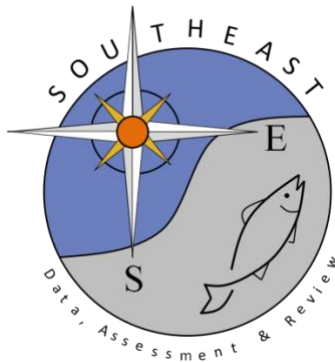


Red snapper (*Lutjanus campechanus*) demographic structure in the northern Gulf of Mexico based on spatial patterns in growth rates and morphometrics

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**Abstract**—Red snapper (*Lutjanus campechanus*) in the United States waters of the Gulf of Mexico (GOM) has been considered a single unit stock since management of the species began in 1991. The validity of this assumption is essential to management decisions because measures of growth can differ for nonmixing populations. We examined growth rates, size-at-age, and length and weight information of red snapper collected from the recreational harvests of Alabama ( $n=2010$ ), Louisiana ( $n=1905$ ), and Texas ( $n=1277$ ) from 1999 to 2001. Ages were obtained from 5035 otolith sections and ranged from one to 45 years. Fork length, total weight, and age-frequency distributions differed significantly among all states; Texas, however, had a much higher proportion of smaller, younger fish. All red snapper showed rapid growth until about age 10 years, after which growth slowed considerably. Von Bertalanffy growth models of both mean fork length and mean total weight-at-age predicted significantly smaller fish at age from Texas, whereas no differences were found between Alabama and Louisiana models. Texas red snapper were also shown to differ significantly from both Alabama and Louisiana red snapper in regressions of mean weight at age. Demographic variation in growth rates may indicate the existence of separate management units of red snapper in the GOM. Our data indicate that the red snapper inhabiting the waters off Texas are reaching smaller maximum sizes at a faster rate and have a consistently smaller total weight at age than those collected from Louisiana and Alabama waters. Whether these differences are environmentally induced or are the result of genetic divergence remains to be determined, but they should be considered for future management regulations.

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## Red snapper (*Lutjanus campechanus*) demographic structure in the northern Gulf of Mexico based on spatial patterns in growth rates and morphometrics

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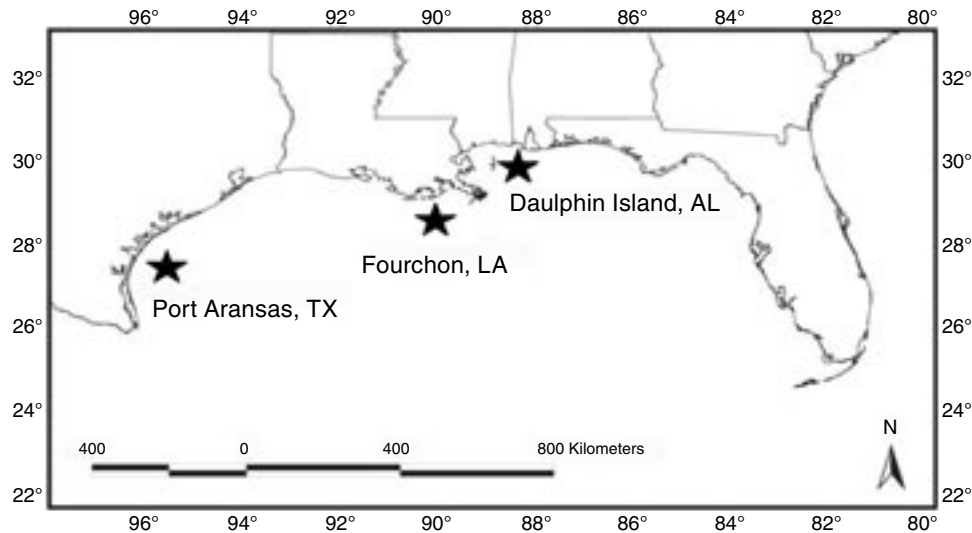
Red snapper (*Lutjanus campechanus*) in the United States waters of the Gulf of Mexico (GOM) are heavily exploited by both recreational and commercial fishermen (Wilson and Nieland, 2001; Shirripa and Legault<sup>1</sup>). Harvest, however, has not proceeded without detrimental affects on the population. Commercial landings have declined substantially from 6048 metric tons (t) in 1964 to 1207 t in 1990; recreational landings exhibited similar declines from 1937 t in 1981 to 481 t in 1990 (NMFS<sup>2</sup>). In 1991, harvest restrictions including reef fish permits, seasonal fishing, fish quotas, creel limits, and minimum size limits were placed upon the red snapper fishermen by the Gulf of Mexico Fishery Management Council (GMFMC<sup>3</sup>) to increase the spawning potential ratio to 20%, which is indicative of recovery. These regulations have also been adopted for state waters in Alabama, Louisiana, and Texas. Despite the management actions, GOM red snapper remain overfished (Goodyear<sup>4</sup>; Shirripa and Legault<sup>1</sup>).

<sup>1</sup> Shirripa, M. J., and C. M. Legault. 1999. Status of the red snapper in the U. S. waters of the Gulf of Mexico: updated through 1998, 44 p. + appendices. Contribution rep. SFD-99/00-75 from Sustainable Fisheries Division, Miami Laboratory, Southeast Fisheries Science Center, National Marine Fishery Service, 75 Virginia Beach Drive, Miami, FL 33149-1099. [Not available from NTIS].

<sup>2</sup> NMFS (National Marine Fisheries Service). 2003. Fisheries Statistics and Economics Division. Website: www.nmfs.noaa.gov.

<sup>3</sup> GMFMC (Gulf of Mexico Fishery Management Council). 1991. Amendment 3 to the reef fishery management plan for the reef fish resources of the Gulf of Mexico, 38 p. Gulf of Mexico Fishery Management Council, 3018 N. U.S. Hwy 301 Suite 1000, Tampa, FL. 33619-2272. [Not available from NTIS].

