Age Estimates from Annuli in Otoliths of Red Snapper, *Lutjanus campechanus*, from the Northern Gulf of Mexico

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ABSTRACT

The red snapper *Lutjanus campechanus* is currently under stringent federal management in the Gulf of Mexico off the southeastern United States due to apparent overfishing of many populations. Management strategies employed to promote recovery of the species are dependent upon knowledge of various demographic variables such as the ages of individuals, the distribution of these ages (cohort strength) within the population, and maximum longevity. Thus a reliable and accurate ageing methodology for red snapper is of paramount importance. Annuli on otoliths have been used to age many species of fishes, including red snapper. However, the utility of this methodology for ageing red snapper has been questioned by those who dispute both the apparent longevity (over 50 yr) of red snapper and the position of the first annulus within the otolith.

We counted annuli and assessed edge condition in sagittal otoliths of 3,791 red snapper collected from the northern Gulf off Louisiana during the periods 1989 to 1992 and 1995 to 1998. Opaque annuli were validated by marginal increment analysis to form once per year from December through June. Among the otoliths examined, estimated ages ranged from 0.5 to 52.6 yr for individuals from 104 mm to 1,039 mm total length and from 0.017 kg to 22.793 kg total weight. The great heterogeneity in red snapper age at a given total length or total weight limits the use of morphometric variables as predictors of age.

KEY WORDS: Age, otoliths, red snapper

INTRODUCTION

The red snapper *Lutjanus campechanus* (Poey) (Family Lutjanidae) has been a significant element of the past and current commercial and recreational fisheries in the Gulf of Mexico (GOM) (Cato and Prochaska 1976, Moran 1988, Goodyear 1994, Schirripa and Legault 1999). However, documented commercial landings from United States territorial waters declined precipitously from historic highs of about 3,738 metric tons (mt) in 1974 to 1,015 mt in 1991 (Goodyear

1996, Schirripa and Legault 1999). Estimated recreational landings similarly waned from 4,734 mt in 1979 to 581 mt in 1990 (Schirripa and Legault 1997). Since 1991 both fisheries have been constrained by size limits, creel or trip limits, and quotas as established by the Gulf of Mexico Fishery Management Council GMFMC). Since 1991 the commercial fishery has achieved its allotted annual catch quota and has been subject to closure; however, the recreational fishery has often exceeded its allocation (Goodyear 1996, Schirripa and Legault 1999) and yet has experienced closure only in 1997, 1998, and 1999. The best efforts of the GMFMC and the commercial and recreational sectors notwithstanding, red snapper in the GOM may continue to be overfished (Goodyear 1995, Schirripa and Legault 1999).

Accurate information on the age structure of the red snapper population in the GOM is necessary to monitor year class strength, to conduct stock assessments, and to document population recovery. Previous efforts at estimating red snapper age have employed a variety of ageing methodologies. Bradley and Bryan (1975) cited the long red snapper spawning season and constant recruitment into the population as reasons for the difficulty in assigning red snapper ages from length frequency data. Moseley (1966) used scale annuli to age red snapper to age 4 years and advanced spawning as the causal factor in check formation. Wade (1978) also used scales to age red snapper to 9 years. Among 240 red snapper taken off the west coast of Florida, Futch and Bruger (1976) estimated red snapper ages of 1 to 5 years from 200 readable otoliths; however, they postulated ages up to 20 years for larger individuals whose otoliths were unreadable. Nelson and Manooch (1982) found red snapper age 1 to 16 years based on both scales and otoliths and demonstrated once yearly scale annulus formation in June and July from monthly mean marginal growth. A recent study has significantly extended the hypothesized longevity of red snapper in the GOM to 42 years (Szedlmayer and Shipp 1994). Render (1995) provided a preliminary validation of yearly annulus formation in sagittal otoliths and reported ages from 0 to 53 years for red snapper in Louisiana waters. Examinations of otoliths from 537 red snapper captured in the northwestern Atlantic Ocean from Beaufort, North Carolina south to the Florida Keys manifested a maximum longevity of 25 years (Manooch and Potts 1997). Among 907 red snapper from the GOM off Alabama, Patterson (1999) reported opaque annulus formation from January through June and maximum ages of 30 years for females and 31 for males.

Despite these efforts the longevity of red snapper remains controversial. Small sample sizes, a paucity of older specimens, and the failure to present legitimate validations of ages from hard parts (Beamish and McFarlane 1983) have variously hampered the above studies. It has further been speculated that larger and presumably older red snapper form numerous false annuli within otoliths (Rothschild et al. 1997). And both the timing of deposition and the position of the putative first annulus remain in question.

