

**Abstract**—The gray snapper (*Lutjanus griseus*) is a temperate and tropical reef fish that is found along the Gulf of Mexico and Atlantic coasts of the southeastern United States. The recreational fishery for gray snapper has developed rapidly in south Louisiana with the advent of harvest and seasonal restrictions on the established red snapper (*L. campechanus*) fishery. We examined the age and growth of gray snapper in Louisiana with the use of cross-sectioned sagittae. A total of 833 specimens, (441 males, 387 females, and 5 of unknown sex) were opportunistically sampled from the recreational fishery from August 1998 to August 2002. Males ranged in size from 222 to 732 mm total length (TL) and from 280 g to 5700 g total weight (TW) and females ranged from 254 to 756 mm TL and from 340 g to 5800 g TW. Both edge analysis and bomb radiocarbon analyses were used to validate otolith-based age estimates. Ages were estimated for 718 individuals; both males and females ranged from 1 to 28 years. The von Bertalanffy growth models derived from TL at age were  $L_t = 655.4\{1 - e^{-0.23(t)}\}$  for males,  $L_t = 657.3\{1 - e^{-0.21(t)}\}$  for females, and  $L_t = 656.4\{1 - e^{-0.22(t)}\}$  for all specimens of known sex. Catch curves were used to produce a total mortality ( $Z$ ) estimate of 0.17. Estimates of  $M$  calculated with various methods ranged from 0.15 to 0.50; however we felt that  $M=0.15$  was the most appropriate estimate based on our estimate of  $Z$ . Full recruitment to the gray snapper recreational fishery began at age 4, was completed by age 8, and there was no discernible peak in the catch curve dome.

Manuscript submitted 19 September 2003 to the Scientific Editor's Office.

Manuscript approved for publication 20 November 2004 by the Scientific Editor. Fish. Bull. 103:307–319 (2005).

## Age, growth, mortality, and radiometric age validation of gray snapper (*Lutjanus griseus*) from Louisiana

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The gray snapper (*Lutjanus griseus*), commonly referred to as the mangrove snapper, is a temperate and tropical reef species that is found along the southeastern Atlantic coast of the United States from North Carolina to Bermuda, throughout the Gulf of Mexico (GOM), and south to Brazil (Johnson et al., 1994; Allman and Grimes, 2002). Gray snapper are fairly common along the Louisiana coast and are usually associated with complex structures such as oil and gas platforms, artificial reefs and other hard bottom substrates. In 1991 restrictions were put on the recreational red snapper (*Lutjanus campechanus*) fishery; these restrictions coincided with a rapid expansion of the gray snapper fishery in south Louisiana. Recreational anglers now typically target gray snapper once they have reached their bag limit of red snapper; thus peak gray snap-

per landings generally coincide with the red snapper recreational season (April–October). As a result, recreational landings of gray snapper in Louisiana have increased exponentially from 3.25 metric tons (t) in 1983 to 175 t in 2002 (NMFS<sup>1</sup>). Currently there is a 305 mm (12 inches) minimum size and a recreational bag limit of 10 fish/person/day for gray snapper in the GOM.

Some background information is available for gray snapper in the southeastern United States, mainly from south Florida. Scientists have reported on early life history (Ruth-

<sup>1</sup> NMFS (National Marine Fisheries Service). 2003. Fisheries Statistics and Economics Division. Unpubl. data. Website: [http://www.st.nmfs.gov/pls/webpls/MF\\_ANNUAL\\_LANDINGS.RESULTS](http://www.st.nmfs.gov/pls/webpls/MF_ANNUAL_LANDINGS.RESULTS). [Accessed 25 August 2003.]

erford et al., 1989; Domier et al., 1997), population dynamics (Rutherford et al., 1989), juvenile food habits (Hettler, 1989), juvenile distribution (Chester and Thayer, 1990), and reproduction (Domeier et al., 1997; Allman and Grimes, 2002).

Few reports have been conducted on the age and growth of gray snapper. Manooch and Matheson (1981) used sectioned otoliths to age gray snappers from eastern Florida but did not validate their methods. Johnson et al. (1994) also used sectioned otoliths to age fish sampled from Fort Pierce, FL, to Grand Isle, LA, again without validation of methods. Burton (2001) validated the periodicity of opaque zone formation in gray snapper from east coast Florida waters with the use of marginal increment analysis of distal edge measurements. But gray snapper have never been fully examined in the northern GOM and comprehensive age, growth, and mortality data from the thriving Louisiana recreational fishery are virtually nonexistent.

The objectives of our study were to describe the age, growth, and mortality of gray snapper from the Louisiana recreational fishery. We obtained age information through examination of cross-sectioned sagittal otoliths, validated our aging techniques with the use of bomb-radiocarbon  $^{14}\text{C}$  and edge analyses, produced mortality estimates with standard procedures, and modeled growth with the von Bertalanffy growth equation.

## Methods and materials

Gray snapper were sampled from the Louisiana recreational harvest from August 1998 to August 2002 by personnel from the Louisiana State University Coastal Fisheries Institute and the Louisiana Department of Wildlife and Fisheries. Fish were opportunistically sampled at charter boat facilities in Port Fourchon, LA, and at spearfishing and hook and line fishing tournaments in Grand Isle and New Orleans, LA. Morphometric measurements (fork length [FL] and total length [TL] in mm, total weight [TW] in g) were taken, sex was determined by macroscopic examination of the gonads, and both sagittae were removed, rinsed, and air dried, weighed to the nearest 0.1 mg, and stored in coin envelopes until processed. For specimens in which TL was unavailable, TL was estimated from FL with the equation  $TL = 1.048(FL) + 8.35$  (linear regression,  $df=275$ ;  $P<0.001$ ;  $r^2=0.98$ ) calculated from specimens in which both TL and FL were available.

In order to estimate age of gray snapper, a transverse section (~1 mm thick) was taken containing the core of the left sagittal otolith of each specimen. Sections were made with a Hillquest model 800, thin-sectioning machine equipped with a diamond embedded wafering blade and precision grinder (Cowan et al., 1995). In instances where the left otolith was unavailable, the right was substituted. Examinations of otolith cross-sections were made under a dissecting microscope with transmitted light and polarized light filter from 20 $\times$  to 64 $\times$ . Opaque zones were enumerated along the ventral side

of the sulcus acousticus from the core to the proximal edge (Wilson and Nieland, 2001). Two readers (AJF and MSB) performed opaque zone counts independently without knowledge of capture date or morphometric data. Otolith marginal edge condition was coded as opaque or translucent by using the criteria described by Beckman et al. (1989). Opaque zones were counted a second time when initial counts differed. In instances where a consensus between readers could not be reached, counts of the more experienced reader (AJF) were used. Between-reader variation in opaque zone counts was examined after the second readings of otolith sections were completed. Differences in counts were evaluated with the coefficient of variation (CV), index of precision ( $D$ ) (Chang, 1982), and average percent error (APE) (Beamish and Fournier, 1981).

