Age and growth of red snapper, *Lutjanus campechanus,* from the northern Gulf of Mexico off Louisiana

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Abstract–The red snapper (*Lutjanus campechanus*) is currently under rigorous federal and state management in the Gulf of Mexico because of apparent overfishing. Management strategies implemented to promote recovery of the species are dependent upon knowledge of various demographic variables, including the ages of individuals, the distribution of these ages (cohort strength) within the population, and maximum longevity. Thus a dependable and precise aging method is of principal importance. Counts of annuli in otolith thin sections have been used to age many species of fish, including red snapper. However, the utility of this method for aging 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 red snapper otolith.

We counted annuli and assessed edge condition in sagittal otoliths of 3791 red snapper collected from the northern Gulf of Mexico off Louisiana during the periods from 1989 to 1992 and from 1995 to 1998. Opaque annuli were validated by marginal increment analysis to form once per year from December through June. Estimated ages ranged from 0.5 to 52.6 yr for individuals from 104 mm to 1039 mm total length and from 0.02 kg to 22.79 kg total weight. Among the 2546 specimens of known sex, both sexes evidenced rapid growth of individuals until about age 8–10 yr, after which growth slows considerably. Von Bertalanffy growth models for total length at age were significantly different for males and females, indicating differential growth between the sexes, with females typically obtaining larger sizes at older ages than do males.

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The red snapper, *Lutjanus campechanus* (Poey) (family: Lutjanidae), is resident on the continental shelves of the Gulf of Mexico (GOM) and northwest Atlantic Ocean from the Bay of Campeche, Mexico, to Massachusetts; however, it is found only occasionally north of Cape Hatteras, North Carolina (Rivas, 1966; Robins and Ray, 1986; Hoese and Moore, 1998). Although Rivas (1966) suggested that red snapper may also occur off Bermuda, the Bahamas, and northern Cuba, it has been reported neither from Bermuda by Smith-Vaniz et al. (1999) nor from the Bahamas by Böhlke and Chaplin (1993), nor from Cuba by Allen (1985). The species is replaced in the Caribbean Sea and southward by the Caribbean red snapper, *L. purpureus* (Rivas, 1966; Robins and Ray, 1986; Hoese and Moore, 1998). Although the appellation "red snapper" has been widely used to identify as many as 12 commercially marketed lutjanids (Camber, 1955; Carpenter, 1965), it is correctly applied only to *L. campechanus* (Robins et al., 1991). The binomina *L. aya, L. blackfordi,* and *Neomaenis aya,* all of which appear in the literature (e.g. Moseley, 1966) are synonyms of *L. campechanus* and refer to the red snapper *sensu* Robins et al. (1991).

The red snapper has been and remains a significant component of both the commercial and recreational fisheries in the GOM. However, documented commercial landings from United States territorial waters declined precipitously from historic highs of about 6389 metric tons (t) in 1965 to 1015 t in 1991; estimated recreational landings similarly waned from 4734 t in 1979 to 581 t in 1990 (Schirripa and Legault[1]). 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). The best efforts of the GMFMC and the commercial and recreational sectors notwithstanding, overfishing of red snapper in the GOM may persist (Schirripa and Legault[2]).

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[1] Schirripa, M. J., and C. M. Legault. 1997. Status of the red snapper in U. S. waters of the Gulf of Mexico: Updated through 1996. Contribution rep. MIA-97/98-05 from Sustainable Fisheries Division, Miami Laboratory, Southeast Fisheries Science Center, National Marine Fisheries Service, 75 Virginia Beach Drive, Miami, FL 33149-1099. [Not available from NTIS.]

[2] Schirripa, M. J., and C. M. Legault. 1999. Status of the red snapper in U. S. waters of the Gulf of Mexico: Updated through 1998. Contribution rep. SFD-99/00-75 from Sustainable Fisheries Division, Miami Lab-

continued

Accurate information on the age structure of the red snapper populations in the GOM is essential for monitoring year-class strength, for conducting stock assessments, and for documenting population recovery. Previous efforts at estimating red snapper age have employed a variety of aging methods. Bradley and Bryan (1975) cited the long spawning season and a 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 yr and advanced spawning as the causal factor in check formation. Among 240 red snapper taken off the west coast of Florida, Futch and Bruger (1976) estimated red snapper ages of 1 to 5 yr from 200 readable whole otoliths; however, they postulated ages up to 20 yr for larger individuals whose otoliths were unreadable. Comparisons of ages derived from whole otoliths, scales, and vertebrae by Bortone and Hollingsworth (1980) revealed all three hard parts to be of equal utility in aging red snapper at age 1 and 2 yr. Wade (1981) also used scales to age red snapper to 9 yr. Nelson and Manooch (1982) reported red snapper ages from 1 to 16 yr based on both scales and sectioned otoliths and demonstrated once yearly scale annulus formation in June and July from monthly mean marginal growth. A recent study of red snapper otoliths significantly extended the hypothesized longevity of red snapper in the GOM to 42 yr (Szedlmayer and Shipp, 1994). Render (1995) provided a preliminary validation of yearly opaque annulus formation in sagittal otoliths and reported ages from 0 to 53 yr for red snapper in Louisiana waters. Examinations of otolith sections 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 yr (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 yr for females and 31 yr 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.[3]) . 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; Crabtree et al., 1992; Murphy and Taylor, 1994; Franks et al., 1998; Thompson et al., 1998). Herein we present our interpretations of the use of sagittal otoliths to estimate ages of red snapper from the GOM off Louisiana. Specifically we address the timing of formation and position of the first annulus, validation of the once yearly accretion of opaque annuli, longevity, and reader reproducibility. We further describe the growth of red snapper with von Bertalanffy growth models for both males and females.