Otolith analyses have proven consistent in estimating ages of many fish species, including several from the temperate waters of the northern GOM (Johnson et al. 1983, Barger 1985, Beckman et al. 1988, Beckman et al. 1990, 1991). Herein we present our interpretations of the use of sagittal otoliths to estimate ages of red snapper from the GOM off Louisiana. Specifically addressed are the timing of formation and position of the first annulus, validation of the once yearly accretion of opaque annuli, and reader reproducibility.

METHODS AND MATERIALS

Red snapper from the northern GOM were sampled from recreational and commercial catches from 1989 to 1992 and from 1995 to 1998 by personnel of the Louisiana State University (LSU) Coastal Fisheries Institute and the Louisiana Department of Wildlife and Fisheries (LDWF). Although the vast majority of our sampling efforts were targeted at both wholesale facilities and charter boat docks located in Grand Isle and Port Fourchon, LA, the area of coverage in the northern GOM extended from off the Mississippi River Delta in the east to off Galveston, TX in the west. Morphometric measurements (fork length (FL) in mm, total (TW) or eviscerated body weight (BW) in g), both sagittal otoliths, and a sex determination when possible were taken from each specimen. Body weight was converted to TW, when necessary, with the equation TW = 1.101(BW) - 26.32 and total length (TL) was estimated with the equation TL = 1.073 (FL) + 3.56.

All otoliths were weighed, embedded in an epoxy resin, and then thin sectioned with a low speed saw equipped with a wafering blade as described in Beckman et al. (1988). Examinations of otolith sections were made with a compound microscope and transmitted light at 40X to 100X magnification. Counts of annuli (opaque zones) were accomplished by reading along the medial surface of the transverse section ventral to the sulcus; annuli were often inconsistent in other regions of the otolith section. Annulus counts were performed by two readers (A. L. Stanley and A. J. Fischer) without knowledge of date of capture or morphometric data. The appearance of the otolith margin was also coded as either opaque or transparent (Beckman et al. 1988, Beckman et al. 1990, 1991). Sections were recounted a second time by both readers when initial counts disagreed. Rather than excluding the small number of individuals for which a consensus could not be reached after a second reading, the assigned annulus count for these was that of Stanley. Fischer's annulus count and edge condition were used in those circumstances where Stanley's were missing. Annulus counting error between the two readers was evaluated after both the initial and second readings of the otolith sections. Reproducibility of the counts was determined with the coefficient of variation, the index of precision (Chang 1982), and average percent error (Beamish and Fournier 1981).

The frequency of opaque annulus formation was determined by marginal increment analysis and by plotting percent occurrence of otoliths with opaque margins by month (Beckman et al. 1988, Beckman et al. 1990, 1991). If one opaque and one translucent zone are shown to be formed each year, validation of annuli as being accreted once yearly is accomplished. Age estimates of red snapper were based on otolith opaque annulus counts and adjusted by edge condition. Based on previous studies of red snapper reproduction (Render 1995, Collins et al. 1996), a uniform hatching date of 1 July was assigned for all specimens.

RESULTS

During eight years of variable collection effort, 3,791 red snapper from recreational (N=274) and commercial (N = 3,517) catches were sampled for morphometric data and sagittal otoliths. Among the 1,438 male and 1,542 female specimens for which sex could be determined, females ranged from 242 to 1,039 mm TL and from 0.160 to 22.793 kg TW; males were 245 - 946 mm TL and 0.190 - 13.695 kg TW. Composite ranges for all specimens of either known or unknown sex were 104 - 1,039 mm TL and 0.017 - 22.793 kg TW. Distributions of 3,787 available TL and 3,718 available TW are shown in Figure 1 A and B, respectively.

Sagittae of red snapper are ovate, laterally compressed and have an indented sulcus on the medial surface. Although one can count purported growth rings in relatively small whole otoliths of red snapper less than age 5, it is difficult to discern annuli in the larger otoliths of older individuals (Futch and Bruger 1976). Thin transverse sections of the otoliths exposed semi-distinct translucent and opaque annuli which alternated from the core to the growing edge (Figure 2). The assumptive first annulus posed the most consistent problem for the readers. This annulus appeared as a diffuse "smudge" of opaque material variously located from contiguous to and continuous with the otolith core to totally isolated and somewhat distant form the core. Nonetheless, annulus counts ranging from 0 to 53 and edge conditions were determined by at least one reader for all 3,791 individuals sampled.