Ages of gray 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 of 1 July assigned for all gray snapper to coincide with peak spawning activity occurring in July (Domeier et al., 1997; Allman and Grimes, 2002). Age in years was assigned by dividing age (in days) by 365. Year of birth (YOB) was back calculated by subtracting our otolith-based age estimates from year of capture.

Validation of the periodicity of opaque zone formation in gray snapper otoliths was examined with two approaches. An advanced and accurate method of age validation uses a quantitative measurement of nuclear bomb-produced radiocarbon ( $^{14}\text{C}$ ) that was accumulated in carbon-containing hard parts of marine organisms before, during, and after the atmospheric testing period of nuclear weapons (1958–65) (Baker and Wilson, 2001). Elevated levels of  $^{14}\text{C}$  have been observed in hermatypic corals (Druffel, 1980, 1989) and this time-specific marker can be used to validate age estimates derived from hard parts in marine fishes (Kalish, 1993; Campana and Jones, 1998). Baker and Wilson (2001) recently validated red snapper otolith section age estimates using this technique with excellent results. This same method was applied in our study to the otolith cores of gray snapper hatched after the nuclear testing periods.

Gray snapper hatched prior to 1973 were not available for our study, and thus the steepest portion of the radiocarbon uptake curve could not be used to confirm age estimates. Consequently, no coral reference data for the general area were available after 1983. Because red snapper otoliths have been previously validated

with this same method (Baker and Wilson, 2001), we anticipated that gray snapper radiocarbon values would be roughly similar to red snapper values for a given YOB.

To obtain the oldest portion of the otolith for radiocarbon analysis, right otoliths of older gray snapper with an estimated YOB after the period of atmospheric testing (1973–95) were embedded in araldite epoxy resin and thin sectioned (~1 mm in thickness) through the core with an Isomet low-speed saw. The otolith core region was isolated from the otolith section by using the technique described in Baker and Wilson (2001). Cores were rinsed in double-distilled de-ionized water, allowed to air dry, weighed to the nearest 0.1 mg, and submitted to the accelerator mass spectrometry (AMS) facility in acid-washed 20-mL glass scintillation vials. The mean sample weight submitted for analyses was 12.8 mg.

At the AMS facility, otolith cores underwent acid hydrolysis with 85% phosphoric acid to yield CO<sub>2</sub> which was then made into graphite (pure C) by reduction at high temperature under vacuum. The graphite was pressed onto a target, loaded on the AMS unit and analyzed for radiocarbon. Samples were also analyzed for <sup>13</sup>C to correct for natural and machine fractionation effects. Radiocarbon values from individual otolith cores were reported as Δ<sup>14</sup>C (mean ±SD), the adjusted deviation from the radiocarbon activity of 19<sup>th</sup> century wood (Stuiver and Polach, 1977).

The periodicity of opaque zone formation was also examined with edge analysis. The marginal edge of each otolith was examined and coded as

- 1 opaque zone forming on otolith margin;
- 4 translucent zone forming on margin up to 1/3 complete;
- 5 translucent zone forming on margin 1/3 to 2/3 complete;
- 6 translucent zone forming on margin 2/3 to fully complete.

Percentages of otoliths with opaque margins were plotted by month of capture (Beckman et al., 1989; Campana, 2001; Wilson and Nieland, 2001) for all months in which specimens were available.

In order to examine the predictive capacity of otolith weight ( $W_o$ ) to determine age in gray snapper, sex specific  $W_o$ -age relationships were fitted by using a power function with least squares with the model:  $Age = aW_o^b$ . A likelihood ratio test (Cerrato, 1990) was used to test for differences between male and female models.

Male and female TW-TL relationships were independently fitted with linear regression to the model  $W = aTL^b$  from log<sup>10</sup>-transformed data. Male and female regression coefficients were compared with an ANCOVA. Variability in age, TL, and TW-frequency distributions of males and females were compared with Komolgorov-Smirnov two-sample tests (Tate and Clelland, 1957; Sokal and Rohlf, 1995). Growth of gray snapper was modeled by using all specimens of known sex. Von Ber-

talansffy growth models of TL at age were fitted with nonlinear regression by least squares (SAS 6.11, SAS Institute, 1996, Cary, NC) in the form:

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

where  $t$  = age in years;

$TL$  = TL at age  $t$ ;

$L_\infty$  = the theoretical maximum TL; and

$k$  = the growth coefficient.

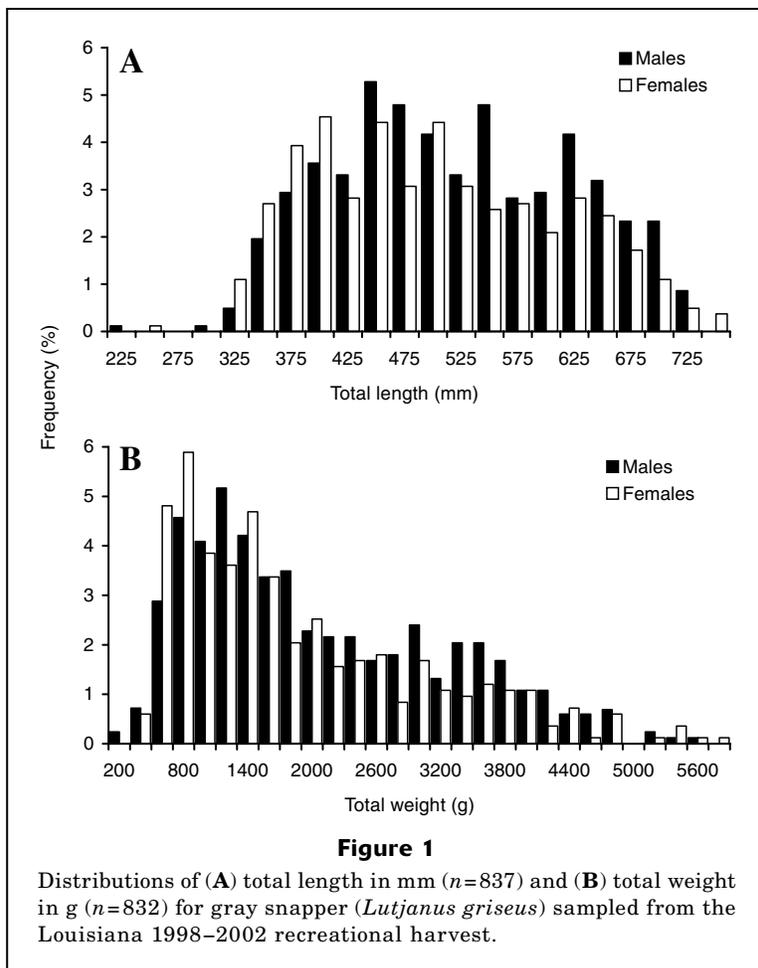
Because of a lack of smaller individuals in our sample population, no  $y$ -intercepts for  $t_0$  were specified and models were forced through 0 (Szedlmayer and Shipp, 1994; Fischer et al., 2004) to better estimate juvenile growth. One growth model was generated for all specimens of known sex. Additional models were fitted independently for males and females. Likelihood ratio tests (Cerrato, 1990) were used to test for differences between male and female models.