Methods and materials

Red snapper from recreational and commercial catches were sampled 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 (total length [TL] or fork length [FL] in mm, total weight [TW] or eviscerated body weight [BW], i.e. mass with liver, digestive tract, and reproductive organs removed, in g) were recorded, both sagittal otoliths were removed, and sex was determined, when possible, for each specimen. Eviscerated body weight was converted to TW, when necessary, with the equation $TW=1.101(BW) - 26.32$ (linear regression, df=418; $P<0.001$; $r^2=0.996$) and TL was estimated from FL with the equation $TL=1.073\ (FL) + 3.56$ (linear regression, df=1015; $P<0.001$; $r^2=0.999$) .

All undamaged, intact otoliths were weighed to the nearer 0.1 g. The left sagittal otolith from each individual was embedded in an epoxy resin and subsequently sectioned with a low-speed saw equipped with a wafering blade as described in Beckman et al. (1988). In those instances where the left sagitta was damaged or unavailable, the right sagitta was substituted. Examinations of otolith sections were made with a compound microscope and transmitted light at 40× to 100× magnification. Counts of annuli (opaque zones) were accomplished by reading along the medial surface of the transverse section dorsal or ventral to the sulcus; annuli were often inconsistent in other regions of the otolith section. Annuli were counted by two readers without knowledge of date of capture or morphometric data. The appearance of the otolith margin was also coded as either opaque or translucent (Beckman et al., 1988). 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 (n=27), the assigned annulus count for these was that of the more experienced reader (reader 1). Reader 2's annulus count and edge condition were used in those circumstances where reader 1's were missing (n=2). Annulus counting error between the two readers was evaluated after both the initial and second readings of the otolith sections. Reproducibility of the resultant age estimates was evaluated with the coefficient of variation, the index of precision (Chang, 1982), and average percent error (Beamish and Fournier, 1981).

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[2] (continued) oratory, Southeast Fisheries Science Center, National Marine Fisheries Service, 75 Virginia Beach Drive, Miami, FL 33149-1099. [Not available from NTIS.]

[3] Rothschild, B. J., A. F. Sharov, and A. Y. Bobyrev. 1997. Red snapper stock assessment and management for the Gulf of Mexico. Report submitted to the National Marine Fisheries Service, Office of Science and Technology, 1315 East-West Highway, Silver Spring, MD 20910 USA. [Not available from NTIS.]

The periodicity of opaque annulus formation was determined by marginal increment analysis and by plotting the proportion of otoliths with opaque margins by month of capture (Beckman et al., 1988). To assess the possibility of false annulus formation among either younger or older red snapper, those individuals of age ≤5 yr and those >5 yr were also analyzed as above. Fork lengths at 100% maturity, 420 mm for males and 440 mm for females (Render, 1995), are achieved at about age 5. If one opaque and one translucent zone are shown to be formed each year, validation of annuli as being accreted once yearly is accomplished.

Ages of red snapper were estimated from opaque annulus counts and date of capture with the equation

$$Age(\text{days}) = -182 + (annulus\ count \times 365) + \big((m-1)\times 30\big) + d,$$

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

The 182 days that were subtracted from each age estimate are an accommodation for the uniform 1 July hatching date which was assigned for all specimens (Render, 1995; Collins et al., 1996). Age in yr was derived by dividing the age in days by 365. Thus a red snapper captured on 1 January which exhibits five opaque annuli (including an opaque margin [see below]) in its otoliths would have an estimated age of 1644 days or 4.5 yr. Our age estimation method also assumed that opaque annulus formation at the otolith margin uniformly commenced in January. The small number of individuals captured in September, October, November, and December that evidenced early formation of opaque annuli had their ages adjusted by subtracting 365 days from their age estimates. Conversely, a larger number of individuals captured in January, February, and March had otoliths with translucent margins—evidence of an assumed delay in opaque annulus formation. The age estimates of these were augmented by the addition of 365 days.

Total length-TW regressions were fitted with linear regression to the model $TL = a\ TW^{b}$ from $\log^{10}$-transformed data. Male and female regressions were compared with analysis of covariance (SAS, 1985). Only those red snapper for which sex could be determined were used to fit growth models. Von Bertalanffy growth models of TL at age were fitted with nonlinear regression by least squares (SAS, 1985) in the form

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

where TL_t = TL at age t;
L_∞ = the TL asymptote;
k = a growth coefficient;
t = age in yr; and
t_0 = a hypothetical age when TL is zero.

Growth models were generated for three groups of red snapper within which the age and TL of all individuals were extant: 1) all specimens, 2) all specimens of known sex, and 3) specimens of known sex for which growth models were fitted independently for each sex. Likelihood ratio tests (Cerrato, 1990) were used to test for differences between males and females, both in growth models and in growth parameter estimates. Significance level for statistical analyses was 0.05 unless indicated otherwise.