<sup>4</sup> Goodyear, C. P. 1995. Red snapper in U.S. waters of the Gulf of Mexico. Stock assesment report MIA-95/96-05, 171 p. Miami Laboratory, Southeast Fisheries Science Center, National Marine Fisheries Service, 75 Virginia Beach Dr., Miami, FL, 33149-1099. [Not available from NTIS].



**Figure 1**

Map of the northern Gulf of Mexico showing the three red snapper (*Lutjanus campechanus*) sampling locations.

An underlying assumption crucial to a fishery management plan is that the fish species being managed is a unit stock (Gulland, 1965). A stock is defined as the part of a fish population that is under consideration as an actual or potential resource (Ricker, 1975). Since management began in 1991, red snapper in the northern GOM have been considered a unit stock. Genetic studies to date have shown that there is little evidence to dispute this assumption (Camper et al., 1993; Gold et al., 1997; Heist and Gold, 2000). On the other hand, tag-recapture studies indicate that red snapper have the capacity to move great distances, making it possible for separate stocks to develop (Patterson et al., 2001).

The validity of an assumption of a single stock of red snapper is essential to management decisions because measures of growth, natural mortality, reproductive capacity, and recruitment can differ among nonmixing populations. Should separate red snapper stocks exist, management plans would have to be enacted for each defined stock in order to follow federal guidelines. Even if a single large red snapper stock exists, management should be sensitive to both the diversity of habitats and user groups within the species area of occurrence. Because red snapper are arguably the most important recreational and commercial offshore fishery from Florida to southern Texas, every effort should be undertaken to develop the most effective and productive management plan.

The objective of this study was to evaluate the stock structure of GOM red snapper based on growth rates and size-at-age information. We hypothesized that red snapper sampled from across the northern GOM would be indistinguishable in their growth rates and size at age—a uniformity indicative of a single unit stock.

### Methods and materials

Red snapper were collected from the recreational harvests of 1999, 2000, and 2001 from the northern GOM at Dauphin Island, Alabama, at Port Fourchon, Louisiana, and at Port Aransas, Texas (Fig. 1). A maximum of 75 fish were randomly selected and sampled from the daily catch of each charter boat or head boat while the captains and deck hands cleaned fish. These fish were not selected by size. Larger individuals (>6.8 kg) were opportunistically sampled from spear fishing and hook-and-line fishing tournaments in Alabama and Louisiana. In addition, a number of smaller fish (<406 mm, <457 mm during summer 1999) were randomly sampled during red snapper tagging cruises in Alabama. Morphometric measurements were recorded (fork length [FL] in mm, total weight [TW] in kg, and eviscerated body weight [BW] in kg), sex was determined by macroscopic examination of gonads, and both sagittal otoliths were removed, rinsed, and stored in coin envelopes until processed. Fish weights were not recorded for 1999 Texas samples.

A transverse thin section (containing the core) was taken from the left sagittal otolith of each individual. Sections were made with the Hillquist model 800 thin-sectioning machine equipped with a diamond embedded wafering blade and precision grinder (Cowan et al., 1995). When the left otolith was unavailable, the right otolith was sectioned. Examinations of otolith sections were made with a dissecting microscope with transmitted light and polarized light filter at 20× to 64× magnification. Opaque annulus counts were made along the ventral side of the sulcus acousticus from the core to the proximal edge (Wilson and Nieland, 2001). Annulus counts were performed by two independent readers (AJF

and MSB) without knowledge of either date of capture or morphometric data. The appearance of the otolith section edge condition was coded as opaque or translucent after Beckman et al. (1989). Annuli were counted a second time when initial counts disagreed. In instances where a consensus between the two readers could not be reached, annulus counts of the more experienced reader (AJF) were used. Between-reader differences in annulus counts were evaluated with the coefficient of variation (CV), index of precision (D) (Chang, 1982), and average percent error (APE) (Beamish and Fournier, 1981). The periodicity of opaque zone formation was verified for each sampling location with edge analysis after Wilson and Nieland (2001). Ages of red snapper were estimated from opaque annulus counts and capture date with the equation described by Wilson and Nieland (2001):

$$\text{Day age} = -182 + (\text{opaque increment count} \times 365) + ((m-1) \times 30) + d,$$

where  $m$  = the ordinal number (1–12) of month of capture; and

$d$  = the ordinal number (1–31) of the day of the month of capture.

The 182 days subtracted from each age estimate are to account for the uniform hatching date assigned for all specimens (Render, 1995; Wilson and Nieland, 2001). Age in years was assigned by dividing day age by 365.

Fork length–TW relationships were fitted with linear regression to the model  $FL = a TW^b$  from  $\log_{10}$ -transformed data for Alabama, Louisiana, and Texas specimens. Analysis of covariance (ANCOVA) was used to compare slopes and intercepts among sampling locations (SAS, 1985). Variability in age, FL, and TW frequency distributions of red snapper were compared among states with the Komolgorov-Smirnov two-sample test (Tate and Clelland, 1957).

Growth of red snapper was modeled for FL and TW with the von Bertalanffy growth equations. Because of differences in sample population size among states, weighted mean FL and mean TW at age were fitted for each state with nonlinear regression in the forms:

$$FL_t = L_\infty(1 - e^{-k(t)})$$

$$TW_t = W_\infty(1 - e^{-k(t)})^b,$$

where  $FL_t$  = FL at age  $t$ ;

$TW_t$  = TW at age  $t$ ;

$L_\infty$  = the FL asymptote;

$W_\infty$  = the TW asymptote;

$k$  = the growth coefficient;

$t$  = age in years; and

$b$  = exponent derived from our length–weight regressions (SAS, version 5, 1985, SAS Inst, Cary, NC).