The instantaneous total mortality rate ( $Z$ ) was estimated from a catch curve (Nelson and Manooch, 1982; Burton, 2001) assuming our collections represented the actual age distribution of the population. These estimates were made with the regression method of plotting the log<sub>e</sub> age frequency on age. We used the absolute value of the slope of the linear descending right limb of the curve after full recruitment to estimate  $Z$ .

Estimates of instantaneous natural mortality ( $M$ ) were computed with several methods. The first estimate of  $M$  was based on Hoenig's (1983) longevity-mortality relationship, where the mortality rate is based solely on the oldest specimen encountered in the data set. We also used Hoenig's (1983) relationship for natural mortality with modifications for sample size. Natural mortality was also computed with the method of Pauly (1980) assuming a mean annual water temperature of 25°C. Our mean annual water temperature estimate was derived from the data buoys operated by the National Oceanic and Atmospheric Administration's National Oceanographic Data Buoy Center from 1995 to 2001. Finally,  $M$  was calculated with the Ralston (1987) method, where the estimate of  $M$  is based solely on a simple regression involving the Brody growth coefficient ( $k$ ). A significance level of 0.05 was used for all statistical analyses.

## Results

We sampled 833 gray snapper (441 males, 387 females, and 5 individuals of unknown sex) from the recreational fishery of Louisiana for morphometric data and otoliths. The male:female ratio was 1:0.88; a  $\chi^2$  test indicated no significant difference between the proportions of males and females ( $\chi^2=3.52$ ,  $P=0.06$ ). Male and female specimens ranged from 222 to 732 mm TL and from 254 to 756 mm TL, respectively (Fig. 1A). Both sexes exhibited multimodal distributions; males were represented in the greatest numbers at 450 mm TL, compared to 400 mm



TL for females. A Komolgorov-Smirnov two-sample test indicated no significant difference between male and female TL frequencies (maximum difference=9.45). Male and female TW ranged from 200 to 5700 g and 300 to 5800 g TW, respectively (Fig. 1B). Both sexes also displayed multimodal distributions in TW. A Komolgorov-Smirnov two-sample test indicated a significant difference between sexes at 1600 g TW (maximum difference=9.67). A single predictive TL-TW regression was generated for both males and females:

$$TW = 3.31 \times 10^{-5} (TL^{2.85})$$

$$(F_{1, 822}=9,326.54; P<0.001; r^2=0.92).$$

Significant differences were found between sexes in TL-TW relationships (ANCOVA test of homogeneity of slopes,  $F_{3,822}=7.25$ ;  $P=0.007$ ;  $r^2=0.92$ ). Therefore, separate models were fitted for each sex:

$$\text{Males} = TW = 2.04 \times 10^{-5} (x^{2.93})$$

$$(F_{1, 436}=7588.29; P<0.001; r^2=0.95)$$

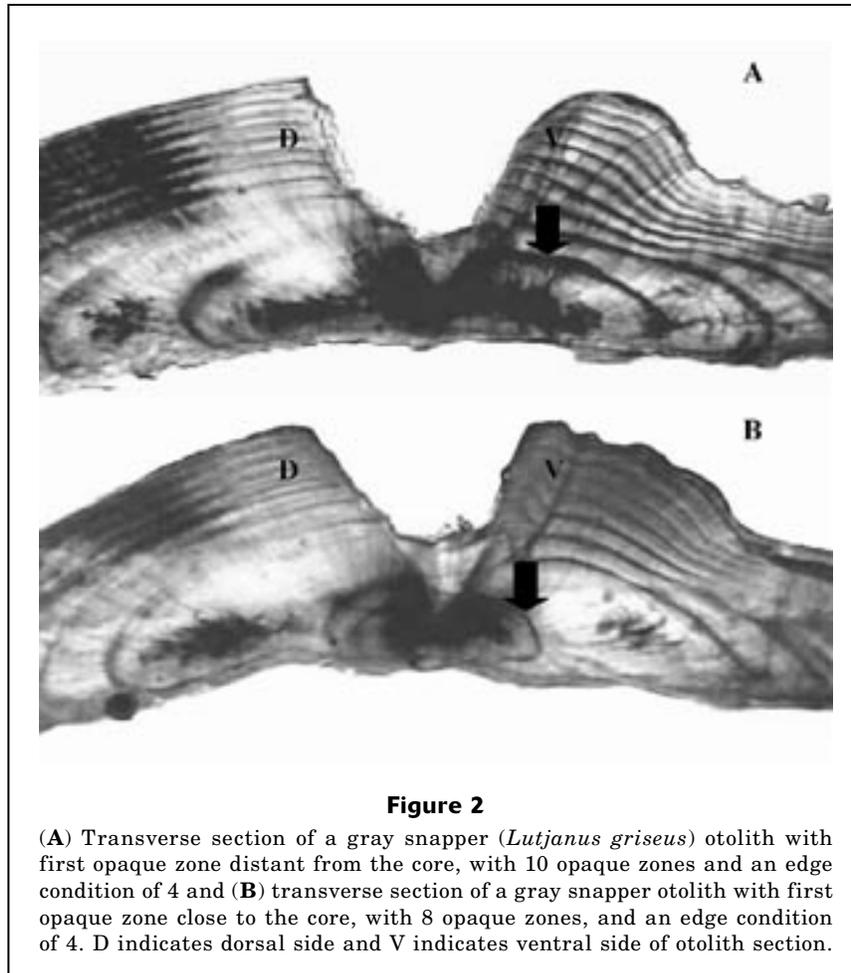
$$\text{Females} = TW = 5.5 \times 10^{-5} (TL^{2.77})$$

$$(F_{1,385}=3,089.16; P<0.001; r^2=0.89)$$

Gray snapper otoliths are very similar in physical structure, although much smaller in actual size, to those of the red snapper. Opaque zones are easily distinguishable on the ventral side of the sulcus groove (Manooch and Matheson, 1981; Johnson et al., 1994; Shipp<sup>2</sup>) (Fig. 2, A and B).

