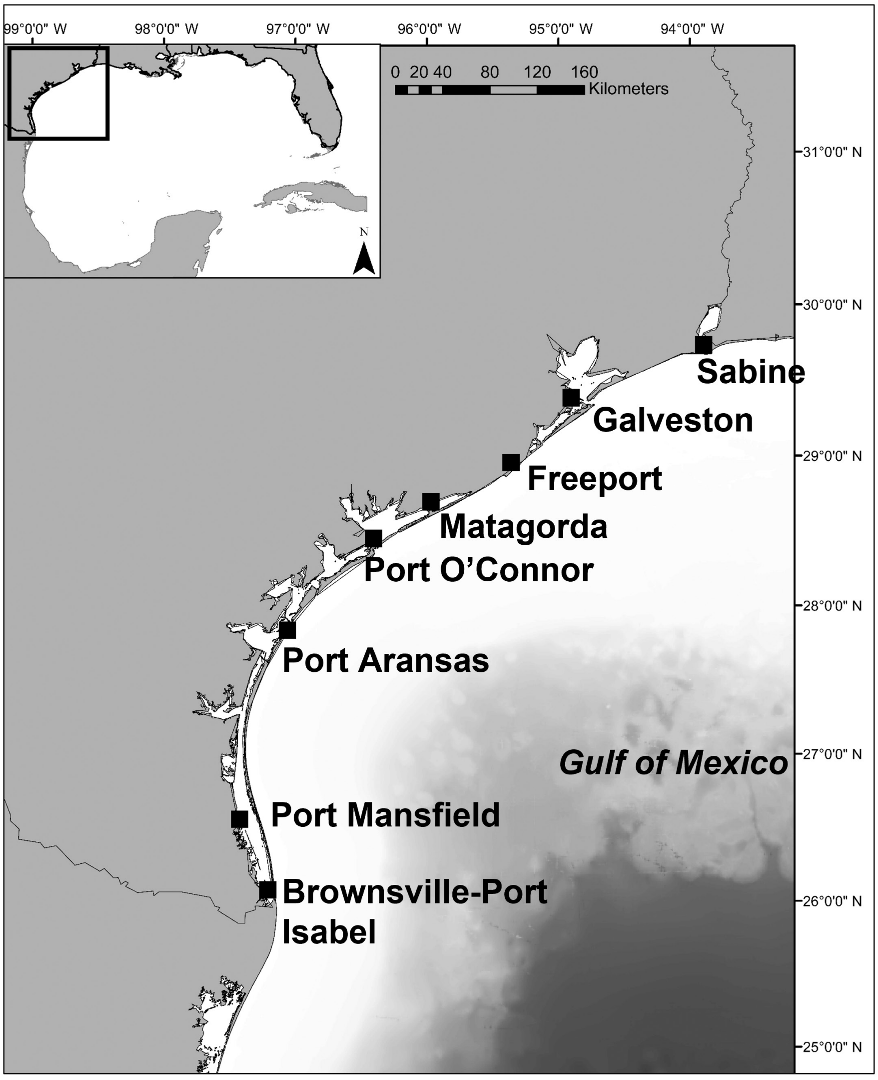

FIGURE 1 Map of sampling locations (black squares) of King Mackerel along the Texas coast.

samples allowed scientists to obtain fish below the minimum size limit (state: 68.6 cm TL; federal: 61.0 cm FL) and were obtained using recreational hook-and-line gear and by scientists that were sorting through shrimp trawl bycatch. Upon collection, each fish was assigned to a fishing sector (private, headboat, tournament, and fishery-independent), measured (FL; cm), and sexed macroscopically with some exceptions if only a partial carcass was available (i.e., lacking gonad tissues). The sagittal otoliths were removed in the field and returned to the lab, where they were rinsed, dried, and stored in small vials that were marked with the individual's unique identification number. An exact test of goodness of fit was used to determine if the sex ratio differed from an expected 1:1 female : male ratio and the 1.8:1 female : male ratio reported by Chih (2014) and Lombardi (2014). Individuals that lacked length data were excluded from length and growth analyses.

Age determination

The annuli (opaque zones) within the otoliths were counted to determine age (DeVries and Grimes 1997). The otoliths from males <80 cm FL and females <90 cm FL were aged whole, whereas the otoliths from larger fish were thin-sectioned (0.5 mm) in the transverse plane using a low-speed sectioning saw (DeVries and Grimes 1997; Palmer et al. 2014). Whole otoliths were placed in a black-bottomed dish with distilled water and examined at 7× magnification using a dissecting microscope with reflected light. For the otoliths that were sectioned, the left otolith was used for aging; otherwise, the right otolith was used. The sections were then mounted on slides using thermoplastic cement and viewed under a dissecting microscope at 32× magnification with transmitted light. For each section or whole otolith, two independent readers made blind (i.e., no knowledge of size of fish, date of capture, or other readers age assignment) counts of opaque annuli and classified the marginal edge using the guidelines in VanderKooy et al. (2020). When the counts differed, the first reader examined these sections or whole otoliths a second time. If the counts still differed, the two readers jointly examined the section or otolith and came to a consensus. If a consensus could not be reached, the section was omitted from further age analysis. Precision between readers was assessed using the average percentage of error (APE; Beamish and Fournier 1981) and the coefficient of variation (CV = SD/mean × 100; Chang 1982), which was averaged across all fish to estimate an average CV (ACV; Campana 2001). Reader bias was assessed using age-bias plots (Campana et al. 1995) and the Evans and Hoenig (1998) test of symmetry. This test was used to determine whether differences between readers were related to systematic bias rather than random error.