Reader One (Fischer) considered all of the otolith sections to be of sufficient quality to produce annulus counts; reader two (Stanley) provided annulus counts from all but two sections. After the initial counts, consensus between readers was achieved for 2804 individuals (Table 1). A second reading of the 987 sections for which annulus counts differed produced consensus for 3,762 individuals. The degree of agreement in red snapper opaque annulus counts between the two readers in each of the two readings was assessed. Average percent error (APE), coefficient of variation (CV), index of precision (D), and percentages of absolute differences in counts are given in Table 1.

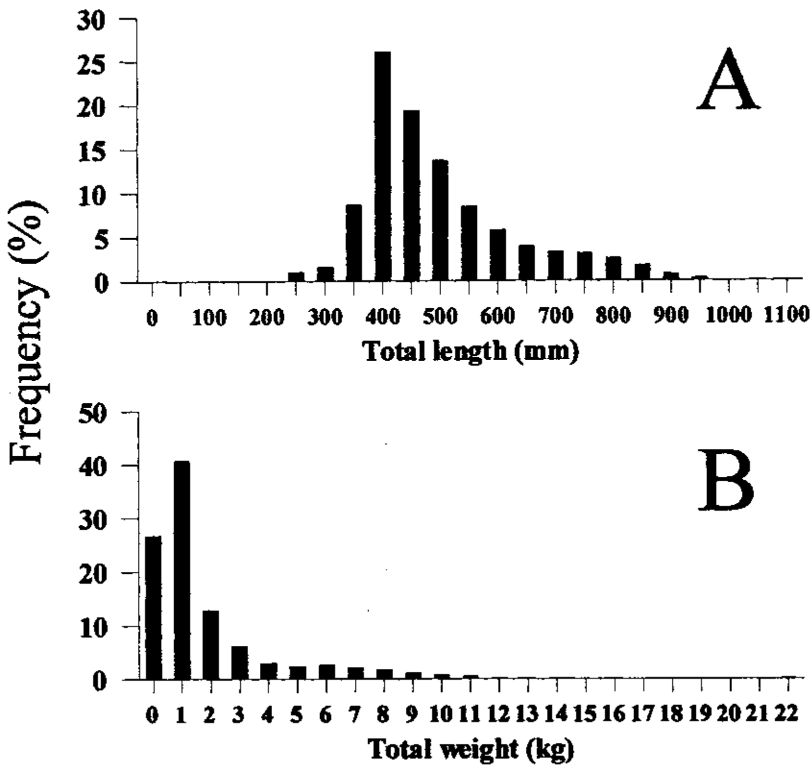

Figure 1. Frequency histograms for (A) total length (N=3,787) and (B) total weight (N = 3,718) of red snapper *Lutjanus campechanus* from the northern Gulf of Mexico.

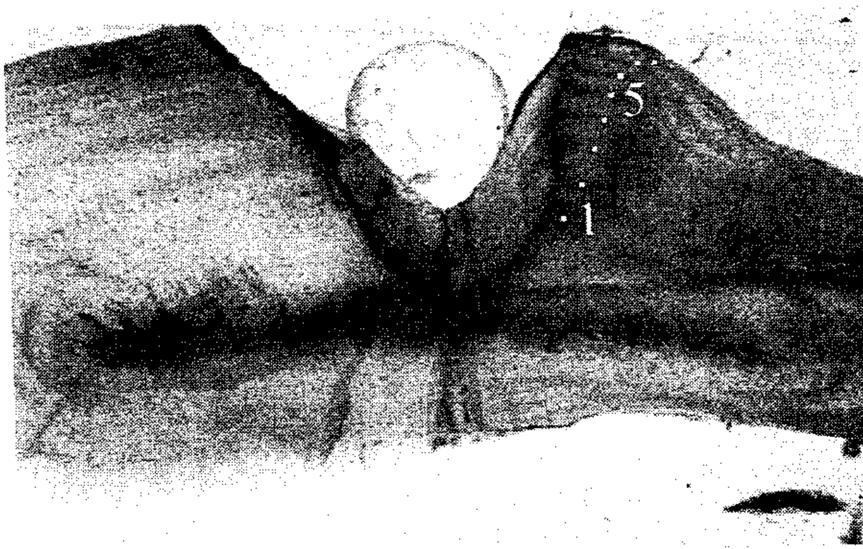

Figure 2. Transverse section of a red snapper, *Lutjanus campechanus*, sagittal otolith showing alternating opaque and translucent annuli. White dots indicate the opaque annuli. The first and fifth annuli are indicated with numerals.