Because of a lack of smaller individuals in all sample populations, no  $y$ -intercepts for  $t_0$  were specified and models were forced through 0. Larger individuals and

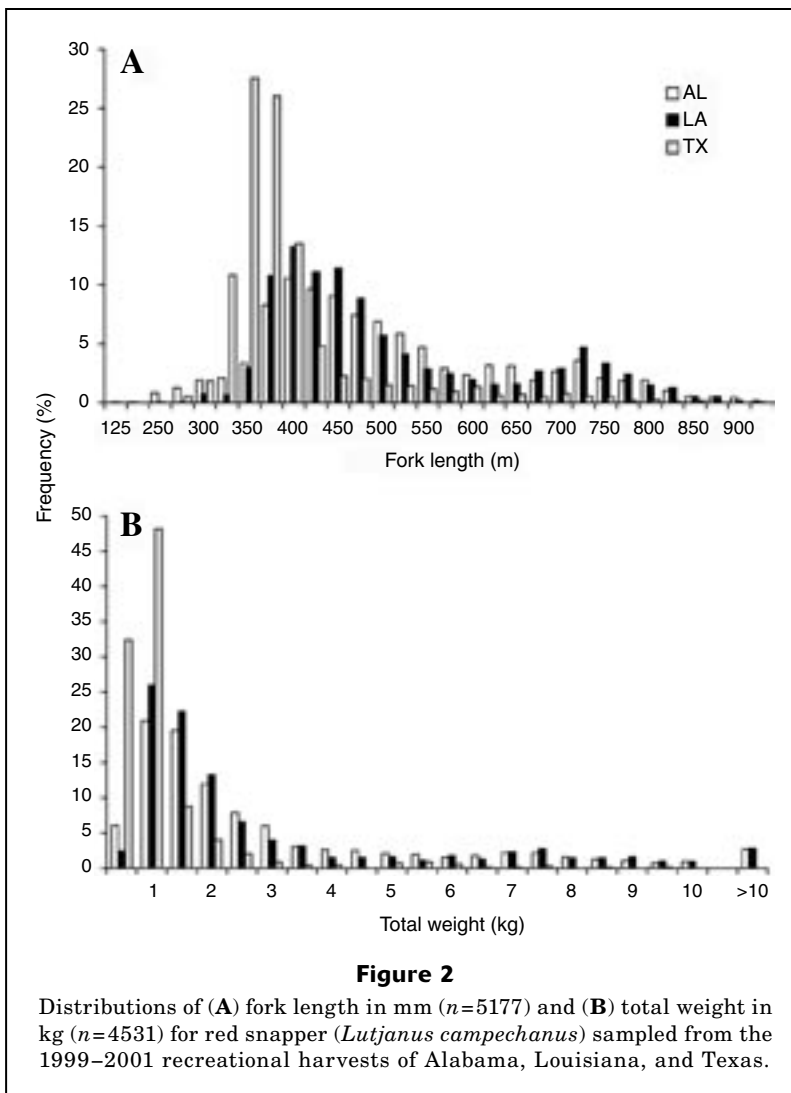
**Table 1**  
Numbers of red snapper (*Lutjanus campechanus*) sampled from recreational sources by state and year.

State	Males	Females	Unknown sex	Total
<b>Alabama</b>				
1999	434	396	5	835
2000	355	415	7	777
2001	189	209	0	398
			Total	2010
<b>Louisiana</b>				
1999	367	339	31	737
2000	399	397	8	804
2001	160	179	25	364
			Total	1905
<b>Texas</b>				
1999	268	293	14	575
2000	278	284	22	584
2001	52	56	10	118
			Total	1277

juveniles selectively sampled by size were excluded from the models to more accurately reflect a random sample. Likelihood ratio tests (Cerrato, 1990) were used to test for differences among states in models and in growth parameter estimates. Differential growth was evaluated for red snapper in the first 10 years of life when somatic growth is most rapid (Szedlmayer and Shipp, 1994; Patterson et al., 2001; Wilson and Nieland, 2001). Linear regressions of mean FL and mean TW at age for fishes aged 1 to 10 years were compared among states with analysis of covariance (ANCOVA) and tested for homogeneity of slopes.

## Results

During the three-year study period, 5192 red snapper were sampled from the recreational harvest of the northern GOM (Table 1): 642 individuals from fishing tournaments, 71 undersize fish from tagging cruises, and 4479 random samples from recreational catches. The samples included 2502 males, 2568 females, and 122 individuals of undetermined sex. The resultant male-to-female ratios were 0.96:1 for Alabama, 1:0.99 for Louisiana, 0.94:1 for Texas, and 0.97:1 for all states combined. A chi-square test indicated no significant difference in the number of males to females ( $\chi^2=0.78$ ,  $P=0.38$ ). Fork lengths ranged from 237 to 916 mm (Fig. 2A). Specimens from Alabama ranged from 237 to 916 mm FL, Louisiana specimens ranged from 282 to 913 mm FL, and Texas specimens ranged from 266 to 846 mm FL. The FL frequency distributions of the random samples were different among all states (AL and LA, maximum difference (MD)=5.26; AL and TX, MD=51.86; LA and TX, MD=51.77)(Fig. 2A).