Annual ages, based on calendar year, were assigned based on the count of opaque annuli, the degree of marginal edge completion, and capture date (DeVries and Grimes 1997; Palmer et al. 2014). Because annulus formation typically occurs in the spring (Beaumariage 1973; Johnson et al. 1983), the advancement of ages is necessary for fish that are captured during that time of year to assign them to the correct cohort (DeVries and Grimes 1997). Following the conventions of the NMFS Panama City Laboratory (Palmer, personal communication), King Mackerel that were collected from January 1 to May 31 with a marginal edge >1/3 of that from the previous year were advanced 1 year. Fish were also advanced 1 year if they were collected between June 1 and July 15 with >2 annuli and a marginal edge >1/3 of the previous year or had ≤2 annuli with a marginal increment >2/3 of the previous year (Johnson et al. 1983; DeVries and Grimes 1997). This distinction was made because younger fish grow faster than older fish and may have a relatively large marginal increment as early as June (DeVries and Grimes 1997). For fish that were collected from mid-July (July 16) through December 31, age equaled the number of visible annuli (i.e., not advanced). To account for the difference between capture date and time of peak spawning (July 1; Fitzhugh et al. 2009), biological ages were also calculated and used for subsequent analyses of growth (Lombardi 2014; VanderKooy et al. 2020), using the following equation:

$$\text{Biological age (years)} = \left\{-182 + (\text{annulus count} \times 365) + \left[(m-1) \times 30 + d\right]\right\} / 365,$$

where m is the ordinal number of the month (1–12) of capture and d is the ordinal number (1–31) of the day of the month of capture.

Size and age structure

Potential differences in mean length and age between sexes and fishing sector were examined with two-way ANOVAs. Length and age data were first log transformed to meet the assumptions of ANOVA. If a significant result was found, Tukey's HSD test was used to determine which means were different. Length and age frequency distributions were compared between sexes and sectors using two-sample Cramér-von Mises tests, which are a more powerful analog to the popular Kolmogorov–Smirnov test and have less sensitivity to gaps in distributions (Baringhaus and Franz 2004; Arnold and Emerson 2011).

The sector comparison of length-frequency distributions excluded tournament-caught fish because of the low sample size. The results of these tests were based on 1000 ordinary bootstrap replicates carried out in R version 4.2.2 (R Core Team 2022) using the "twosamples" package version 2.0.0 (Dowd 2022) with $\alpha = 0.05$.

Growth

Following recommendations for multimodel inference (Burnham and Anderson 2002; Katasanevakis and Maravelias 2008), four growth models were fit to length-at-age data for all King Mackerel using nonlinear least squares. The growth model parameter estimates were calculated in R with assisting functions from the FSA package (Ogle et al. 2022). The first model fit to the length-at-age data was the three-parameter von Bertalanffy growth model (VBGM; von Bertalanffy 1938):

$$L_t = L_\infty \left[1 - e^{-k(t-t_0)}\right],$$

where L_t is the expected FL (mm) at age (years) t, L_∞ is the average maximum FL, k is the growth coefficient (year^{-1}), and t_0 is the theoretical age when the fish had a length of zero. The Gompertz growth function (Ricker 1979) was the second model fit and was specified as

$$L_t = L_\infty \left[e^{-ke^{(-gt)}}\right],$$

where g is the instantaneous rate of growth when $t = t_0$ and k is a dimensionless rate parameter such that kg is the instantaneous growth rate when $t = t_0$ and $L = L_0$. The third model fit to the length-at-age data was the logistic growth model (Ricker 1979):

$$L_t = \frac{L_\infty}{1 + e^{-g(t-t_0)}},$$

where g is the instantaneous rate of growth when $L \rightarrow 0$ and t_0 is the time when the absolute rate of increase begins to decrease (i.e., inflection point of curve). The Richards (1959) growth function was the last model fit to the length-at-age data and followed the parameterization of Tjorve and Tjorve (2010):

$$L_t = L_\infty \left[1 - ae^{(-kt)}\right]^b,$$

where k is the growth coefficient (the slope at the inflection point), a is a dimensionless parameter affecting the horizontal position (i.e., age) of the inflection point, and b is a dimensionless parameter affecting the vertical position (i.e., size) of the inflection point.

After fitting each model to the data, the Akaike information criterion (AIC; Akaike 1973) with the small-sample bias adjustment (AIC_c; Hurvich and Tsai 1989) was used to assess goodness of fit of each model. The model with the lowest AIC_c is considered the best-fitting model, and models with an AIC_c difference ≤2 (i.e., $\Delta_i \leq 2$) are considered to be strongly supported (Burnham and Anderson 2002). Akaike weights (w_i), ranging from 0 to 1, were also calculated to assess the likelihood of each model given the data, with the greatest Akaike weight corresponding to the most plausible model of the candidate set (Burnham and Anderson 2002). A size-modified version of the best-fitting model was also estimated to account for the nonrandom sampling that is associated with fishery-dependent sampling. This size-modified model used a restrictive maximum-likelihood estimation procedure with minimum size (68.6 cm FL) as the left truncation limit for the fishery-dependent samples (Diaz et al. 2004; Lombardi 2014).