Sagittae were collected from 721 gray snapper of which 718 were aged. Readers were unable to resolve opaque zones in three otolith sections because of poor sectioning. Readers agreed on the ages of 568 individuals (78.8%) after initial counts and differed by one opaque annulus for 154 specimens, two annuli for 18 specimens, and three annuli for 2 specimens. Readers agreed on 709 ages (98.7%) after the second reading. The average percent error (APE) was 0.5, coefficient of variation (CV) was 0.00078, and index of percent ( $D$ ) was 0.0006.

<sup>2</sup> Shipp, R. L. 1991. Investigations of life history parameters of species of secondarily targeted reef fish and dolphin in the northern Gulf of Mexico. Proc. Fourth Annu. MARFIN Conf., San Antonio, TX, p 80–85. [Available from National Marine Fisheries Service, State/Federal Liaison Office, 9721 Executive Center DR. N., St. Petersburg, FL 33702.]

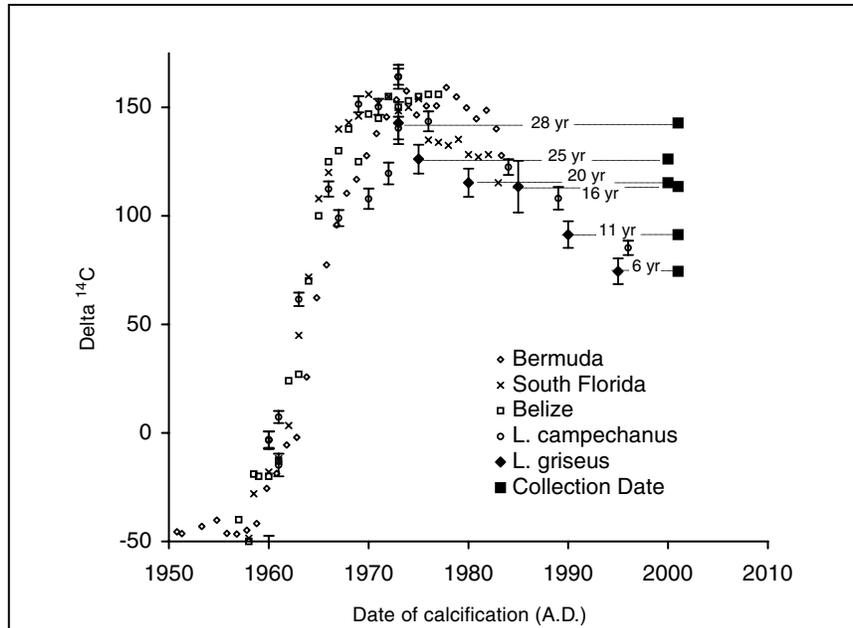
**Table 1**

List of gray snapper (*Lutjanus griseus*) otoliths analyzed for stable carbon and bomb radiocarbon. “AMS wt.” is the amount of otolith separated from the otolith section and submitted for accelerator mass spectrometry (AMS) radiocarbon analysis; FL=fork length. I.D.= our identification number.

NOS-AMS number	I.D.	Date caught	Otolith section age (yr)	Birth date	Otolith wt. (mg)	AMS wt. (mg)	$\delta^{13}\text{C}$ (‰)	$\Delta^{14}\text{C}$ (‰)	
								Mean	$\pm$ SD
OS-36337	320	2001	28	1973	639.1	9.9	-2.67	142.8	9.7
OS-36338	33	2000	25	1975	635.2	14.7	-2.55	126.2	6.7
OS-36339	5	2000	20	1980	536.7	15.0	-3.34	115.3	6.5
OS-36340	322	2001	16	1985	414.6	15.1	-5.27	113.5	11.9
OS-36341	316	2001	11	1990	306.5	9.8	-4.49	91.4	6.1
OS-36342	304	2001	6	1995	154.0	12.2	-5.73	74.5	5.9

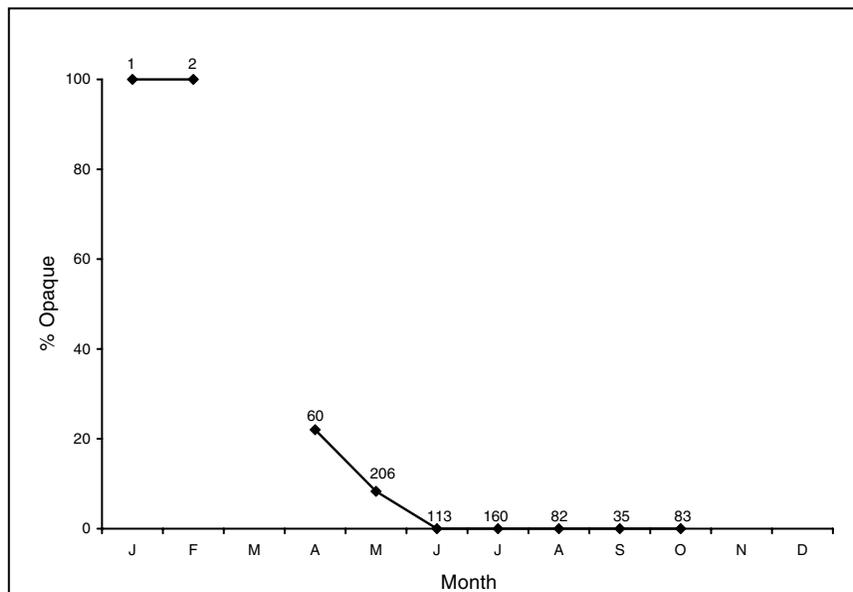
The gray snapper ( $n=6$ ) used for the radiocarbon age validation procedure ranged from 6 to 28 years of estimated age and were collected during 2000 and 2001 (Table 1). Furthermore, YOB ranged from 1973 to 1995. Gray snapper radiocarbon values were plotted

along with red snapper radiocarbon values from the northern Gulf of Mexico (Baker and Wilson, 2001) and coral radiocarbon values from Bermuda (Druffel, 1989), South Florida (Druffel, 1989), and Belize (Druffel, 1980) (Fig. 3). Radiocarbon values of gray snapper cores were