Total weights of all fish sampled ranged from 0.11 to 17.35 kg (Fig. 2B). Specimens from Alabama ranged from 0.22 to 15.42 kg TW, Louisiana specimens were 0.42 to 17.35 kg TW, and Texas specimens ranged from 0.33 to 9.42 kg TW. Total weight-frequency distributions (in 0.5 kg increments) differed significantly between all states (AL and LA,  $MD=5.37$ ; AL and TX,  $MD=53.68$ ; and LA TX,  $MD=52.28$ ) (Fig. 2B). Significant differences in red snapper FL-TW regression models were detected among states (ANCOVA test of homogeneity of slopes,  $F_{5, 4522}=23.36$ ;  $P<0.001$ ;  $r^2=0.98$ ; ANCOVA test for equal intercepts,  $F_{5, 4522}=22.77$ ,  $P<0.001$ ,  $r^2=0.98$ ); therefore, separate models were fitted for each state. The resultant equations were

$$AL\ TW = 1.51 \times 10^{-5} (FL^{3.03}) \\ (F_{1,1965}=102740; P<0.0001; r^2=0.98);$$

$$LA\ TW = 1.02 \times 10^{-5} (FL^{3.09}) \\ (F_{1,1856}=77981; P<0.0001; r^2=0.98);$$

$$TX\ TW = 2.88 \times 10^{-5} (FL^{2.92}) \\ (F_{1,699}=13345; P<0.0001; r^2=0.95).$$

Ages were obtained from 5035 transverse otolith sections. Thirty fish had otolith sections deemed unreadable by both readers. The age estimates determined by the two readers were evaluated for reader agreement, precision, and average percent error for first and second readings of otolith sections by sample year. Table 2 gives APE, CV, D, percentage agreement (O), and percentages of differences in age estimates ( $\pm 1$ , 2, and 3 years). The readers agreed on age estimates for 4053 otoliths (80.5%) after the initial reading. Re-examination of the 982 otolith sections for which annulus counts differed produced agreement for 5007 individuals.

We compared the timing of opaque annulus formation among red snapper sample sites by plotting the monthly occurrence of maximum and minimum proportions of opaque otolith edges. Sample limitations of red snapper in Texas, however, prevented meaningful comparisons of

opaque annulus formation for this state. However, minimum proportions of opaque edges during the months of April through October may indicate that red snapper from Texas form an opaque annulus during the winter months. Proportions of opaque edges for Alabama and Louisiana were essentially the same: maximum proportions of opaque edges during the months of February and March followed by a decrease to minimum proportions during the months of May through November (Fig. 3). These findings are consistent with previous age and growth studies on red snapper in the northern GOM (Patterson et al., 2001; Wilson and Nieland, 2001), indicating that the formation of one opaque annulus in the winter months is followed by the formation of one translucent annulus in summer. Annulus-based age estimates of red snapper from the northern GOM have also been validated to 55 years with otolith radiocarbon chronologies based on accelerator mass spectrometry  $^{14}\text{C}$  measurements (Baker and Wilson, 2001).

Red snapper ages ranged from 1 to 45 years and the majority (90%) of individuals were between 2 and 6 years (Fig. 4). Alabama fish ranged from 1 to 35 years ( $n=1985$ ), Louisiana fish ranged from 2 to 37 years ( $n=1864$ ), and Texas fish ranged from 1 to 45 years ( $n=1186$ ). Modal ages were 4 years for Alabama and 3 years for Louisiana and Texas red snapper. We found significant differences among age-frequency distributions from all states (AL and LA,  $\text{MD}=9$ ; AL and TX,  $\text{MD}=33.84$ ; and LA and TX,  $\text{MD}=24.84$ ). Texas had a much higher proportion of younger individuals; 63% of sampled fish were aged at 3 years or less compared to only 30% of Alabama and 39% of Louisiana fish aged at 3 years or less.

Red snapper growth was modeled from weighted mean FL at age and mean TW at age by using the von Bertalanffy growth equation (Fig. 5, A and B). Resultant von Bertalanffy growth equations were

$$\text{AL } FL_{\infty} = 839(1 - e^{(-0.38(t))}) \\ (F_{1,15}=2824.9; P<0.0001; r^2=0.95);$$

$$\text{LA } FL_{\infty} = 847.8(1 - e^{(-0.25(t))}) \\ (F_{1,13}=5024.4; P<0.0001; r^2=0.76);$$

$$\text{TX } FL_{\infty} = 778.2(1 - e^{(-0.49(t))}) \\ (F_{1,19}=1452.1; P<0.001; r^2=0.85);$$

$$\text{AL } TW_{\infty} = 17.05(1 - e^{(-0.15(t))})^{3.03} \\ (F_{1,15}=457.9; P<0.0001; r^2=0.89);$$

$$\text{LA } TW_{\infty} = 12.61(1 - e^{(-0.32(t))})^{3.03} \\ (F_{1,14}=122.02; P<0.0001; r^2=0.18);$$

$$\text{TX } TW_{\infty} = 8.89(1 - e^{(-0.21(t))})^{2.84} \\ (F_{1,12}=613.01; P<0.0001; r^2=0.96).$$

Models of mean red snapper FL at age for Alabama and Louisiana were markedly similar with likelihood ratio tests indicating no significant differences between red snapper from the two states (Table 3). However, the

**Table 2**

Differences between two readers in average percent error (APE), coefficient of variation (CV), index of precision (D), and in percentages of agreement (O) for counts of opaque annuli in red snapper (*Lutjanus campechanus*) otoliths after first and second readings for each sample year.  $n$ =number of otoliths sampled.

Year	1 <sup>st</sup> reading	2 <sup>nd</sup> reading
1999 ( $n=2100$ )		
APE	0.483	0.499
CV	0.014	0.0008
D	0.010	0.0006
O	89.48%	99.43%
±1	8.62%	0.48%
±2	1.19%	0.095%
±3	0.71%	
2000 ( $n=2069$ )		
APE	0.487	0.499
CV	0.034	0.0006
D	0.024	0.0004
O	73.79%	99.47%
±1	22.49%	0.53%
±2	1.78%	
±3	1.93%	
2001 ( $n=866$ )		
APE	0.459	0.498
CV	0.032	0.0005
D	0.023	0.0003
O	74.73%	99.42%
±1	22.06%	0.58%
±2	2.27%	
±3	0.94%	

Texas model differed from both Alabama and Louisiana models. The Texas model displayed significant differences from the other models in both  $L_{\infty}$  and in  $k$ . A comparison of the models of mean TW at age indicated no significant differences between Alabama and Louisiana red snapper (Table 3). Differential growth in TW was found when comparing Alabama and Louisiana with the Texas model; significant differences were manifested in both  $W_{\infty}$  and in  $k$ . The model failed to converge for estimating a common value of  $k$  for both Louisiana and Texas.