The most plausible model was used to examine differences in growth between males ($n = 235$) and females ($n = 381$), as previous works have indicated sexually dimorphic growth in King Mackerel (DeVries and Grimes 1997; Lombardi 2014). For these sex-specific models (also size-modified), tournament fish were excluded given their nonrandom sampling and age-0 individuals that could not be sexed were included in the growth models for both sexes to help anchor the growth curves (sensu Shepard et al. 2010). Differences in growth curves were assessed using a likelihood-ratio test (Kimura 1980). Welch's t-test (Welch 1938) was used to assess differences in mean length at age between males and females for age-classes with at least 15 samples/sex.

Mortality

Mortality was examined using cross-sectional catch curve analysis. The instantaneous total mortality rate (Z) was estimated using the Chapman–Robson method (Chapman and Robson 1960). Because the modal age-class may not be fully recruited to the fishing gear, the descending limb of the catch curve was defined using the Peak Plus (modal age + 1) criterion of Smith et al. (2012). Chapman–Robson catch curves and Z were also estimated for private samples and headboat samples separately.

RESULTS

Between 2017 and 2018, a total of 727 King Mackerel was sampled from the Texas coast, ranging in size from 12.8 cm to 147.3 cm FL (Figure 2). By sector, the largest portion of samples was obtained from headboats ($n = 460$), followed by private recreational anglers ($n = 208$), tournaments ($n = 49$), and shrimp trawl bycatch ($n = 10$). The sample

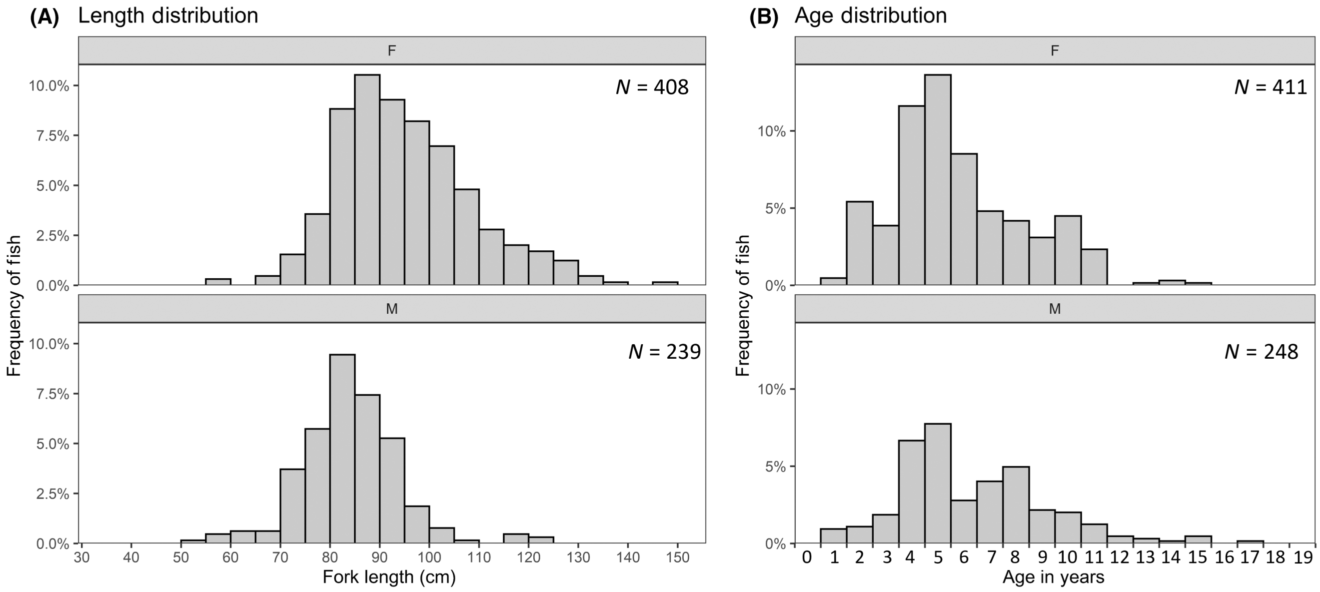

FIGURE 2 (A) Length and (B) age distribution by sex for King Mackerel along the Texas coast.

composition by sex included 411 females, 248 males, and 68 fish for which sex could not be determined. The observed sex ratio (1.7:1.0 female : male) deviated from the expected 1:1 ratio (exact test of goodness of fit, $p<0.001$), but it was similar ($p=0.310$) to the 1.8:1 female : male ratio that was reported by Chih (2014) and Lombardi (2014).

Age determination

The sagittal otoliths of all 727 King Mackerel that were sampled during this study were extracted and used to obtain annual age estimates. Age-0 fish were obtained from the shrimp trawl bycatch. After the first read, the APE between readers was 7.3% and the ACV was 10.3%. A systematic bias was detected ($\chi^2=120.46$, df=6, $p<0.001$), with reader 1 tending to underage relative to reader 2. Reader 1 reviewed the NOAA Fisheries King Mackerel aging guide (Palmer and DeVries 2003) before the second read, which lowered the APE to 2.5% and the ACV to 3.6%. Systematic bias was not detected after the second read ($\chi^2=4.34$, df=6, $p=0.630$). Consensus on the remaining otoliths was achieved in the third joint reading. The King Mackerel ages ranged from 0 to 17 years.