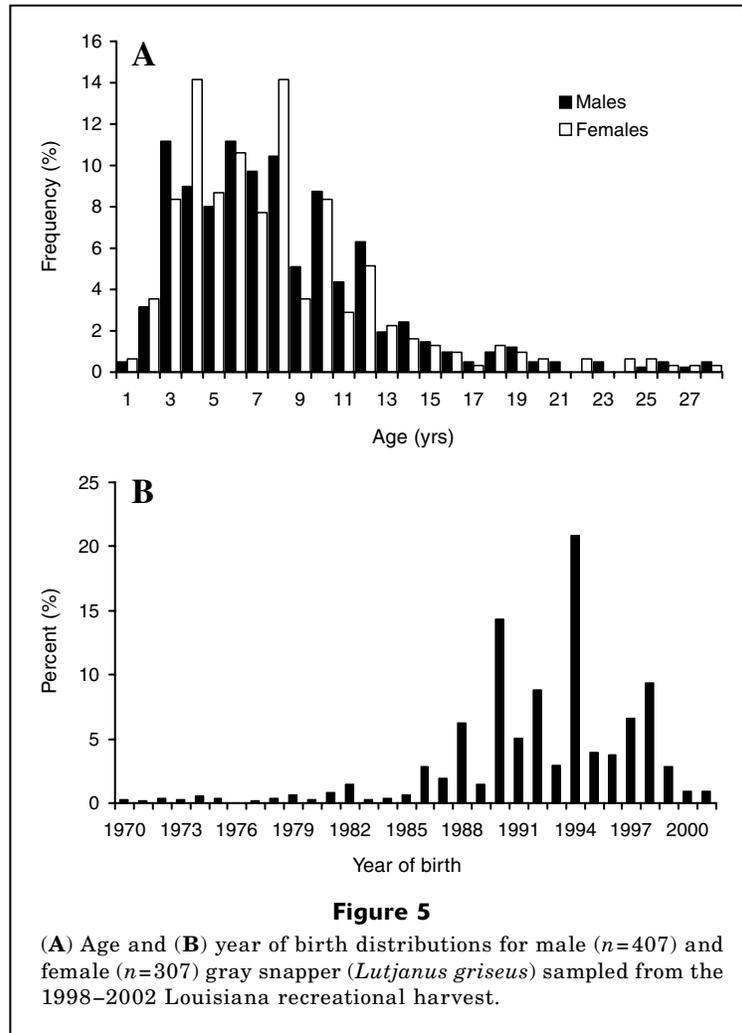
**Figure 3**

Plot of radiocarbon (<sup>14</sup>C) values versus date of calcification for gray snapper (*Lutjanus griseus*) (present study) and red snapper (*Lutjanus campechanus*) (Baker and Wilson, 2001) from the northern Gulf of Mexico and from corals off Bermuda (Druffel, 1989), South Florida (1989), and Belize (Druffel, 1980). Solid squares (■) indicate collection dates for the gray snapper samples (n=6) and the age listed are the estimated ages as read from the otolith sections.



**Figure 4**

Marginal edge analysis of gray snapper (*Lutjanus griseus*) otoliths sampled from the 1998–2002 Louisiana recreational harvest (n=718). Numbers above data points indicate the number of otoliths analyzed for each month.



highest in 1973 and exhibited a steady decline to a low in 1995.

The periodicity of opaque annulus formation in gray snapper otoliths was further examined by plotting the monthly percentages of otoliths with opaque margins (Fig. 4). Although little data were available for the winter months, one specimen sampled in January and two specimens sampled in February 2001 each exhibited opaque marginal otolith edges indicating that opaque annulus formation occurs during the winter. Minimum percentages of otoliths with opaque margins during the months of April (22%) and May (8%) followed by an absence of opaque margins during the months of June through October indicate the cessation of opaque annulus formation by early spring and the onset of translucent annulus formation beginning in April and continuing through November.

Male and female gray snapper ranged in age from 1 to 28 years (Fig. 5A). There was no significant difference in age distributions between males and females (maximum difference=6.92 yr), but both sexes exhibited variable multimodal distributions in age frequency.

Year of birth (YOB) frequency was also multimodal, and the population was dominated by younger fish; 77% of males and 80% of females were aged at 10 years or younger (Fig. 5B).

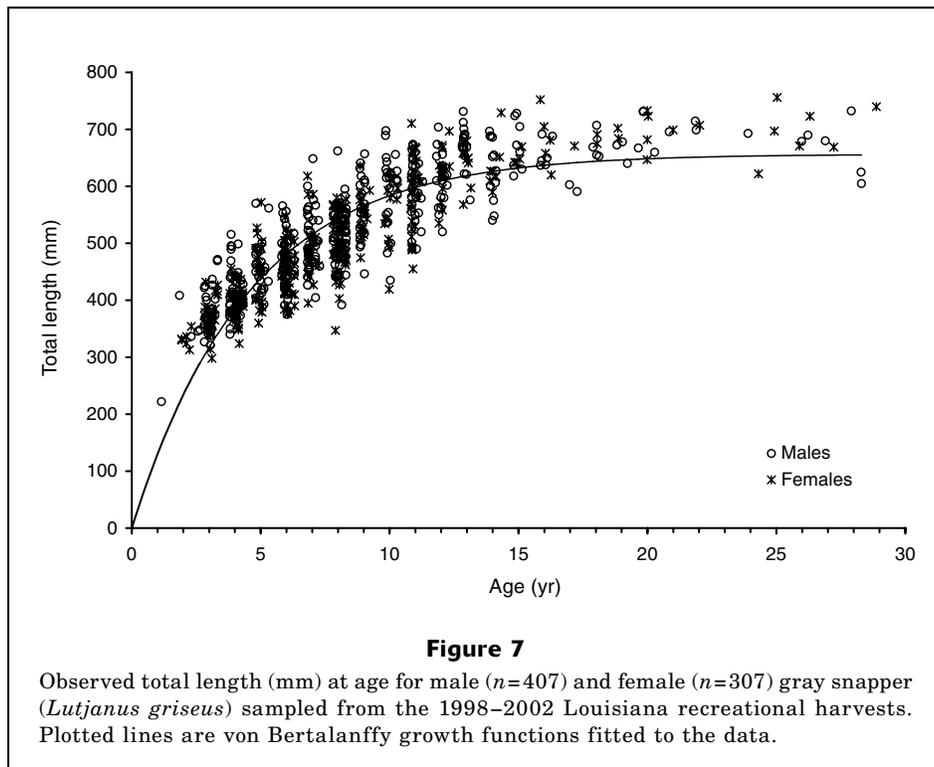
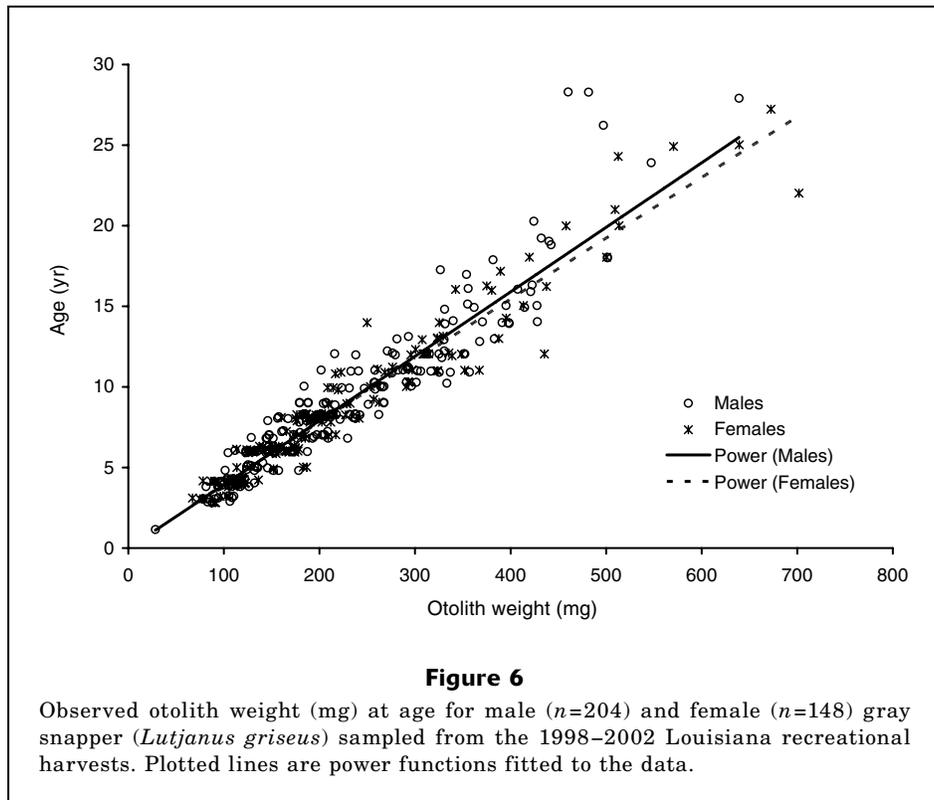
Significant differences in slopes were detected when plotting age- $W_0$  relationships between sexes (ANCOVA test of homogeneity of slopes,  $F_{3,353} = 8.06$ ;  $P=0.0005$ ). Therefore, predictive models of age- $W_0$  were fitted separately for males and females using a power function with least squares as (Fig. 6)