We recognized that the larger red snappers from Louisiana might bias the data; therefore we compared growth for fish from 2 to 10 years of age—a time period when red snapper have demonstrated rapid linear growth (Szedlmayer and Shipp, 1994; Patterson et al., 2001; Wilson and Nieland, 2001). Linear regressions of mean FL at age for all individuals 2 to 10 years (Fig. 6A) were compared among states. We found no significant differences among states (ANCOVA test of homogeneity of slopes,  $F_{2,28}=2.7$ ;  $P=0.08$ ; ANCOVA test for equal intercepts,  $F_{2,28}=0.52$ ;  $P=0.6$ ).

Mean TW at age was also examined among states for red snapper 2 to 10 years in age as above (Fig. 6B). No significant differences were found between Alabama and Louisiana (ANCOVA test of homogeneity of slopes,  $F_{1,17}=0.1$ ;  $P=0.75$ ; ANCOVA test for equal intercepts,  $F_{1,17}=0.26$ ;  $P=0.66$  for intercepts). However, a significant difference between slopes was detected when comparing Alabama and Texas red snapper (ANCOVA test of homogeneity of slopes,  $F_{1,16}=19.68$ ;  $P<0.0007$ ; ANCOVA test for equal intercepts,  $F_{1,16}=2.74$ ;  $P<0.12$ ). The same was found when comparing slopes for Louisiana and Texas red snapper (ANCOVA test of homogeneity of

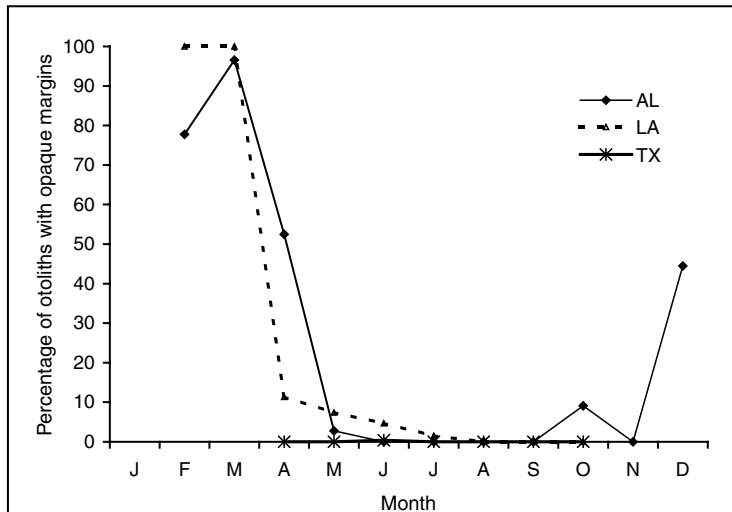
slopes,  $F_{1,16}=9.62$ ;  $P<0.008$ ) but not when comparing intercepts ( $F_{1,16}=0.64$ ;  $P<0.44$ ).

## Discussion

Demographic variations in growth rates and in size-frequency distributions may indicate the existence of isolated management units of red snapper in the northern GOM. The recreational harvests of Alabama and Louisiana red snapper were dominated by individuals ranging from 375 to 425 mm FL, whereas the majority of Texas fish (69%) were 375 mm FL or less. It was within this size range (375–400 mm FL) that the significant differences in red snapper among states were detected. The FL distribution of red snapper sampled in Texas also differed from those for Alabama and Louisiana; there were very few large fish represented in the Texas sample population, partly because fishing tournaments (where larger individuals are targeted) were not sampled in Texas. Significant differences in TW frequencies among states were also detected at approximately 1 kg (the approximate weight of a red snapper 375–400 mm FL); 86% of Texas fish weighed 1 kg or less, compared to only 27% of Alabama fish and 28% of Louisiana fish in this size range.

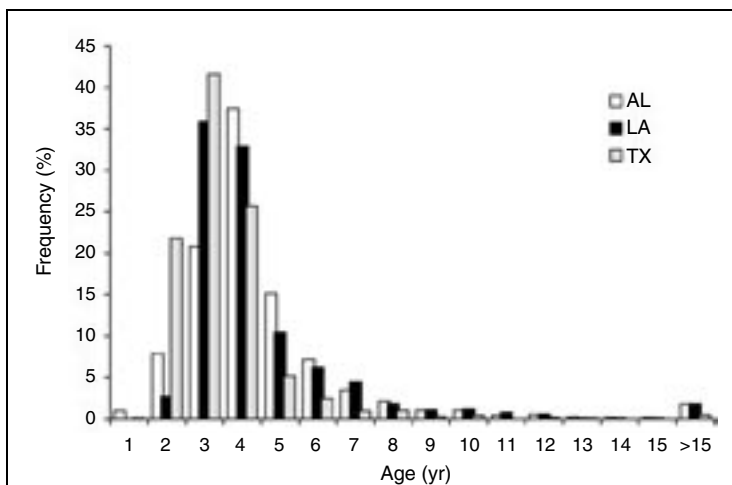
One factor possibly contributing to the modal size class difference was the type of fishing vessel used to catch the fish. The majority of Texas specimens (~95%) were sampled from headboats; whereas Louisiana and Alabama fish were obtained almost exclusively from charterboats. This is not to say that charterboats were purposely excluded from the Texas survey. On the contrary, red snapper were sampled from any and all available recreational fishing parties at the three individual sampling locations. Differences in modal size and number of red snapper caught per person onboard charterboats versus headboats may be inconsequential considering that both trip types used similar gear and targeted similar or the same fishing locations. It should be noted however that in the Texas study area, charterboats routinely frequented a wider array of fishing spots (rigs, hardbottom, wrecks, etc.) than did headboats, which typically return to the same few rigs and large structures over and over again (Tolan<sup>5</sup>).