Results

During eight years of variable collection effort, 3791 red snapper from recreational (n=274) and commercial (n=3517) catches were sampled for morphometric data and sagittal otoliths. Among the 1438 male and 1542 female specimens for which sex could be determined, females ranged from 242 to 1039 mm TL and from 0.16 to 22.79 kg TW; males were 245–946 mm TL and 0.19–13.70 kg TW. Composite ranges for all specimens of either known or unknown sex were 104–1039 mm TL and 0.02–22.79 kg TW; however, 67.6% of 3787 available TL were between 325 and 525 mm and 80.0% of 3718 available TW were less then 2.5 kg (Fig. 1). Neither the slopes (df=2,932; F=3.41; P<0.065) nor the intercepts (df=2,932; F=3.16; P<0.075) of the TL-TW regressions were found to differ significantly between males and females; thus data for the two sexes were combined and a single predictive equation was generated

$$TW = 1.17 \times 10^{-8}\,(TL)^{3.04}.$$

Sagittae of red snapper are ovate, laterally compressed, and have an indented sulcus acousticus on the proximal surface (Fig. 2A). Although one can count purported annuli in relatively small whole otoliths of red snapper less than age 5 (Futch and Bruger, 1976), it is difficult to discern annuli in the larger otoliths of older individuals. Thin transverse sections of these older otoliths showed semidistinct translucent and opaque annuli that alternated from the core to the growing edge (Fig. 2, B and C). The presumptive first annulus posed the most consistent problem for the readers. This annulus appeared as a diffuse "smudge" of opaque material variously located from totally isolated and somewhat distant from the core (Fig. 2B) to contiguous to and continuous with the otolith core (Fig. 2C).

Annulus counts ranging from 0 to 53 and edge conditions were determined by at least one reader for all 3791 individuals sampled. Reader 2 considered all the otolith sections to be of sufficient quality to produce annulus counts; reader 1 provided annulus counts from all but two sections. After the initial counts, consensus between readers was achieved for 2804 individuals A second reading of the 987 sections for which annulus counts differed produced consensus for 3762 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.

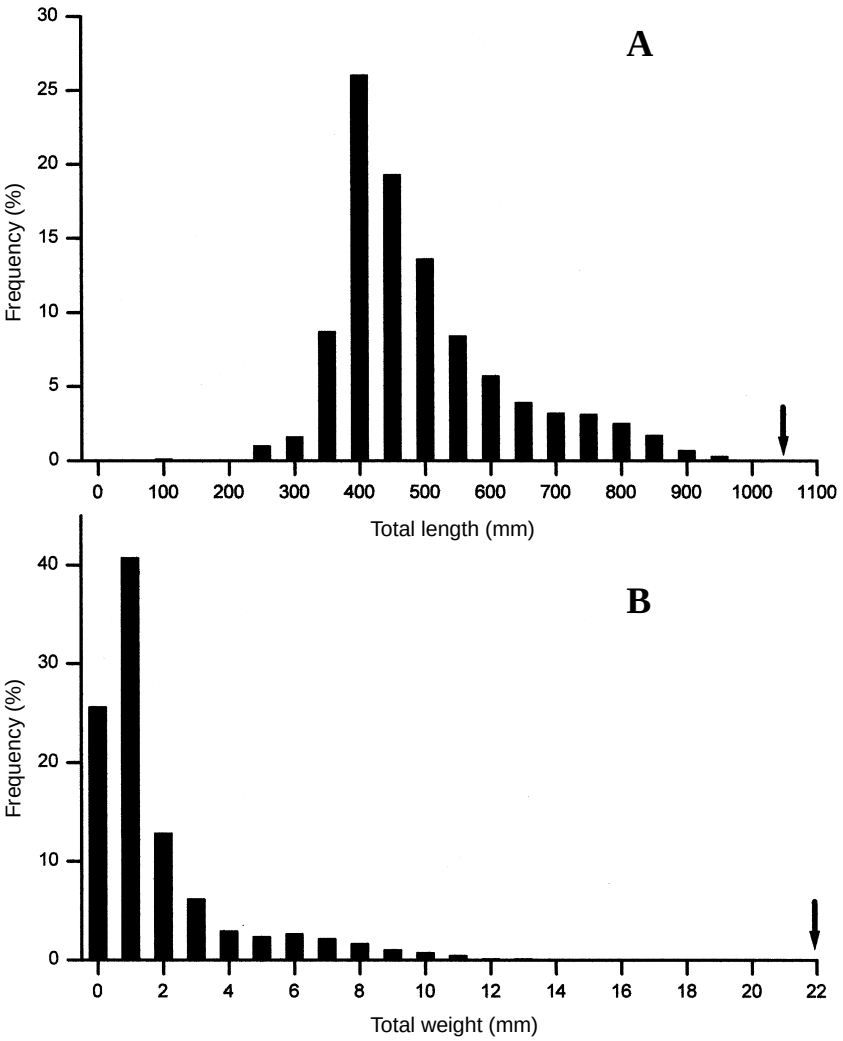

Figure 1

Frequency histograms for (**A**) total length in mm (n=3787) and (**B**) total weight in kg (n=3718) for red snapper, *Lutjanus campechanus*, from the northern Gulf of Mexico off Louisiana. Specimens collected from the recreational and commercial fisheries from 1989 to 1992 and from 1995 to 1998. The vertical arrow denotes the rod and reel world record red snapper caught on 23 June 1996.

Proportions of otoliths with opaque margins were plotted by month of capture for all individuals (n=3791), for those individuals presumed to be sexually immature (ages less than or equal to 5, n=2143), and for those from individuals of presumptive sexual maturity (ages greater than 5, n=948). Each of the three plots (Fig. 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.