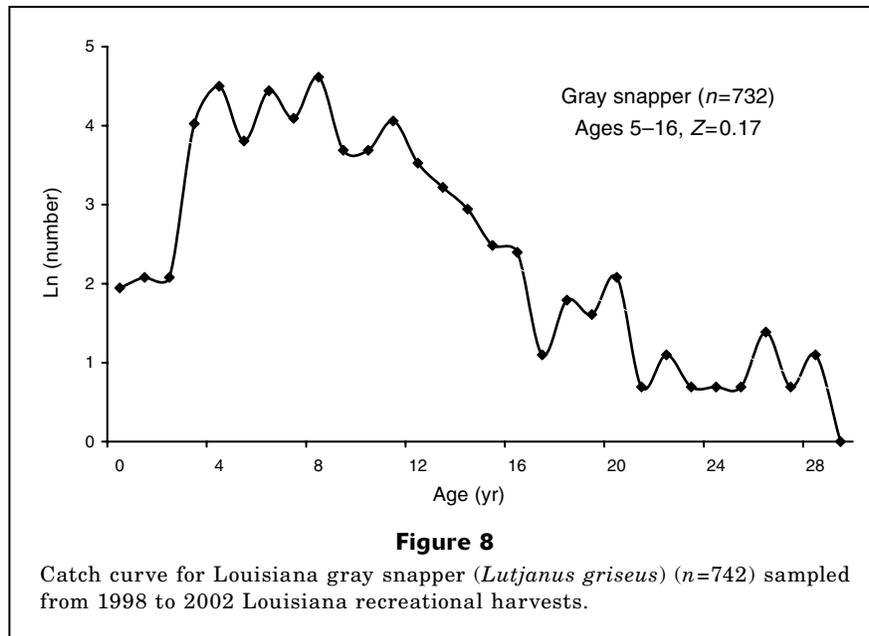
$$\text{Male age} = 0.0278 (W_0)^{1.06} \\ (F_{2,204}=3,956.29, P<0.001, r^2=0.89).$$

$$\text{Female age} = 0.0460 (W_0)^{0.97} \\ (F_{2,148}=4,504.05, P<0.001, r^2=0.90).$$

The single von Bertalanffy growth model to describe gray snapper TL at age (Fig. 7) was

$$L_t = 656.4\{1 - e^{[-0.22(t)]}\} \\ (F_{2,714}=32,217.6; P<0.0001; r^2=0.72).$$



**Table 2**

Degrees of freedom (df), sum of squares (SS), mean square (MS),  $F$  value, and  $P$  values for the likelihood ratio test by which the full von Bertalanffy growth model (in which sexes were fitted independently) is compared with the reduced von Bertalanffy model (by fitting all specimens of known sex).

Model	df	SS	MS	$F$	$P$
Full	4714	$1.9493 \times 10^8$	48,732,614	16,341	<0.0001
Reduced	2714	$1.9489 \times 10^8$	97,447,139	32,217.6	<0.0001

However, a likelihood ratio test indicated growth models for males and females were significantly different from one another ( $\chi^2=494.77$ ;  $df=2,714$ ;  $P<0.001$ ) (Table 2). The resultant sex-specific von Bertalanffy growth models were

$$\text{Male } L_t = 655.4\{1 - e^{-0.23(t)}\}$$

$$(F_{2,407}=19,732.9; P<0.001; r^2=0.73)$$

$$\text{Female } L_t = 657.3\{1 - e^{-0.21(t)}\}$$

$$(F_{2,307}=13,015.2; P<0.0001; r^2=0.72).$$

Instantaneous total mortality ( $Z$ ) was calculated with catch curve analysis. Full recruitment to the gray snapper fishery began at age 4 and was completed by age 8 and there was no discernible peak in the catch curve dome (Fig. 8). For the purposes of  $Z$  estimation, age 4 was used as the age of full recruitment to the fishery.  $Z$  was estimated at 0.18 for all fish (age range: 5–28 years) and 0.17 for all fish when the age range was truncated at 16 years. The age range was truncated at 16 years because older age classes contained fewer than 10 individuals.

Estimates for natural mortality ( $M$ ) for gray snapper varied substantially and were dependent upon the method used. Hoenig's (1983) longevity-mortality relationship produced the lowest estimate of 0.15. Hoenig's (1983) relationship modified for sample size yielded an estimate of 0.30. The regression method of Ralston (1987) produced an estimate of 0.40. Finally, Pauly's (1980) method using a mean annual water temperature of 25°C and parameter estimates  $L_\infty$  and  $k$  derived from the von Bertalanffy growth equations produced the highest estimate of 0.51.