Size and age structure

Significant differences were detected in mean FL among fishing sectors ($F_{2,640}=7.05$, $p=0.001$) and by sex ($F_{1,640}=85.27$, $p<0.001$). Tournament-captured fish (mean = 98.6 cm FL, SD = 16.5) were significantly larger than fish that were captured by headboats (mean = 90.6 cm FL, SD = 13.3) or private anglers (mean = 88.6 cm FL, SD = 12.0). Female King Mackerel averaged 95.0 cm FL (SD = 13.6), and males averaged 83.9 cm FL (SD = 10.0). Cramér-von Mises tests indicated that the length-frequency distributions were similar between sectors (headboat vs. private; $p=0.074$) but differed between sexes ($p<0.001$). Visual assessment of the length-frequency distributions revealed that males had a smaller modal size (80 cm) and a significant decline in fish larger than 90 cm than females (Figure 2).

The observed age structure for King Mackerel was dominated by younger fish. Age 5 was the most frequently observed age-class (21.9%), followed by age 4 (18.6%) and age 6 (10.5%). The mean age was 5.8 years (SD = 2.7). No significant differences in mean age by sex ($F_{1,652}=2.74$, $p=0.098$) or among sectors ($F_{2,652}=2.77$, $p=0.063$) were detected, but on average, tournament-caught fish were older (mean = 7.2 years, SD = 3.2) than fish that were captured by headboats (mean = 5.9 years, SD = 2.5) or private recreational anglers (mean = 5.6 years, SD = 2.6). The age-frequency distributions were significantly different between headboats and private anglers ($p=0.041$). The age-frequency distribution for fish that were caught by headboats showed greater representation of age-6 King Mackerel than did that for private anglers (12.8% vs. 6.7%), as well as less representation of age-2 and age-3 individuals (approximately 5% vs. 9% for private anglers; Figure 3).

Growth

Of the growth models fit to all available length-at-age data ($n=707$), the Richards model provided the best fit (Table 1; Figure 4). Visually, the Richards model improved the fit

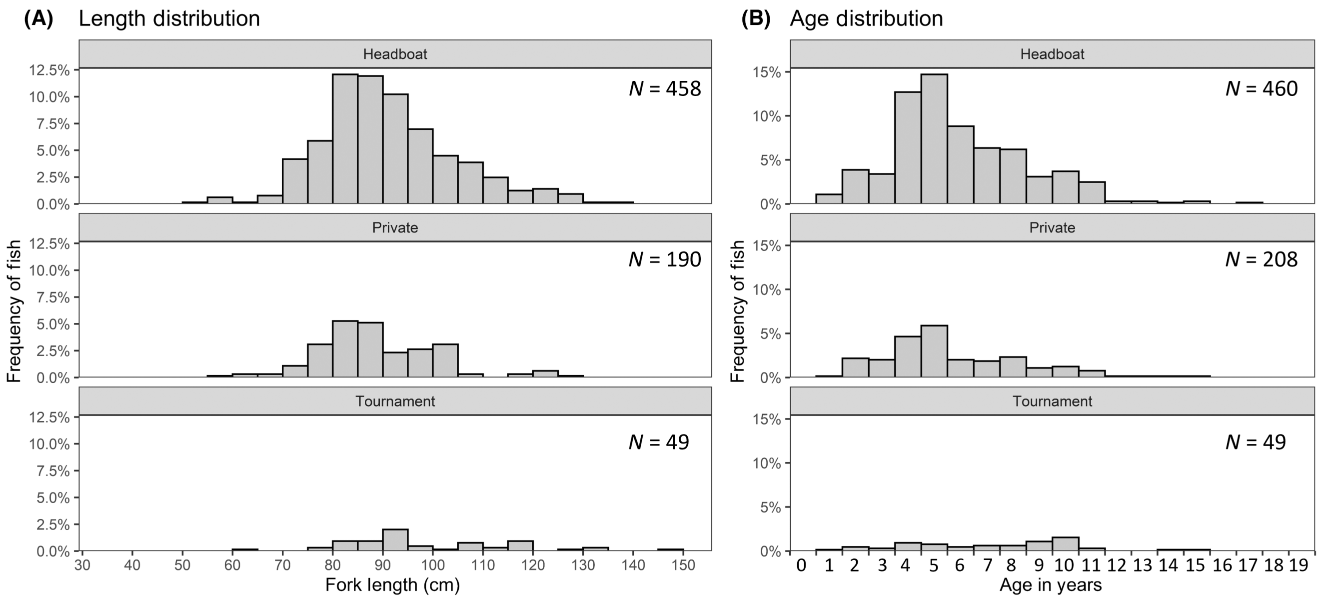

FIGURE 3 (A) Length and (B) age distribution by sector for King Mackerel along the Texas coast.

TABLE 1 Growth model results for the four models tested for all data combined. L_∞ is in fork length (cm).