Having demonstrated once yearly accretion of opaque annuli, we estimated ages from 0.5 to 52.6 yr from the annulus counts of the red snapper in our study. The vast majority of specimens examined were ages 2–5 and only 1.2% of the total number were greater than age 15 yr (Fig. 4). The few ages greater than 15 yr, which were not represented in our sample, were 24, 28, 31, 34, 39, 40, 42–46, and 49–50. The otolith section from the oldest specimen examined is shown in Figure 5.

Among 3787 individuals, the single von Bertalanffy growth model which best describes red snapper TL at age was

$$TL\ (\text{mm}) = 941\ [1 - e^{-0.18\ (t\ +\ 0.55)}], \qquad (r^2=0.72).$$

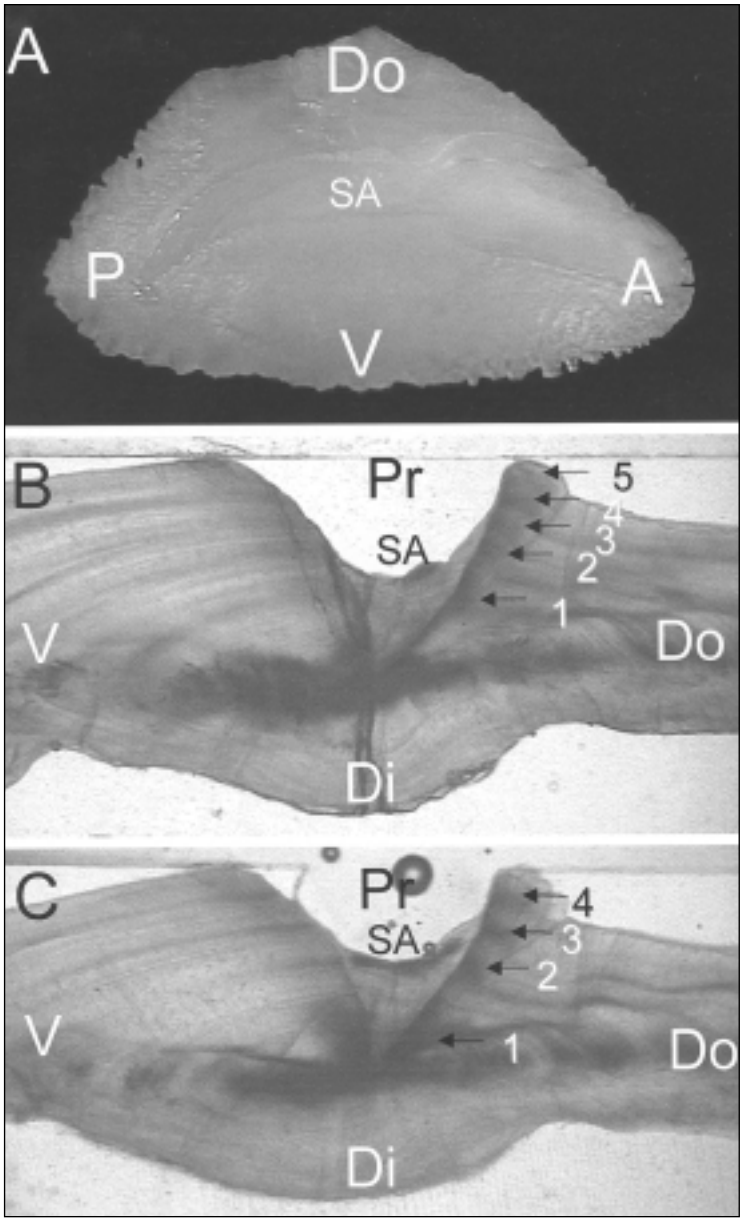

Figure 2

Medial view (**A**) and transverse sections (**B** and **C**) of red snapper (*Lutjanus campechanus*) left sagittal otoliths. Abbreviations for all are Do = dorsal, V = ventral, P = posterior, A = anterior, SA = sulcus acousticus, Di = distal, and Pr = proximal. Arrows with numbers indicate positions of opaque annuli and their enumeration.

Not surprisingly, the von Bertalanffy growth model generated for all individuals of known sex (n=2979) was quite similar to the above:

$$TL\ (\text{mm}) = 935\ [1 - e^{-0.18\ (t\ +\ 0.54)}], \qquad (r^2=0.72).$$

However, a likelihood ratio test revealed that von Bertalanffy growth models for males (n=1438) and females (n=1541) were significantly different from one another ($\chi^{2=}75.09$; df=1,2979; P<0.0001). The resultant models for TL at age were

$$Female\ TL\ (\text{mm}) = 977\ [1 - e^{-0.16\ (t\ +\ 0.63)}], \qquad (r^2=0.71)$$
$$Male\ TL\ (\text{mm}) = 904\ [1 - e^{-0.19\ (t\ +\ 0.48)}], \qquad (r^2=0.73)$$