Table 1. Average percent error (APE), coefficient of variation (CV), index of preecision(D), and absolute differences in red snapper otolith annulus counts for two readers on first and second readings.

	1st Reading	2nd Reading
APE	0.037	0.009
CV	0.045	0.0011
D	0.032	0.0008
0	73.96%	99.29%
± 1	23.27%	0.61%
± 2	2.24%	0.08%
> ± 3	0.54%	0.03%

The assumption of once yearly opaque annulus formation was tested with marginal increment analysis. Proportions of otoliths with opaque margins were plotted by month of capture for all individuals (N = 3,791), for those from individuals presumed to be sexually immature (ages less than or equal to 5, N = 2,143), and for those from individuals of presumptive sexual maturity (ages greater than 5, N = 948). Each of the three plots (Figure 3) features a single broad peak and a single broad valley and conclusively demonstrates opaque annulus formation from December through June and translucent annulus formation from July through November. Thus, the assumption of one to one correspondence between opaque annulus counts and estimated red snapper age in years is validated. Furthermore, this correspondence is validated for immature and mature individuals of all ages.

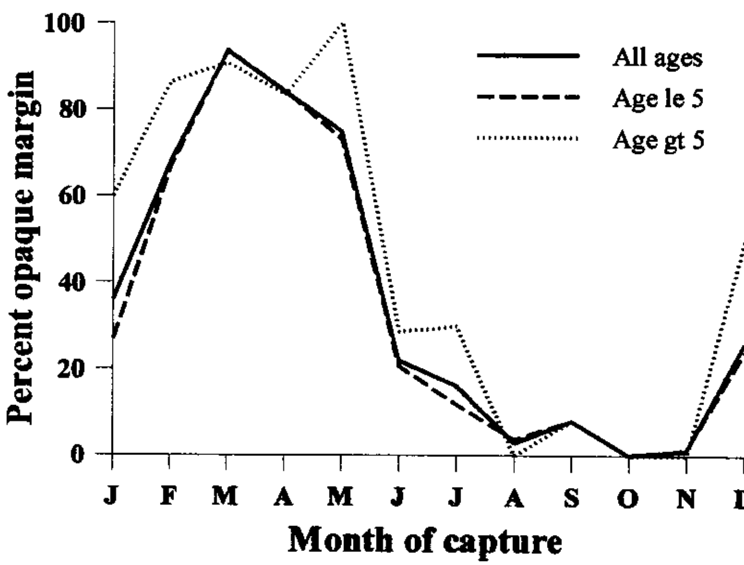

Figure 3. Percent of red snapper, *Lutjanus campechanus,* otoliths with opaque margin by month of capture. Sample sizes are 3,791 for all ages, 3,497 for ages than or equal to 5, and 294 for ages greater than 5.

Assuming once yearly accretion of opaque annuli, ages from 0.5 to 52.6 years were estimated from the annulus counts of the red snapper considered herein. The vast majority of specimens examined were ages 2 - 5 years and only 1.2% of the total number were greater than age 15 years (Figure 4). The otolith section from the oldest specimen examined is shown in Figure 5. Due to the large variability in age at a given TL (Figure 6), this variable is not a good estimator of red snapper age even at the smaller sizes where the age-size relation shows the greatest degree of linearity. Our data indicate that red snappers of 300 mm, 600 mm, and 800 mm TL could be ages 1 - 4 years, 3-9 years, and 3-50+ years, respectively.

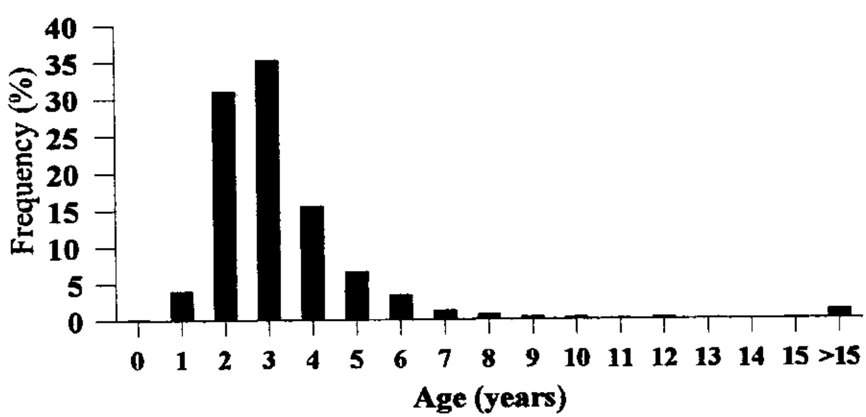

Figure 4. Frequency histogram of age in years for red snapper, *Lutjanus campechanus,* from the northern Gulf of Mexico. Sample size = 3,791.