Our von Bertalanffy growth models on FL at age showed that red snapper from all three states exhibit a pattern of rapid, linear growth to approximately 10 years, after which maximum theoretical (asymptotic) FL is soon



**Figure 3**

Marginal increment analysis of red snapper (*Lutjanus campechanus*) otoliths for specimens from Alabama ( $n=1985$ ), Louisiana ( $n=1864$ ), and Texas ( $n=1186$ ).



**Figure 4**

Age distributions for red snapper (*Lutjanus campechanus*) sampled from the 1999–2001 recreational harvests from Alabama, Louisiana, and Texas.

<sup>5</sup> Tolan, J. 2003. Personal commun. Texas Parks and Wildlife Department, Resource Protection, 6300 Ocean Dr., Corpus Christi, TX 78412.

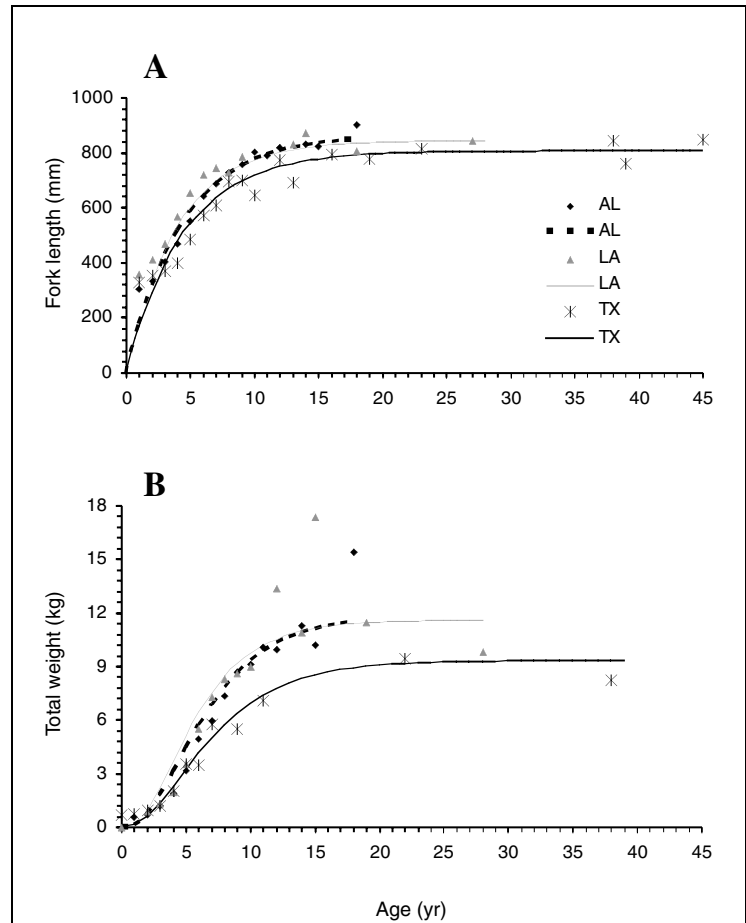
**Table 3**

Chi-square ( $\chi^2$ ), degrees of freedom (df), and *P*-values for likelihood ratio tests for comparing FL and TW von Bertalanffy growth models and parameters among sample locations (states). AL= Alabama; LA= Louisiana; and TX=Texas. n/a=not available.

	AL-LA		AL-TX		LA-TX		
	FL model	FL model	<i>L</i>	<i>k</i>	FL model	<i>L</i>	<i>k</i>
$\chi^2$	2.54	5.14	13.67	21.53	5.8	10.16	9.8
df	1, 28	1, 34	1, 34	1, 34	1, 32	1, 32	1, 32
<i>P</i>	0.11	0.023	0.0002	$3.48 \times 10^{-6}$	0.015	0.001	0.002
	TW model	TW model	<i>L</i>	<i>k</i>	TW model	<i>L</i>	<i>k</i>
$\chi^2$	2.15	38.8	21.3	37.8	16.77	15.1	n/a
df	1, 29	1, 27	1, 27	1, 27	1, 26	1, 26	n/a
<i>P</i>	0.14	$4.7 \times 10^{-6}$	$3.9 \times 10^{-6}$	$7.97 \times 10^{-10}$	$4.2 \times 10^{-5}$	0.001	n/a

reached and growth in length becomes negligible. This pattern of rapid growth was similar to that reported in previous studies (Szedlmayer and Shipp, 1994; Manooch and Potts, 1997; Patterson, 1999; Wilson and Nieland, 2001). However, our models predicted smaller  $L_\infty$  and higher values of *k*. Because of the minimum size limits on the recreational fishery, very few fish under age 2 years (>300 mm FL) were included in our sample populations. We forced our models through  $t_0=0$  to more accurately predict juvenile growth, which in turn increased our estimates of *k*. In addition, we had a much larger sample population that included more older, larger fish than most of the previously cited studies. These larger fish pulled the curve down, driving the lesser estimations of  $L_\infty$ . The lack of significant differences in growth parameters between the Alabama and Louisiana models supports the findings of previous research, which indicates that Alabama and Louisiana red snapper grow at similar rates and reach comparable sizes (Patterson et al., 2001). However, values of  $L_\infty$  for Texas red snapper were significantly smaller than parameters predicted for Alabama and Louisiana red snapper. Interestingly, Texas had a value of *k* that was significantly larger than that for Alabama and Louisiana and this would indicate that Texas fish obtain a smaller maximum theoretical FL but reach it at a faster rate than fish from Alabama and Louisiana.