## Discussion

Validation of the periodicity of opaque zone formation is critical when using otoliths to determine the ages of fish (Beamish and McFarlane, 1983). The lack of data during the winter months prevented us from making a definitive statement on the timing of opaque zone formation based on edge analysis alone. However, we present evidence that suggests that opaque zone formation may

begin as early as December and proceed through May. Opaque zone formation beginning in December through spring has been shown to occur in the congeneric red snapper (Render, 1995; Patterson et al., 2001; Wilson and Nieland, 2001) as well as in a number of other teleosts in the northern GOM (Beckman et al., 1989, 1990, 1991; Thompson et al., 1999). Burton (2001) validated the periodicity of opaque zone formation for gray snapper along the Atlantic coast but reported the period of formation to occur during the summer months of June and July.

The natural decay of radiocarbon in the world ocean after the nuclear testing period is well documented (Broecker et al., 1985) and close agreement between gray snapper data and existing radiocarbon chronologies from the Gulf of Mexico, U.S. South Atlantic, and Caribbean provided additional evidence that our otolith-section-based age estimates of gray snapper were valid (Fig. 3). The  $^{14}\text{C}$  values obtained from gray snapper otolith cores formed after the period of atmospheric testing of nuclear weapons were comparable to, if not slightly less than, those values found in red snapper from the northern Gulf of Mexico (GOM) (Baker and Wilson, 2001).

Although published coral radiocarbon chronologies are available for review and are made available in the present study, we are most confident in comparing gray snapper to the red snapper data for several reasons. First and foremost, these two species were collected from the same general area of the northern Gulf of Mexico and thus in theory should have similar radiocarbon chronologies (Broecker et al., 1985). Second, although the coral samples would seem to be the best possible items for comparison because of their known age, stationary location, and most importantly because multiple "birth dates" can be analyzed from one coral head, the gray snapper and red snapper samples were taken from different geographic areas and thus different water bodies. No known coral radiocarbon chronologies exist for the northern Gulf of Mexico. Radiocarbon chronologies have been shown to vary significantly in the world ocean by latitude (Broecker et al., 1985) and this trend in the reference corals can be seen in Figure 3, especially during the period of rapid radiocarbon uptake (1958–75). Finally, all otolith samples (gray snapper and red snapper) were analyzed for radiocarbon by the same AMS facility by using identical laboratory methods (Baker and Wilson, 2001). Delta  $^{14}\text{C}$  data from the otoliths of gray snapper with presumed YOB back to 1973 (the oldest fish in our data set) clearly reflected the same pattern found in red snapper; high levels of oceanic radiocarbon attributable to previous nuclear testing followed by a slow but steady decline to a low in 1995 (Fig. 3). The gray snapper curve is slightly lower but parallel to the red snapper curve. Because of the inherent variability associated with individual fishes, it is inconceivable to think that the two species of snapper would have curves that completely lie on top of each other or on top of the coral chronologies for that matter. Although the two species are very similar in

many regards, we can only speculate that differences in juvenile life history patterns, habitat preferences, water column chemistry, and possibly otolith formation may account for the variation in radiocarbon chronologies. However, both the gray snapper and previously validated red snapper chronologies exhibit the same trend and indicate that our otolith-based age estimates are accurate.

The majority of radiocarbon fisheries age validation has produced otolith-based chronologies that resemble those from nearby reference corals or other fish species in the same general location (Campana, 2001). Campana and Jones (1998) observed extremely high and erratic radiocarbon values for black drum (*Pogonias cromis*) in the Chesapeake Bay. In that study, the radiocarbon values resembled the intermediate of surface oceanic (corals) and the much higher atmospheric values (Campana and Jones, 1998). The reasons for the erratic  $\Delta^{14}\text{C}$  values remain unknown, but Campana and Jones speculated that the estuarine dependency of the species produced the variable activities of radiocarbon in individual fish for a given YOB. This was not the case with gray snapper, also a species that uses the shallow estuarine environment during the first years of its life. Because gray snapper is estuarine dependent, we fully expected the gray snapper radiocarbon values to be erratic and much higher than the reference corals. In contrast, gray snapper radiocarbon values were strikingly similar to, if not less than, red snapper and the reference coral radiocarbon values at all comparable YOBs (Fig. 3). Contrary to the opinions expressed by Campana and Jones (1998), our limited data suggested that estuarine dependency may have no effect on observed radiocarbon values, at least for gray snapper.

Although opaque zones are distinct in gray snapper otolith cross sections, the small size and apparent longevity of the species pose some challenges for age interpretation. In older fish, opaque zones are formed more closely together in the otolith, making accurate counts and accurate interpretation of the otolith margin more difficult. We observed considerable variability in the location of the first opaque zone in gray snapper; the first annulus was variously located somewhat distant from the core to close to and continuous with the otolith core (Fig. 2, A and B). Wilson and Nieland (2001) noted the same pattern in red snapper otoliths suggesting that this variability may be a function of the protracted red snapper spawning season, which is similar to that of gray snapper, and of the rapid growth rate during the juvenile stage. This variability in first opaque zone position accounted for the majority of disagreement between readers in initial age estimates; there was only 76.5% agreement. However, experience by both readers (AJF and MSB) with red snapper otoliths produced consensus of 98.8% after second readings.

Male and female gray snapper ranged in age from 1 to 28 years. Younger individuals composed the major portion of the fishery; 90% of the catch was aged less than 15 years. Maximum ages were greater than those reported in previous studies. Johnson et al. (1994) re-

ported maximum ages of 23 and 25 years for males and females, respectively; the oldest fish in the study was actually sampled from Grand Isle, LA. Burton (2001) reported a non-sex-specific maximum age of 24 years. Sampling for both of these studies was focused in Florida where there is higher fishing pressure on gray snapper (Burton, 2001) and this fishing pressure may explain the lesser maximum ages and paucity of older individuals in their sample populations.

Gray snapper exhibit multimodal distributions in age and YOB frequencies. Due to minimum size limits, very few individuals were represented below age 3. Age distributions exhibited an initial peak at 3 years, when gray snapper are beginning to recruit to the recreational fishery. Successive peaks in age-class abundance in our data set occurred every two years. In an examination of abundance by YOB a similar pattern was observed; strong year classes were followed by diminished year classes. Similar patterns of variability in year-class strength have been observed in black drum (*Pogonias chromis*) and red drum (*Scienops ocellatus*) in the northern GOM. Beckman et al. (1989) suggested that year-class variability in these species might be due to environmental factors during early life stages or biological controls on the population. If this observed consistent pattern is reflective of the gray snapper population off Louisiana, we suggest that the variation in year-class strength may be reflective of intra-species-specific year-class competition of juveniles competing for resources within the estuaries before recruiting to the offshore fishery.