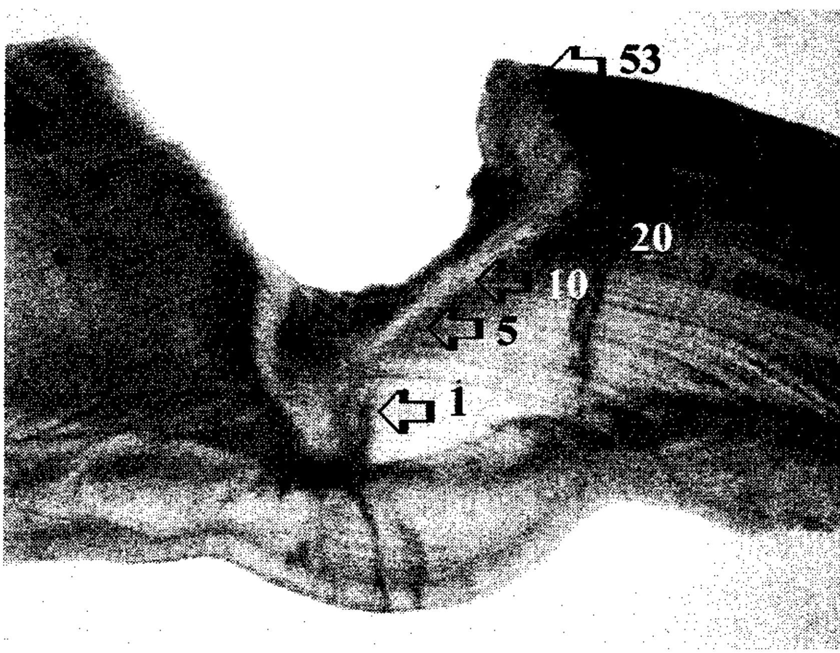

Figure 5. Transverse section of red snapper, *Lutjanus campechanus*, otolith indicating the first, fifth, tenth, twentieth, and fifty-third opaque annuli.

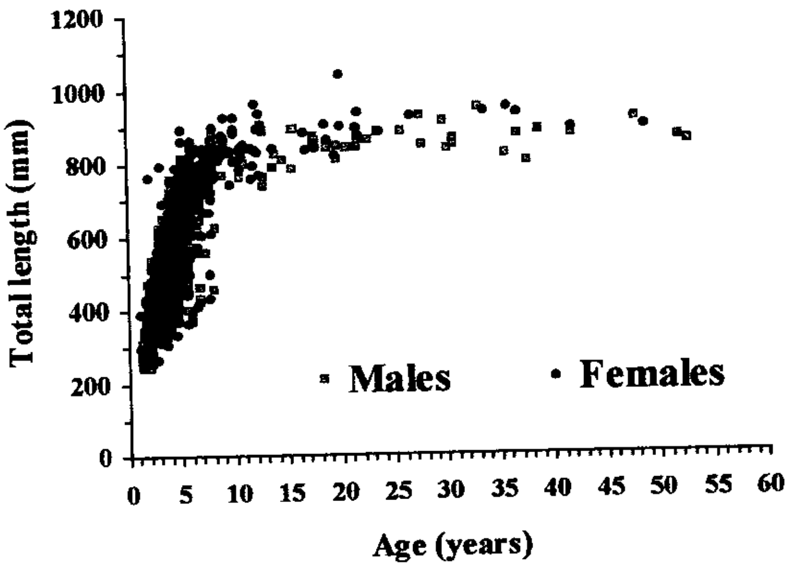

Figure 6. Scatterplot of red snapper, *Lutjanus campechanus*, age versus total length for 3,791 specimens from the northern Gulf of Mexico.