All data											
Model	L_∞	k	t_0	g	a	b	**Parameters**	**LL**	**AICc**	Δ_i	w_i
Richards	147.2	0.021			1.002	0.216	5	−2645.33	5300.74	0	1
von Bertalanffy	104.4	0.311	−1.37				4	−2685.92	5379.89	79.15	0
Gompertz	104.1	0.867		0.35			4	−2696.92	5401.89	101.15	0
Logistic	104.1		0.35	0.39			4	−2704.75	5417.55	116.82	0

for both the youngest and oldest fish in the sample relative to the other growth models that were evaluated. Based on Akaike weights (w_i), there was no support for the von Bertalanffy, Gompertz, or logistic models (Table 1). The size-modified Richards model had parameter estimates that were nearly identical to those in the non-size-modified model (L_∞=147.3 cm FL, k=0.021, a=1.002, b=0.217). The size-modified Richards models were estimated for female (L_∞=192.0 cm FL, k=0.010, a=1.001, b=0.235) and male (L_∞=143.8 cm FL, k=0.010, a=1.001, b=0.188) King Mackerel to examine potential differences in growth. The subsequent likelihood-ratio test indicated that the growth curves were significantly different between sexes (χ^2=378.80, p<0.001; Figure 5). The L_∞ estimate for females was nearly 50 cm FL larger than the estimate for males. Although k was similar between sexes, females had a larger b estimate than males. Significant differences in mean FL at age between sexes were detected for age-4 (t=5.69, df=89.7, p<0.001), age-5 (t=9.74, df=130.8, p<0.001), age-6 (t=4.63, df=38.5, p<0.001), age-7 (t=6.96, df=41.7, p<0.001), and age-8 King Mackerel (t=5.48, df=47.2, p<0.001). On average, females achieved larger size at age than males for each of these age-classes, with differences ranging from 8.4 cm (age 4) to

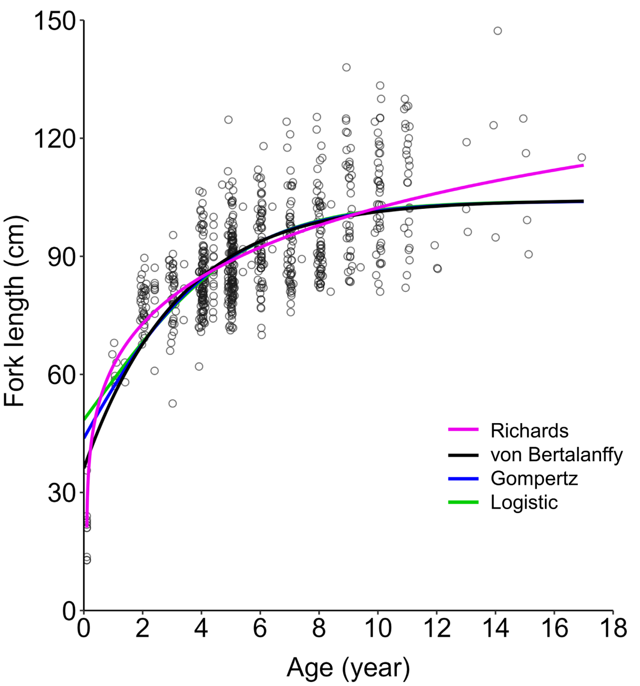

FIGURE 4 Model comparisons of predicted fork length for King Mackerel as a function of age for all observations (n=707). The open circles represent the observed length at age.

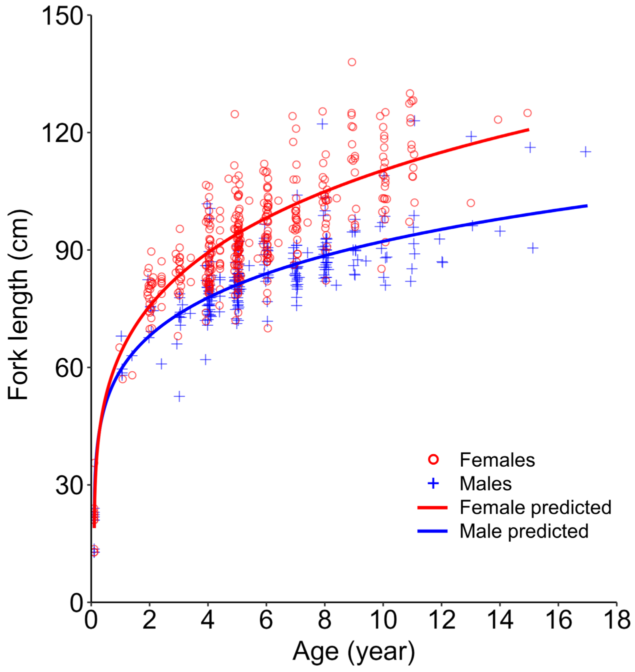

FIGURE 5 Sex-specific, size-modified Richards growth curves for King Mackerel ($n = 616$; excluding tournament fish). The observed length-at-age data is represented by red circles (females; $n = 381$) and blue crosses (males; $n = 235$).

15.1 cm (age 7; Figure 6). An insufficient sample size per age-class ($n < 15$) prevented comparisons of mean size at age for all the other age-classes.

Mortality

Although peak catch was observed at age 5, King Mackerel were not fully recruited to the recreational fishery until age 6—this trend was also true for private samples and headboat samples. Thus, the age-classes that were included in the cross-sectional catch curve analysis ranged from 6 to 17 years. The Chapman–Robson Peak Plus estimate of Z was 0.37. For the private versus headboat comparison, no fish that was older than 15 was present in the private samples, so the age-classes that were included in these catch curves ranged from 6 to 15 years for each group. Private Z was estimated at 0.35, whereas headboat Z was estimated at 0.41.