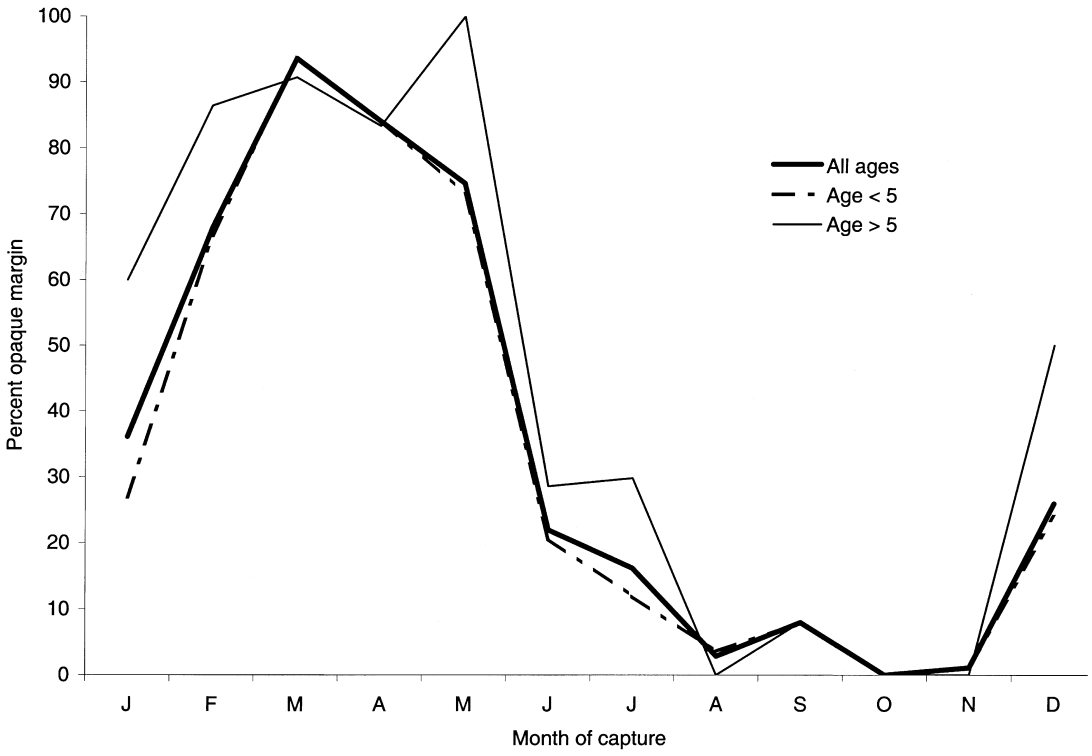

Figure 3

Marginal increment analysis of red snapper (*Lutjanus campechanus*) otoliths for specimens of all ages (n=3791), for ages >5 (n=2143), and for ages >5 (n=948).

Predicted TL at age for males and females (Figs. 6 and 7) generated with the above equations illustrated rapid and roughly equivalent growth to an age of approximately 8–10 yr after which the growth curves diverge. Differential growth between males and females was further demonstrated with likelihood ratio tests which indicated significant differences in L_∞ (χ^2=13.05; df=1,2979; P<0.0003) and k (χ^2=7.16; df=1,2979; P<0.0075). No significant difference was detected in t_0 (χ^2=1.34; df=1,2979; P<0.247). Owing to the large variability in observed TL at age (Fig. 6), TL was a poor estimator of red snapper age within the range of TL encountered in our sampling efforts.

Table 1

Average percent error (APE), coefficient of variation (CV), and index of precision (D) differences in red snapper (*Lutjanus campechanus*) otolith annulus counts for two readers on first and second readings. n = 3791.

	1st reading	2nd reading
APE	3.736	0.0934
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	0.53%	0.02%

Discussion

Otolith annuli as indicators of age in years have been validated for many freshwater and marine fish species, including the Australian lutjanids *L. adetii* and *L. quinquelineatus* (Newman et al., 1996) and *L. argentimaculatus, L. bohar, L.carponotatus, L. erythropterus, L. gibbus, L. johnii, L. malabaricus, L. monostigma, L. rivulatus, L. sebae,* and *L. vitta* (Cappo et al., 2000). Previous studies of red snapper have used scales (Moseley, 1966; Wade, 1981), otoliths (Futch and Bruger, 1976; Szedlmayer and Shipp, 1994; Render, 1995; Manooch and Potts, 1997; Patterson, 1999), scales and otoliths (Nelson and Manooch, 1982) and scales, otoliths, and vertebrae (Bortone and Hollingsworth, 1980) to estimate 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 yr. Nevertheless, they have produced a general consensus