DISCUSSION

The use of otolith annuli as indicators of age has been validated for many freshwater and marine fish species, including the lutjanids *L. adetii* and *L. quinquelineatus* (Newman et al. 1996). Previous studies have utilized scales (Moseley 1966, Wade, 1978), otoliths (Futch and Bruger 1976, Render, 1995, Manooch and Potts 1997, Patterson 1999), scales and otoliths (Nelson and Manooch 1982) and scales, otoliths, and pectoral fin rays (Bortone and Hollingsworth 1980) to estimate red snapper ages. Among these, early attempts to validate age estimation from circuli of scales and annuli of otoliths have suffered from two shortcomings: 1) a small sample size and 2) a paucity of individuals over age 10 years. Nevertheless, they have produced a general consensus that transparent annuli (Nelson and Manooch, 1982) are formed during the spawning season (May to September in the GOM (Collins et al. 1996)). Our validation of opaque annulus formation in otoliths of red snapper during the winter and spring seasons is in substantial agreement with previous efforts. Given that yearly formation of opaque annuli has been validated for substantial numbers of red snapper from the Atlantic waters off North Carolina south to Florida (Manooch and Potts 1997) and the GOM waters off Alabama (Patterson

1999) and Louisiana (Render 1995, this study), the one to one correspondence between annuli and age in years should be indisputable.

Certainly, the reproducibility statistics indicate that the annuli of red snapper otoliths are more difficult to count than those of other fishes. Comparisons of between reader age estimates in several species of the family Sciaenidae have yielded near 100% agreement (Beckman et al. 1988, Beckman et al. 1990, Barbieri et al. 1993, Lowerre-Barbieri et al. 1995). Sciaenid otoliths are comparatively massive and annuli are especially well defined. Conversely, red snapper otoliths are relatively thin and fragile and the annuli become increasingly less well defined with advanced age. But, even given the above, a first reading followed by a second reading produced consensus in age estimates for 99.29% of those red snapper considered herein. Patterson (1999) reported 93.8% between reader consensus of red snapper annulus counts after two readings.

The variable position and the diffuse appearance of the first annulus formed during the first winter following hatching are functions of both the protracted red snapper spawning season and the rapid growth rate of juvenile red snapper. Those individuals which are spawned early in the season will experience proportionally more growth (and more translucent zone accretion) than will a late spawned individual before opaque annulus accretion begins during the following winter; thus the first opaque annulus will be more distant from the otolith core in the former instance than under the later circumstances. Also with the first opaque annulus accreting at a rate theoretically corresponding to the rapid growth rate experienced during the juvenile stage, the resulting first annulus is broader and more diffuse in appearance than annuli produce during times of reduced growth rates in later life.

It is difficult to compare the maximum observed red snapper longevity reported here to those reported in earlier studies due to the assortment of ageing techniques (scales, otoliths, length frequencies) and the variety of sources (commercial, recreational, or both) utilized. All show a predominance of young individuals (<10 years). However, recent advances and refinements in otolith preparation technology have allowed red snapper to be reliably aged up to 42 years (Szedlmayer and Shipp 1995), 53 years (Render 1995), 31 years (Patterson 1999), and 52 years (this study). Furthermore, Baker's (1999) radiometric validation of red snapper longevity to at least 40 years provides additional substantiation to those ages derived from otolith annuli.

As is much the case in humans, red snapper size is little indication of red snapper age. For example, consider the International Game Fishing Association world rod and reel record red snapper whose otoliths were given to us for age analysis. This individual was caught off the coast of Louisiana by Doc Kennedy of Grand Isle, LA on 23 June 1996; it was 22.793 kg (50 lb, 4 oz) TW, 1039 mm (40.9 in) TL, and 965 mm (38 in) FL. Given the immense size of this red snapper, one would reasonably expect it to be ancient by red snapper standards. However, our analysis revealed it to be only 19.98 years old. Conversely, the two oldest red snapper we encountered, 52.63 and 51.73 years old, were a comparatively small 851 mm TL and 862 mm Tl, respectively, and 7.886 kg TW and 9.188 kg TW, respectively. A similar pattern was noted by Patterson (1999) among the red snapper which he sampled from the GOM off Alabama.

Personnel at the LSU Coastal Fisheries Institute continue to investigate the nuances of deriving red snapper ages from sagittal otoliths. We have expanded our sampling efforts to include age 0 and age 1 red snappers collected during the National Marine Fishery Service's Summer SEAMAP and Fall Groundfish cruises in the GOM. Core to first annulus measurements made on otolith sections from these young individuals will give us a better understanding of when and how the first annulus is accreted. We will also soon be analyzing the otoliths of the several oldest red snapper we have encountered for the presence and quantity of Carbon-14 which was released into the atmosphere during atomic testing during the 1940s, 1950s, and 1960s. Elevated levels of this isotope in the otoliths, when compared to contemporaneous levels of the isotope in the water of the GOM, would support the longevity we have observed and report herein.

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