DISCUSSION

Temporal and spatial variation in growth can have significant implications for the assessment and

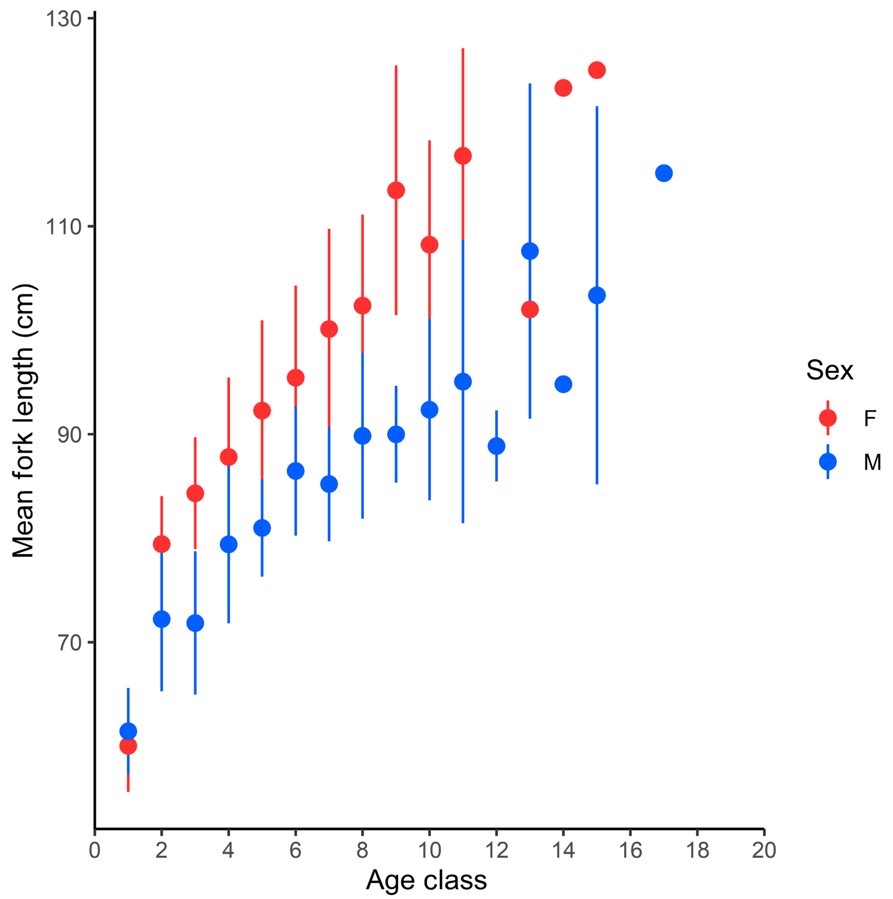

FIGURE 6 Mean (±SE) fork length at age for male and female King Mackerel sampled off the Texas coast, 2017–2018.

management of exploited populations (Rahikainen and Stephenson 2004). As noted by the latest stock assessment, age data for King Mackerel from Texas are limited and can bias the age structure estimates in the western GOM (SEDAR 2014). From 2002 until 2013 (when the last benchmark stock assessment was completed), only 225 King Mackerel from Texas were aged for the stock assessment (Palmer et al. 2014). The data presented here provide a contemporary snapshot of size structure, age, and growth for King Mackerel for this underrepresented region of the GOM and notably suggest that the Richards growth model (Richards 1959) rather than the typical VBGM may be better suited for estimating growth for King Mackerel.

Age and growth were successfully estimated using direct annual aging methods from otoliths that were sampled from multiple fishery-dependent recreational sources in Texas. Annuli are diffuse in King Mackerel otoliths, especially for those fish that may spend more time in warmer waters like south Texas, making distinguishing distinct annuli challenging. Additionally, the first annulus can appear as a broad, diffuse band or as a composite of several very closely spaced faint bands, complicating the identification of the first annulus (SEDAR 2009; Palmer, personal communication). Nevertheless, the APE among readers (first read: 7.3%; second read: 2.5%) was below the 5% APE threshold that is the commonly suggested target for moderately difficult-to-age species like King Mackerel (Palmer et al. 2014). Misidentifying the first annulus may lead to over or underestimation of King Mackerel ages. Previous studies have reported a tendency toward overestimating ages using sectioned otoliths but underestimating those of older (>80 cm FL males; 90 cm FL females) fish using whole otoliths (Collins et al. 1989; DeVries and Grimes 1997). Early studies used ages that were determined by whole otoliths to model growth (Beaumariage 1973; Johnson et al. 1983; Manooch et al. 1987), but a mixed approached of using whole otoliths for males <80 cm FL and females <90 cm FL and otolith thin sections for all larger fish is now accepted to make age determinations for King Mackerel (DeVries and Grimes 1997; Palmer et al. 2014). Difficulty distinguishing annuli may have contributed to the reader bias that was detected after the first read in this study. No bias was detected following the second read, so this bias should not have affected the final age estimates or subsequent analyses.