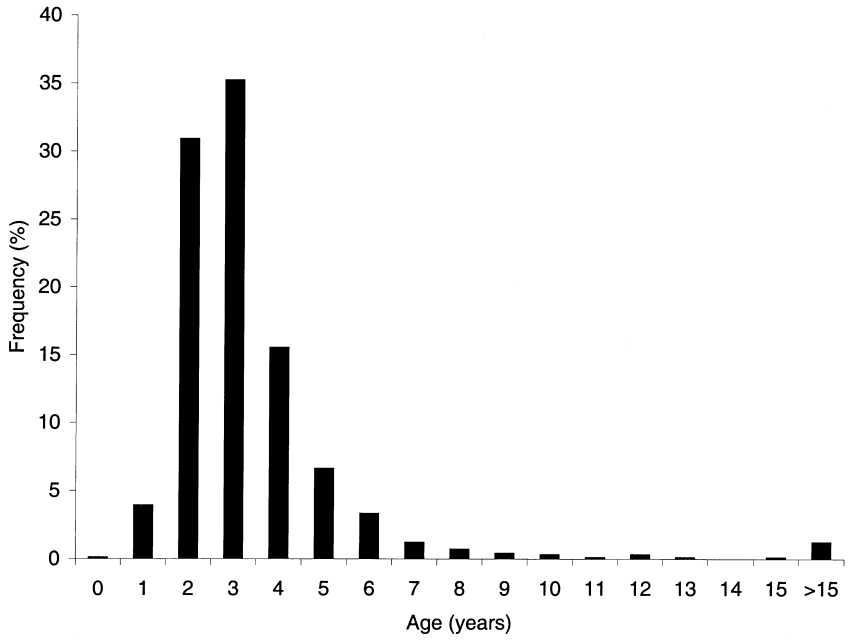

Figure 4

Age-frequency histogram (n=3791) for red snapper, *Lutjanus campechanus*, from the northern Gulf of Mexico. Specimens were collected from the recreational and commercial fisheries of the Gulf of Mexico off Louisiana from 1989 to 1992 and from 1995 to 1998.

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; our study), and the validation among Australian congeneric species cited above, 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 in otoliths of some other species. Comparisons of between-reader age estimates in several species of the family Sciaenidae have yielded almost 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 less well defined with increasing 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 in our study. Patterson (1999) reported 93.8% between-reader consensus of red snapper annulus counts after two readings. Quite unlike the situation in sciaenids, training and experience are critical to achieving high between-reader consensus on red snapper annulus counts.

The variable position and the diffuse appearance of the first annulus formed during the first winter following hatching (age approximately 6 months) are presumed to be functions of both the protracted red snapper spawning season and the rapid growth rate of juvenile red snapper. Those individuals that are spawned early in the season will experience proportionally more growth (and presumably more translucent zone accretion adjacent to the otolith core) 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 latter circumstance. 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 produced during times of reduced growth rates in later life. A more complete understanding of first annulus formation in red snapper could improve insights into both recruitment patterns and growth rates of individuals within a spawning season.

The distribution of ages among our sample population (Fig. 4) is certainly not reflective of the age distribution of red snapper in the GOM off Louisiana. Age-0 and age-1 specimens have been largely unavailable to our sampling efforts owing to minimum size limits applied to the recreational and commercial fisheries during the 1990s. Also

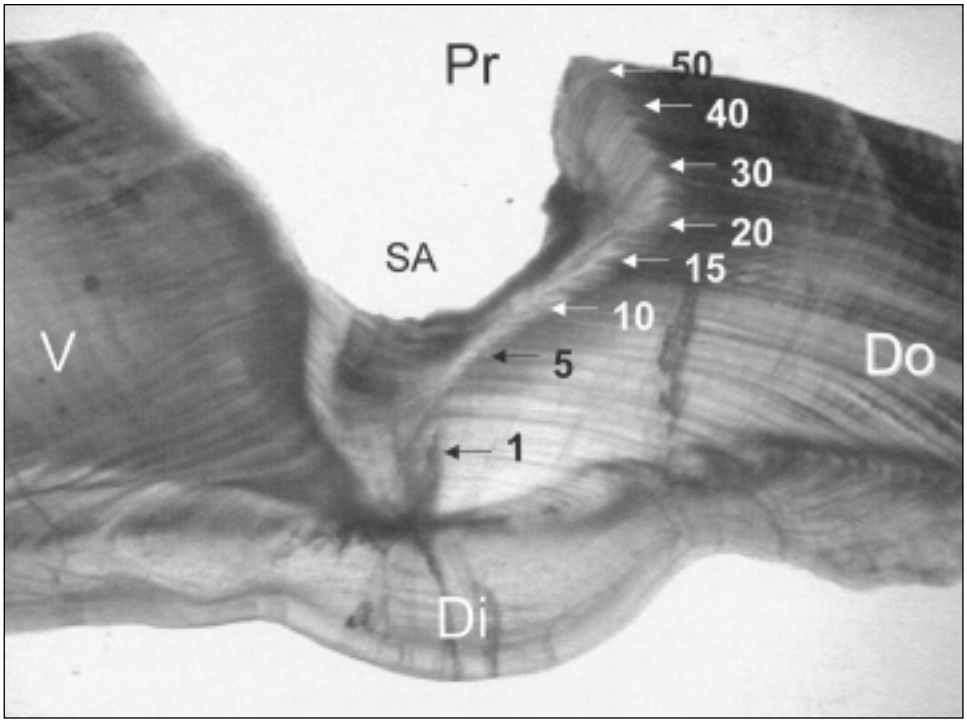

Figure 5

Cross section of sagittal otolith from the oldest red snapper, *Lutjanus campechanus,* from among 3791 specimens sampled from the recreational and commercial fisheries of the Gulf of Mexico off Louisiana from 1989 to 1992 and from 1995 to 1998. Abbreviations are Do = dorsal, V = ventral, SA = sulcus acousticus, Di = distal, and Pr = proximal. Arrows with numbers indicate positions of opaque annuli and their enumeration.

the dominance of ages 2–5 may reflect the practices of the fishermen who target red snapper and a migratory aspect of the species' life history. Age-0, and to a lesser extent age-1, red snapper are known to inhabit shallow water areas devoid of complex habitats or vertical relief where some are vulnerable to capture in trawls. This behavior is illustrated in fishery-independent trawl data from the GOM, specifically the Fall Groundfish Survey and the Summer SEAMAP Survey, in which the great majority of red snapper captured are age 0 and 1 (Schirripa and Legault[2]). It has been hypothesized that the disappearance of red snapper from the trawl data at age 1 represents their migration to structures such as oil and gas platforms that presumably provide refuge from large predators (Render, 1995). It is during this residence at the numerous oil and gas platforms off Louisiana that red snapper become vulnerable to fishing gear. Because the platforms are easily located and potentially harbor large populations of red snapper and other fish species (Stanley and Wilson, 1996, 1998), they are the preferred destinations for both commercial and recreational fishermen. The very low numbers of individuals of age >6 in our sample population likely result from both removal from the population through fishing and natural mortalities and emigration away from the oil and gas platforms to alternative habitats where they are less susceptible to capture.