Von Bertalanffy growth models of mean weight at age produced similar results, indicating that Texas red snapper obtain significantly smaller maximum theoretical TW than fish from Alabama and Louisiana. Fish sampled from tournaments were excluded from all growth models to more accurately reflect



**Figure 5**

Observed (A) mean fork length (mm) at age and (B) mean total weight (kg) at age for red snapper (*Lutjanus campechanus*) from Alabama, Louisiana, and Texas. Plotted lines are weighted von Bertalanffy growth functions fitted to the data.



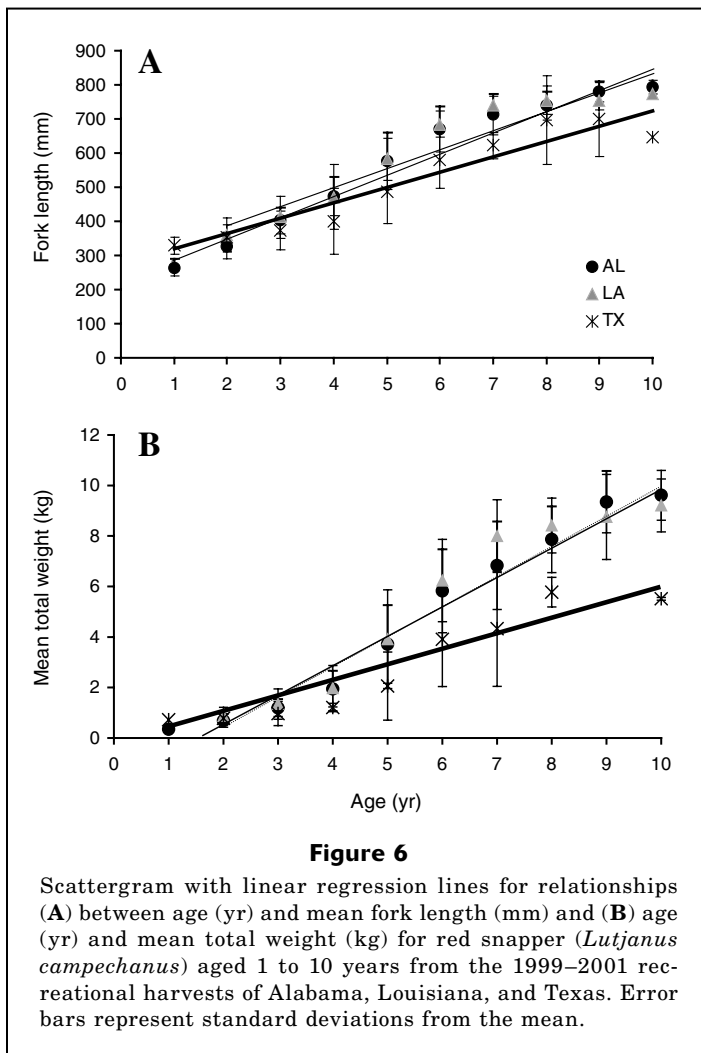
growth of a random population. Tournament anglers target large fish, possibly the fastest growing individuals at a given age, and their catches may bias growth estimates (Ottera, 1992; Vaughan and Burton, 1993; Goodyear, 1995). Without these tournament fish, however, the Alabama red snapper TW model did not reach an asymptote. Therefore the growth parameters for that model were poorly estimated. Notwithstanding, Alabama and Louisiana models did not differ significantly. Estimates of  $W_{\infty}$  and  $k$  predicted for Louisiana red snapper were slightly larger than previously reported for fish from the Louisiana commercial and recreational catches (Render, 1995). Although the Texas model predicted a value of  $W_{\infty}$  that was significantly less than those for both Alabama and Louisiana red snapper, Texas had a growth coefficient ( $k$ ) that was larger than that for Alabama. It appears that, as in the length models, Texas fish reach a smaller theoretical maximum weight but at a faster rate than Alabama fish. Louisiana fish attained maximum weight at a faster rate than Alabama or Texas red snapper. Our growth models indicate that although Texas red snap-

per grow in mass at a faster rate than Alabama fish, Texas red snapper are consistently smaller at age and reach smaller maximum sizes than those from Alabama and Louisiana and that there is a veritable difference in size at age and growth rates among regions. Similar demographic variations in growth rates among populations have been previously noted for other marine fish species of the South Atlantic and GOM, such as gray snapper (Johnson et al., 1994; Burton 2001), and king mackerel (DeVries et al., 1990; DeVries and Grimes, 1997).

Linear regressions of mean FL and mean TW at age for red snapper aged one to 10 years indicated that only TW was significantly different among sample regions. Texas red snapper were shown to differ significantly from both Alabama and Louisiana red snapper in regressions of mean weight at age. Although comparisons of FL at age for all regions were not significantly different, Texas fish were significantly smaller in mass (TW) at age than fish from Alabama and Louisiana. This difference was observed in all age classes.

Our research efforts indicate that there is mounting evidence for discrete differences in size at age and in overall growth rates between red snapper sampled from the north central GOM (Louisiana and Alabama) and the southwest GOM (Texas). Texas red snapper are clearly reaching smaller maximum sizes and are consistently smaller (TW) at age than those collected from Louisiana and Alabama waters. Although the reasons behind these differences remain uncertain, logic indicates that factors such as food availability, habitat preference, and actual population size may cause these differences between regions.

The more productive, nutrient-rich waters of the Mississippi River and north-central GOM off Louisiana and Alabama may be more conducive to faster growth than the less fertile waters off Texas. Approximately 70–80% of GOM fishery landings come from the waters surrounding the Mississippi River delta (Grimes, 2001). The western GOM (including the sampling area of Port Aransas, TX) is devoid of a contributing river system anything remotely similar to the Mississippi River. Draining 43% of the continental United States, the Mississippi River is the largest river system in North America and provides an enormous amount of nutrient-laden fresh water to the shallow continental shelf of the northern GOM. Although the mechanics by which the Mississippi River enhances fishery production remain uncertain, Grimes (2001) postulated that the discharge from the Mississippi primarily influences recruitment in the plume field. Increased growth rates associated with the Mississippi River plume compared with other regions of the GOM have been noted for a number of species, such as gulf menhaden (Warlen, 1988), king mackerel (DeVries et al., 1990), striped anchovy (Day, 1993), and yellowfin tuna (Lang et al., 1994).