The size distributions were marginally different for fishing sectors and suggested that headboats catch greater proportions of larger fish than private anglers. This size difference may be due to slight differences in the methods that are used for targeting King Mackerel by each sector. Private anglers may be more likely to troll than headboats, which typically have more anglers than private recreational vessels. Although headboats can use both trolling methods and flat lines (i.e., lines drifting out from the vessel), they can have more active fishing with customers through the use of flat lines than they can with the limited number that can successfully troll at a time. Estimating growth models based largely on individuals that are sampled from size-selective fishery landings such as tournaments can lead to biased results (Goodyear 1995). In this study, most of the fish were sampled from the recreational fishery (e.g., headboat or private), which uses hook and line. This gear typically selects for larger King Mackerel, omitting the smaller, younger fish that have yet to enter the fishery. To minimize this potential bias, smaller, younger King Mackerel (age 0), which are often unrepresented, were collected from shrimp trawl bycatch and included in each group to allow for better estimation of the t_0 parameter (VBGM and logistic) and juvenile growth (Taylor et al. 2005); however, our sample size was relatively small ($n=10$). The few individuals that were sampled below the size limit likely explains the nearly identical parameter estimates between the typical Richard's model and the size-modified models. Similarly, our limited sample size of older fish likely influenced our L_∞ estimate because our oldest fish was 17 years old and the oldest fish used in the stock assessment for the Gulf stock was 24 years old (Lombardi 2014; Palmer et al. 2014). Shepard et al. (2010) reported 19- and 20-year-olds as the oldest fish for GOM females and males, respectively.

The multimodel approach allows for more robust analyses of growth by comparing different models rather than a priori adopting the VBGM. In this study, the Richards model was a significant improvement in fit relative to the von Bertalanffy, Gompertz, or logistic growth models that were fit to observed length-at-age data. With additional shape parameters (a and b), the Richards model can account for a shift in growth rate and allows for more flexibility in fitting the youngest and oldest ages. The commonly used VBGM does not fit the data of many species or families that may have two-phase (or two-stanza) growth trajectories (Katasanevakis and Maravelias 2008; Flinn and Midway 2021). Recently, preference for the Richards model over the VBGM has also been reported for other Scombrid fishes, including Yellowfin Tuna *Thunnus albacares* (Farley et al. 2020; Pacicco et al. 2021), Bigeye Tuna *T. obesus* (Farley et al. 2020), and Bluefin Tuna *T. thynnus* (Ailloud et al. 2017). The Assessment Workshop Panel for the most recent benchmark GOM King Mackerel stock assessment (SEDAR 2014) requested revisions to the growth modeling that included running a two-phase model because the typical VBGM poorly predicted length at age for younger and older fish (overestimating length at age for young fish and underestimating for older fish). Because King Mackerel are fast growers in their first year, Lombardi (2014) reported a two-phase growth model that used a linear model for young fish (age 0 to age 0.5) and switched to the VBGM to predict growth from age 0.75 to age 20. This model better predicted growth for the youngest and oldest fish and resulted in larger asymptotic lengths. The size-modified Richards model that is reported in our study also had larger asymptotic length ($L_\infty = 147.3$ cm FL) than that observed in many previous studies (which used the VBGM). Given that King Mackerel appear to still be growing larger at the oldest ages encountered (see Figures 6 and A4 in Lombardi 2014), a non-VBGM model such as the Richards model may better serve future King Mackerel growth modeling efforts.

The growth models that were calculated in this study suggested the need for sex-specific parameters, which supports previous findings of sexual dimorphism in this species (DeVries and Grimes 1997; Shepard et al. 2010; Lombardi 2014; Palmer et al. 2014). Females reach larger asymptotic sizes than males. Females were also observed more often than males in this study, which differed from the expected 1:1 female : male sex ratio. Our 1.7:1 female : male ratio is consistent, however, with the results from other studies and stock assessments that reported a 1.8:1 female : male ratio (Trent et al. 1987; Ortiz and Palmer 2008; Chih 2014; Lombardi 2014; SEDAR 2020). Although this difference is likely due to the size-selective nature of fishery-dependent sampling (Chih 2014), deviations from the 1:1 sex ratio can influence sexual selection (e.g., intrasexual competition, breeding success; Clutton-Brock 2007), but a slight variation in a wild population should exhibit negligible effects (Ginsberg and Milner-Gulland 1994; Milner-Gulland et al. 2003).

The sampling area in this study sits between two possible mixing zones for multiple migratory groups in the GOM (Fable et al. 1987; SEDAR 2009). There are possible mixing zones off the Louisania coast for the eastern and western stocks and at the Texas–Mexico border for the western and Mexico stocks (SEDAR 2014). Previous studies (Table 2) have reported differences in regional growth models, with the eastern GOM having the highest growth rate, followed by the western GOM stock (DeVries and Grimes 1997). The few studies that have explored the VBGM for King Mackerel that were collected in Mexico produced growth models with the sexes combined (Aguilar-Salazar et al. 1981; Arreguín-Sánchez et al. 1995), making a direct comparison to models calculated in this study difficult. When the sexes were combined in the present study, the asymptotic length estimate ($L_\infty = 147$ cm FL) from the Richards model was similar to the asymptotic length that was reported by Arreguín-Sánchez et al. (1995) ($L_\infty = 140$ cm FL). Though their study used the VBGM, the biological interpretation of L_∞ (theoretical mean maximum size) is comparable. Had the VBGM been selected a priori in this study, our estimate of $L_\infty = 104$ cm FL would suggest that King Mackerel reach larger sizes off Mexico than Texas. This example highlights the importance of model selection and requires cautious interpretation because these most-recent Mexican studies are over 25 years old and may not reflect current population parameters.