It is difficult to compare the maximum observed red snapper longevity reported in our study with those reported in earlier studies (Moseley, 1966; Futch and Bruger, 1976; Wade, 1981; Nelson and Manooch, 1982; Render, 1995; Szedlmayer and Shipp, 1994; Patterson, 1999) because of the assortment of aging techniques (scales, whole or sectioned otoliths, length frequencies) and the variety of sources (commercial, recreational, or both) used. All show a predominance of relatively young individuals (<10 yr). However, recent advances and refinements in otolith preparation technology have allowed red snapper to be aged reliably up to the following ages: 42 yr (Szedlmayer and Shipp, 1994), 53 yr (Render, 1995), 31 yr (Patterson, 1999), and 52 yr (our study). Despite the sparsity of old red snapper among these research efforts, there can be little doubt that red snapper at least have the potential to achieve ages of 40–50 yr and more.

The red snapper growth models that we present are similar to those of earlier studies (Nelson and Manooch, 1982; Szedlmayer and Shipp, 1994; Manooch and Potts, 1997; Patterson, 1999) which did not produce separate models for the two sexes and variously applied weighted

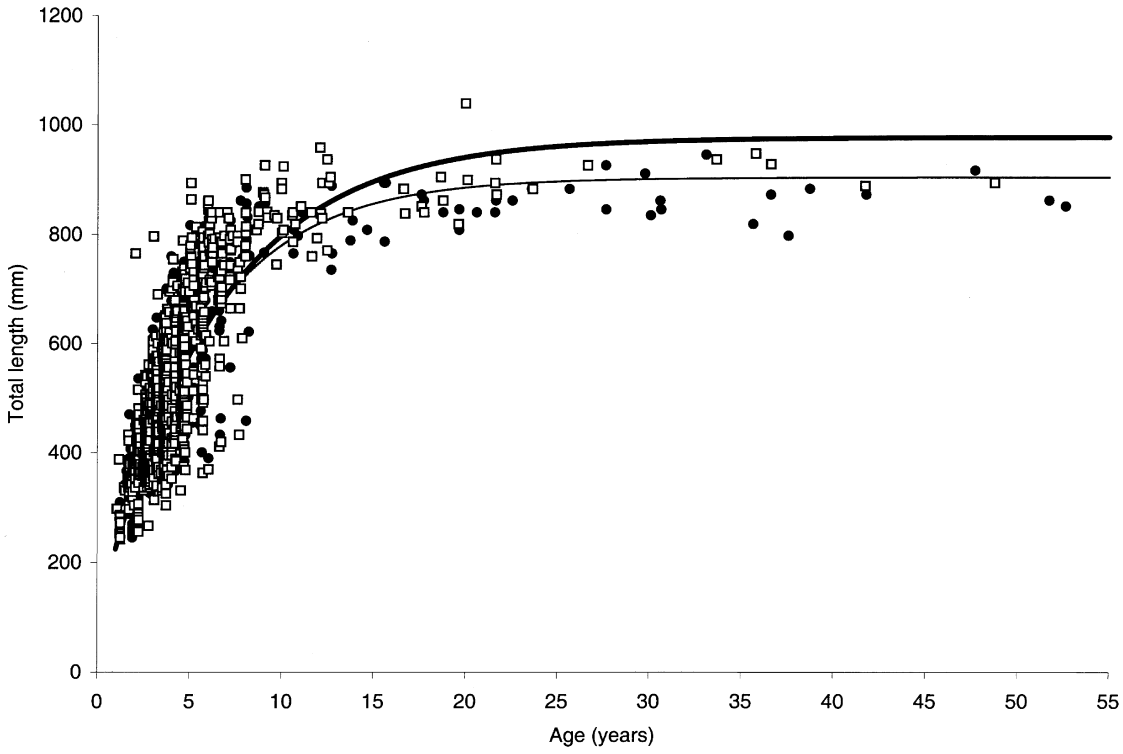

Figure 6

Observed total length (mm) at age and relationship of age to total length predicted from von Bertalanffy growth models for male (n=1438) and female (n=1542) red snapper, *Lutjanus campechanus*, from the northern Gulf of Mexico. Closed circles and narrow line represent males; open squares and thick line represent females.