**Figure 6**

Scattergram with linear regression lines for relationships (A) between age (yr) and mean fork length (mm) and (B) age (yr) and mean total weight (kg) for red snapper (*Lutjanus campechanus*) aged 1 to 10 years from the 1999–2001 recreational harvests of Alabama, Louisiana, and Texas. Error bars represent standard deviations from the mean.

In addition to increased food availability off of the north-central GOM, the amount and condition of preferred habitat may have some effect on the observed differences in growth rates for Texas and those for Louisiana and Alabama. Approximately 95% of all Louisiana fishes sampled in this study were harvested from waters surrounding nearshore (<50 km) oil and gas platforms. Similarly, about 95% of all Alabama fishes sampled were caught over artificial reef sites. The fact that there was no detectable difference in size at age and overall growth rates between Louisiana and Alabama red snapper therefore is not surprising, given the similarity in the habitats sampled and the proximity of both locations to the Mississippi River discharge plume. Texas was the only area in which samples were routinely obtained from natural hard bottoms (40%), as well as from oil and gas platforms and artificial reefs (60%). Given that more than half of the Texas specimens were captured in the waters immediately surrounding artificial structures (i.e., oil and gas platforms), we can assume that habitat type is not be the sole source for the observed differences in growth rates among regions.

Despite the current acceptance of a unit stock hypothesis for GOM red snapper, the species is not, and to our knowledge never has been, uniformly distributed across the northern GOM. The fishery for red snapper began in northwest Florida approximately 20 years before the Civil War (Collins, 1887) and during that time period was centered between Mobile, AL, and Fort Walton, FL (Camber, 1955). One hundred years of landings data indicate that the fishery, and possibly the population, has undergone a major shift from the natural outcroppings of the West Florida Shelf to oil and gas platforms of the north-central portion of the GOM (Shirripa and Legault<sup>1</sup>). Fishery-dependent data indicate that currently there is a center of abundance of red snapper off southwest Louisiana and a second, smaller center off Alabama (Patterson et al., 2001; Goodyear<sup>4</sup>; Shirripa and Legault<sup>1</sup>). Patterson et al. (2001) stated that Louisiana and Alabama accounted for 32.6% and 11.4%, respectively, of the combined recreational and commercial GOM landings from 1981 to 1998. This is especially surprising for Alabama, considering that its coastline accounts for only 3% of the GOM coastline from the Texas-Mexico border to the southern tip of Florida (Patterson et al., 2001).

Red snapper have never been reported to be plentiful in Texas waters, despite the availability of suitable habitat in the form of natural hard bottom and the current high concentration of oil and gas platforms. In a historical report on red snapper fishing in the GOM, Camber (1995) reported that although a few red snapper were taken from the "Galveston Lumps" or the "Western" fishing grounds off Texas, the fishery never fully developed in this region during the latter part of the nineteenth century. Commercial landings for red snapper from the GOM indicated that Texas accounted for approximately only 18% of the total catch during the time period 1981–95 (Goodyear<sup>6</sup>). In a recent fish-

ery-dependent survey of recreational headboat discards and landings in Texas coastal waters, red snapper less than the minimum legal size (15 inches) made up 64% of the catch (Dorf, 2000). In the latter study, Galveston, Port Aransas, and Port Isabel were surveyed to canvas a large portion of the Texas coast. Discard-to-landing ratios were as high as 211:1 in the waters off Galveston and were possibly indicative of the paucity of legal-size red snapper in Texas waters. Of the three sampling locations, Port Aransas had the lowest discard-to-landing ratio (5.2:1) and the largest mean fish length and weight (387 mm, 0.9 kg)—length and weight data that are consistent with a 3-yr-old fish from our Texas (Port Aransas) specimens. The majority of Texas fish (63%) were aged at 3 years or less. Age distribution, along with FL and TW distributions, may indicate that red snapper are being harvested from Texas waters just as they reach legal size. Given the vast differences in historical landings data between the northern and southwest GOM, the highly disproportionate discard-to-landing ratio reported for headboats in Texas waters (Dorf, 2000), and the large number of young fish sampled in Texas, it is not inconceivable to speculate that there are fewer red snapper available for harvest in Texas waters.

Demographic variation in growth rates may indicate the existence of separate management units of red snapper in the GOM. Our data indicate that the red snapper inhabiting the waters off Texas are reaching smaller maximum sizes at a faster rate, but are consistently smaller (TW) at age than those collected from Louisiana and Alabama waters. Whether these differences are environmentally induced or result from genetic divergence remains to be determined. The more productive, nutrient-rich waters of the Mississippi River and north-central GOM off Louisiana and Alabama may be more conducive to faster growth than the less fertile waters off Texas. Fishing pressure and its effects on population size may also be leading to the observed differences in growth rates. Fishery-dependent landing data and disproportionate discard-to-landing ratios in Texas waters loosely support the concept that fewer red snapper are available for harvest in the southwest GOM. Regardless of the cause, the existence of demonstrable demographic differences argues for the delineation of multiple red snapper management units in the GOM.

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<sup>6</sup> Goodyear, C. P. 1996. An update of red snapper harvest in U.S. waters of the Gulf of Mexico. Report MIA-95/96-60, 21 p. Miami Laboratory, Southeast Fisheries Center, National Marine Fisheries Service, 75 Virginia Beach Dr. Miami, FL., 33149-1099. [Not available from NTIS].

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