Researchers continually search for effective, cost-efficient ways to acquire fish age data. Body size has been shown to be a poor value to use for estimating age in a number of fish species because of the considerable variability in size at age. Otolith growth has been shown to continue with age, independent of somatic growth. Otolith weight ( $W_o$ ) has been used as a predictive tool to determine age in a number of fish species (Templeman and Squires, 1956; Beamish, 1979; Wilson and Dean, 1983; Secor et al., 1989; Beckman et al., 1991). Although a strong relationship has been demonstrated between  $W_o$  and age, especially for the younger age classes, considerable variability exists in  $W_o$  at age in older age classes. For example, the  $W_o$  of a 10-yr-old male gray snapper can range from 180 mg to 357 mg thus preventing a precise age estimate based on  $W_o$  alone. Although  $W_o$  data may provide general information on overall age distribution patterns of a population, we feel that annulus counts from otolith cross sections provide the most accurate age estimates for gray snapper.

Our overall (sexes combined) von Bertalanffy growth model estimated a maximum theoretical length ( $L_\infty$ ) of 656.4 mm TL. Although a likelihood ratio test indicated a significant difference between male and female models, this difference may be of limited biological significance because male and female models appear to be very similar. The presence of larger, older fish in our sample population resulted in our overall model

coming to an asymptote at a smaller  $L_\infty$  and having a larger respective  $k$  than previously reported (Manooch and Matheson, 1981; Johnson et al., 1994). Johnson et al. (1994) predicted an  $L_\infty$  of 792.25 mm using the regression method of Manooch and Matheson (1981) to back calculate lengths at age. Johnson et al. (1994) also obtained a much smaller estimate of  $k$  at 0.08 compared with a  $k$  value of 0.22 predicted in our model. A smaller estimate was not unexpected given the inverse correlation between  $L_\infty$  and  $k$  noted by Knight (1968). Because of the minimum size limitations on the recreational fishery, smaller (presumably younger) individuals below 304 mm TL were almost absent in our sample population. We chose to not specify a  $y$ -intercept for  $t_0$  and to force our growth models through zero in order to obtain more accurate estimates of  $k$ . Forcing our models through zero also contributed to the differences in growth parameters between our study and those of Johnson et al. (1994). Like Johnson et al. (1994), Burton (2001) also estimated growth parameters by fitting back-calculated lengths at age. Burton's (2001)  $L_\infty$  estimates of 717 mm and 625 mm for north and south Florida, respectively, are similar to those found in our study. Burton's (2001) sample populations consisted of a number of fish below 200 mm TL. These smaller individuals had similar effects on his models as that of forcing our models through zero. Burton's estimates of  $k$  were 0.17 and 0.13 for north and south Florida, respectively, compared with a  $k$  of 0.22 for our overall model.

We estimated total instantaneous mortality ( $Z$ ) to be 0.17 and full recruitment to the fishery at age 4. We chose to use the truncated age range of 5–16 years (versus 5–28 years) for  $Z$  estimation in order to have at least 10 samples in each age category. Our estimation of  $Z$  based on all age categories (5–28) was 0.18. Our estimate of  $Z$  is at the low end of the range of values reported by Johnson et al. (1994) ( $Z=0.17-0.26$ ) for the Gulf of Mexico. It should be noted, however, that Johnson et al. (1994) pooled fish from five distinct geographical locations. Of the 432 fish analyzed in their study, 69% came from Grand Isle, LA ( $n=104$ ) and Panama City, FL ( $n=193$ ). The remaining 31% came from the central and southern coasts of Florida. Perhaps Johnson et al.'s (1994) estimates of  $Z$  would be lower if only the Louisiana samples were used. Our  $Z$  values, however, are much lower than those reported by Manooch and Matheson (1981) ( $Z=0.39-0.60$ ) and Burton (2001) ( $Z=0.34-0.95$ ) for the east coast of Florida.

Our low estimate of  $Z$  for gray snapper in Louisiana waters is clearly associated with the abundance of older, larger individuals in the population. Unlike the catch curves in previous studies that dealt with gray snapper populations on the east coast of Florida (Manooch and Matheson 1981; Burton 2001) and in the southeast in general (Johnson et al. 1994), the mode of our catch curve is not well defined. It is evident that gray snapper in the South Atlantic are heavily exploited (Burton, 2001), as evidenced from their age-frequency distribution and high estimates of  $Z$ .

Estimates of  $M$  ranged from 0.15 to 0.51 and were comparable to previous studies on gray snapper from the southeastern United States. Johnson et al. (1994) used the Pauly (1980) and Ralston (1987) methods to estimate  $M$  to range from 0.12 to 0.32 for the west coast of Florida, including Louisiana. Manooch and Matheson (1981) used the Pauly (1980) relationship to calculate  $M = 0.22$ . Burton (2001) used the same four methods as in our study and found  $M$  to range from 0.18 to 0.43. It is well known that estimates of mortality are highly variable and depend upon the parameters used to calculate them. The purpose of providing various estimates of  $M$  was to demonstrate to the reader the variability in this important life history parameter and to demonstrate how little we actually know about it. Adopting our estimate of  $Z$ , we feel that the Hoenig (1983) method ( $M=0.15$ ) produced the most suitable estimate of  $M$  for gray snapper in Louisiana waters of the northern Gulf of Mexico. Based on the apparent age-size structure of the stock, historical landings data, and personal observation, all indications are that this species is lightly fished in this study area. Hoenig (1983) indicated that  $M$  should be roughly equivalent to  $Z$  if the population is lightly exploited. Our estimate of  $Z$  (0.17) was indeed roughly equivalent to  $M$  (0.15), supporting our belief that fisheries mortality ( $F$ ) is not yet a significant threat to this fishery.

Gray snapper could become over-exploited if a large, intensive fishery developed in the northern Gulf of Mexico. Landings of gray snapper in Louisiana have increased dramatically over the last few years, partly because of the recent restrictions imposed on red snapper in the Gulf of Mexico. Compared to the gray snapper population structure in the South Atlantic, especially off the coast of south Florida (Manooch and Matheson, 1981; Burton, 2001), the Louisiana population appears to be healthy. Long-term heavy fishing pressure has probably affected the south Florida gray snapper population (Burton, 2001). As a result, the population structure of south Florida is dramatically different from that of Louisiana. Our estimates of  $Z$  are extremely low and indicate that fishing mortality ( $F$ ) is currently not a significant factor for the gray snapper population in Louisiana waters. A low-intensity gray snapper fishery could take most of the resource without endangering future production.

### Acknowledgments

Funding and assistance with sampling was provided by the Louisiana Department of Wildlife and Fisheries. We would also like to thank Josh Maier, Brett Blackmon, and Candace Aiken for sampling efforts and otolith processing as well as Brain Milan for providing juvenile gray snapper samples. We thank Steve Tomeny, the boat captains, and deck hands of Captain Steve Tomeny's charters in Port Fourchon, LA, as well as all the recreational fishermen that allowed us to sample their catch. We wish to thank Ann P. McNichol of National Ocean

Sciences (Accelerator Mass Spectrometry facility at the Woods Hole Oceanographic Institution) for otolith radiocarbon analyses.

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