or unweighted analyses (Fig. 7). All models predict rapid, and very much similar, growth during the first 8–10 years of life and slower growth thereafter. Asymptotic lengths among the above varied from 936 to 1025 mm. Our von Bertalanffy growth models also predicted a greater asymptotic TL and slightly faster growth for female red snapper. Among marine teleosts from the GOM, a similar pattern of growth has been shown for red drum, *Sciaenops ocellatus* (Beckman et al., 1988), sheepshead, *Archosargus probatocephalus* (Beckman et al., 1991), and cobia, *Rachycentron canadum* (Franks et al., 1998). However, this phenomenon in red snapper may be the result of a preponderance of data from the commercial fishery included in our analyses. Owing to minimum size limits enforced in both the commercial and recreational fisheries, we had access to few red snapper less than age 2 and few less than 250 mm TL. Conversely, the preference of commercial red snapper fishermen and wholesalers for smaller, plate-size individuals afforded us little opportunity to sample larger, and presumably older, red snapper; these are the individuals that can influence estimation of k and which ultimately drive estimation of L_∞. The addition of another 20–30 old specimens of both genders could have profound effects on the estimations of L_∞ for both sexes. Furthermore, growth studies of lutjanids in Australian waters (Davis and West, 1992; McPherson and Squire, 1992; Newman et al., 1996) report faster growth and larger size at age among males. Proportionally greater expenditures of energy in the production of gametes by females is advanced to explain this observation (Newman et al., 1996). Thus, although the growth rates and asymptotic lengths for male and female red snapper are shown to differ statistically in our study, questions of the biological veracity and the biological significance of these differences remain unresolved.

In addition to the differences in red snapper estimated growth rates between the sexes, there is an obvious high degree of diversity in individual growth rates. Owing to the large variability in age at a given TL (Fig. 6), this variable is a poor estimator of red snapper age. Our data indicate that red snappers of 400 mm, 600 mm, and 800 mm TL could be ages 2–7 yr, 3–9 yr, and 5–35+ yr, respectively. As a more concrete example, consider the International Game Fishing Association world-record red snapper caught by rod and reel, the otoliths of which 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 22.79 kg (50 lb, 4 oz) TW, 1039 mm (40.9 in) TL, and 965 mm (38 in) FL. Given the immense size of this specimen, one would reasonably expect it to be ancient by red snapper standards. However, our analysis

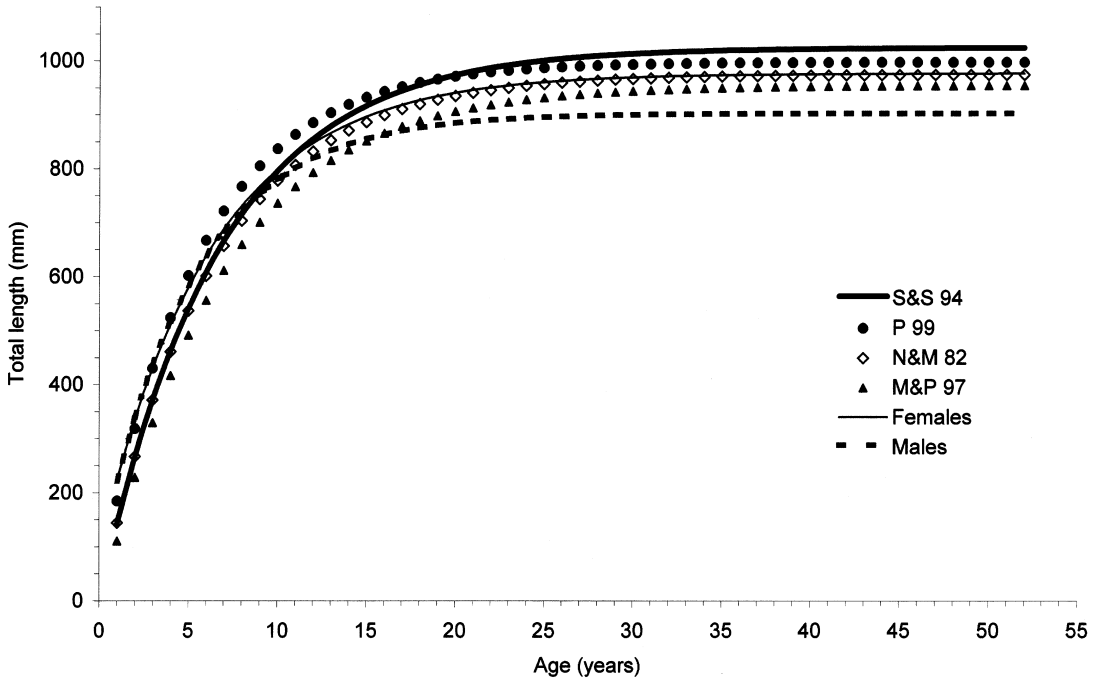

Figure 7

Comparative von Bertalanffy growth models for red snapper, *Lutjanus campechanus*, from the western north Atlantic Ocean. S&S 94 = Szedlmayer and Shipp (1994), P 99 = Patterson (1999), N&M 82 = Nelson and Manooch (1982), and M&P 97 = Manooch and Potts (1997). Males and Females are from our study.

revealed it to be only 19.98 yr. Conversely, the two oldest red snapper we encountered, age 52.63 and 51.73 yr, 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 that 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. Although our marginal increment analysis demonstrates that a single opaque increment is formed each year, our sample size among older individuals, albeit larger than any previous investigation, is probably inadequate for absolute validation of this phenomenon. Thus, some have and will continue to question once yearly annulus accretion among red snapper older than 20 yr. A solution for this problem may lie in radiometric aging techniques with protocols that analyze various radionuclides in the otoliths. Also, core-to-first-annulus measurements made on otolith sections from age-0 and age-1 individuals would contribute to a better understanding of when and how the first annulus is accreted.

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