Instantaneous total mortality was lower in this study ($Z = 0.37$) than in the current stock assessment ($Z = M + F$: $0.55 = 0.17 + 0.38$; SEDAR 2014, 2020). Recruitment estimates for King Mackerel have demonstrated a cyclical pattern, with periods of relatively low recruitment followed by periods of relatively high recruitment (SEDAR 2014). Ricker (1979) noted that moderate to random variation in recruitment would not change the general form of the catch curves, allowing for mortality rates to be estimated. Although our lower Z may be an artifact of our sampling design, alternatively, it may represent a western GOM stock that is influenced by different fishing styles and levels of fishing effort. Historically, the eastern GOM has represented most of the fish that are sampled in the stock assessment (all sectors from 1985 through 2014: Gulf Florida, Alabama, Mississippi: $n = 13{,}672$ fish) relative to the western stock (all sectors from 1985 through 2014: Texas: $n = 2513$). In fact, the eastern GOM commercial sample size (1985 through 2014: Gulf Florida, Alabama, Mississippi: $n = 2654$) is similar in size to that of the entire Texas sample ($n = 2513$). Only 39 fish were sampled commercially in Texas between 1985 and 2013. The fish that were collected off Louisiana are largely from the commercial fishery ($n = 7283$; Palmer et al. 2014) and may consist of a combination of western and eastern substocks because a mixing zone is hypothesized here (SEDAR 2014). For fish that were caught in the recreational sector (excluding tournaments), the eastern GOM (Gulf Florida, Alabama, Mississippi) comprised 79.2% ($n = 7218$) of the fish that were used in the stock assessment, which is significantly more fish from the western stock and potential mixing zone (Texas: 18.1%, $n = 1651$; Louisiana: 1.6%, $n = 142$, respectively; Palmer et al. 2014).

This study found age-5 fish to be the most frequently sampled fish, which is inconsistent with Palmer et al. (2014), in which age-2 fish were the most frequently sampled. Most of the fish that were sampled in the GOM for the stock assessment were ages 1–5 (74% for females and 64% for males, as reported in Palmer et al. 2014). However, differences in age between sectors (e.g., recreational vs. commercial) and zones (e.g., western vs. eastern GOM) were not reported. Palmer et al. (2014) reported a larger modal fork length (~80 cm) for commercially caught fish relative to recreationally caught fish (~72 cm) in the GOM, which may be attributed to differences in

TABLE 2 Parameters of the von Bertanlanffy growth equation for King Mackerel sampled in the Gulf of Mexico. M = males, F = females, and B = both sexes combined. L_∞ is in centimeters, and size is fork length.

L_∞	*k*	t_0	Sex	Site	Reference
84	0.350	−2.50	M	Florida	Beaumariage (1973)[a]
114	0.210	−2.40	F		
148	0.115	−2.36	B	Florida and Texas (all ages)	Manooch et al. (1987)
142	0.136	−1.98	F	(Ages 1–14)	
111	0.208	−1.48	M	(Age 1–11)	
130	0.182	−1.55	F	(Age 1–10)	
104	0.258	−1.12	M	(Age 1–9)	
107	0.290	−0.97	F	Florida	Johnson et al. (1983)
97	0.280	−1.17	M		
123	0.230	−0.26	B	Northwestern Yucatan (1984–1985)	Aguilar-Salazar et al. (1981)
138	0.240	−0.24	B	(1986–1987)	
123	0.230	−0.26	B	Northern Yucatan (1983–1984)	
117	0.230	−0.27	B	(1984–1985)	
134	0.350	−0.25	B	(1985–1986)	
140	0.190	−0.54	B	Campeche Bank	Arreguín-Sánchez et al. (1995)
138	0.172	−1.83	F	Eastern GOM (1982–1992)	DeVries and Grimes (1997)
137	0.160	−2.12	F	(1977–1978)	
103	0.247	−1.84	M	(1982–1992)	
99	0.269	−1.63	M	(1977–1978)	
134	0.150	−2.63	F	Western GOM (1982–1992)	
152	0.127	−2.78	F	(1977–1978)	
103	0.203	−2.74	M	(1982–1992)	
116	0.094	−6.78	M	(1977–1978)	
172	0.082	−3.83	F	Northern GOM	Shepard et al. (2010)
118	0.095	−6.51	M		
110	0.338	−0.91	F	Texas	This study
92	0.426	−0.64	M		
104	0.31	−1.37	B		
129	0.122	−4.09	B	Northern GOM	Lombardi (2014)
143	0.121	−3.41	F		
98	0.227	−2.63	M		

[a]The VBGM included King Mackerel samples from the Atlantic side of Florida.

fishing style by commercial anglers (e.g., handline or gill net) or the disproportionate sample contribution between the eastern and western GOM (see below for discussion). Given the potential for temporal changes in age and growth (e.g., Shepard et al. 2010) and the limited data that are available for the western GOM migratory group, this sample-size discrepancy could have significant implications for the assessment and management of exploited GOM King Mackerel populations.

Estimates of growth and mortality influence stock assessment models, which ultimately affect the estimates of productivity and stock-status benchmark calculations (i.e., overfished and overfishing status). Overall, this study characterized the growth and mortality of the western GOM King Mackerel stock, which is largely underrepresented in the stock assessment. We suggest the Richards growth model (Richards 1959) rather than the typical VBGM may be better suited for estimating King

Mackerel growth and should be explored for future stock assessments.

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CONFLICT OF INTEREST STATEMENT

There is no conflict of interest declared in this article.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

This research was conducted in accordance with guidelines approved by Texas Parks and Wildlife Department (Scientific Research Permit SPR-0303-279) and the Institutional Animal Care and Use Committee at Texas A&M University–Corpus Christi (Animal Use Protocols #07-15 and #04-18).

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