

Abstract—Age and growth were examined of red snapper, *Lutjanus campechanus*, captured in an extensive (3100 km²) artificial reef area off Alabama in the northern Gulf of Mexico. Sagittal otoliths were removed from individuals ($n=1755$) sampled from recreational catches and tournament landings. Marginal increment analysis of sectioned otoliths revealed that a single opaque zone formed annually in sagittae from January through May. Fish ages were estimated from the number of opaque zones in otoliths, timing of opaque zone formation, sampling date, and a presumed birthdate of 1 July. Estimated growth of recaptured red snapper ($n=288$) from a tagging experiment was similar to growth estimated from otolith-aged fish and corroborated otolith aging methods. The von Bertalanffy growth function fitted to length-at-age data was $TL = 969 \text{ mm} (1 - e^{-0.192(t-0.020)})$ ($P < 0.001$; $r^2 = 0.99$), which was similar to reported growth functions for western Gulf of Mexico and Atlantic red snapper. Results of our study are consistent with the single stock hypothesis for Gulf of Mexico red snapper.

Age and growth of red snapper, *Lutjanus campechanus*, from an artificial reef area off Alabama in the northern Gulf of Mexico

William F. Patterson III

Coastal Fisheries Institute
204 Wetlands Resources Building
Louisiana State University
Baton Rouge, Louisiana 70803
E-mail address: wpatte2@LSU.edu

James H. Cowan Jr

Department of Marine Sciences
University of South Alabama
Mobile, Alabama 36688

Charles A. Wilson

Department of Oceanography and Coastal Studies
Louisiana State University
Baton Rouge, Louisiana 70803-7503

Robert L. Shipp

Department of Marine Sciences
University of South Alabama
Mobile, Alabama 36688;

Red snapper, *Lutjanus campechanus*, are large, predatory reef fish belonging to the family Lutjanidae. They generally are found from Cape Hatteras, North Carolina, to the Yucatan Peninsula, including the waters of the Gulf of Mexico (GOM) but not the Caribbean Sea (Hoese and Moore, 1998). Throughout their range red snapper are distributed along the continental shelf out to the shelf's edge and demonstrate affinity for vertical structure. Adults aggregate on or near coral reefs, gravel bottoms, or rock outcrops, as well as on artificial reefs, oil rigs, and wrecks (Moseley, 1966; Szedlmayer and Shipp, 1994; Stanley and Wilson, 1997).

Red snapper support economically valuable recreational and commercial fisheries in U.S. waters of the GOM (GMFMC, 1989). Federal management of GOM red snapper is based on the assumption that fish from Florida to Texas constitute a single stock. Although genetic evidence supports this assumption (Camper et al., 1993; Gold et al.,

1997; Heist and Gold, 2000), fish are not distributed uniformly across the northern GOM. Fisheries-dependent data suggest there is a center of red snapper abundance off southwest Louisiana and a second, smaller center of abundance off Alabama (Goodyear, 1995a; Schirripa and Legault, 1999). For example, from 1981 to 1998 estimated Louisiana landings of red snapper (commercial and recreational catch from state and federal waters) accounted for 32.6% (mean) $\pm 1.5\%$ (SE) of the total GOM harvest, whereas Alabama landings accounted for 11.4% $\pm 0.9\%$ of the total catch (Schirripa and Legault, 1999).

Although fewer red snapper are harvested from waters off Alabama than from the northwestern GOM, the red snapper fishery off Alabama is unique in several ways. Given that Alabama's GOM coastline represents only about 3.0% of the coastline from Tampa, Florida, to Brownsville, Texas, a disproportionately high percentage of the GOM red snapper harvest is caught and land-

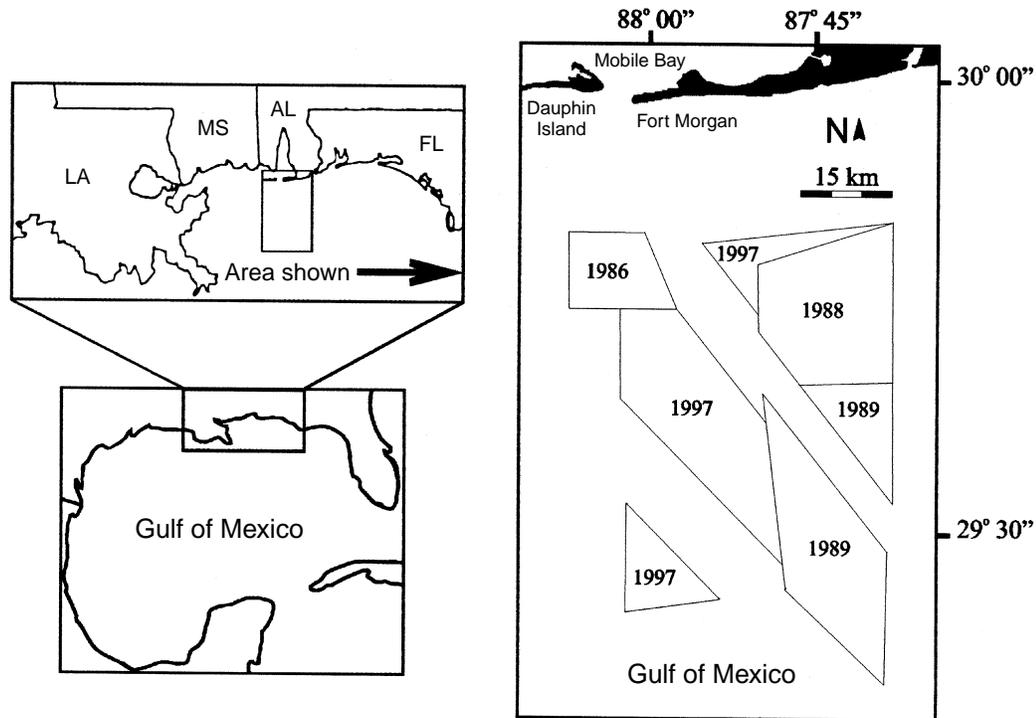


Figure 1

Map of artificial reef permit areas off Alabama. Date of creation is given for each area.

ed there. The productivity of the red snapper fishery off Alabama occurs despite the fact that few high-relief (>1 m) natural reefs exist on the continental shelf in the north central GOM (Parker et al., 1983; Shultz et al., 1987; Schroeder et al., 1989); however, off the coast of Alabama exists a 3100-km² area designated for artificial reef deployment (Fig. 1). The correlation between high catch rates and the creation of artificial reefs off Alabama has caused some to speculate that artificial reefs have increased the productivity of the GOM red snapper stock in this area (Szedlmayer and Shipp, 1994; Minton and Heath, 1998).

Despite the implied effect of artificial reefs on the red snapper fishery off Alabama, few studies have focused on red snapper in this area. The objective of our study was to estimate growth rates of adult red snapper captured off Alabama with otolith-aging and mark-recapture methods and to compare growth estimates with growth of adult red snapper from the western GOM and the southeastern United States. As a corollary to our primary objective, we also attempted to validate presumed annual growth rings in otoliths with marginal increment analysis and present a comparison of estimated growth of otolith-aged red snapper with estimated growth of tagged individuals.

Methods

Otolith aging

Red snapper were sampled from July 1995 to September 1999. All fish were caught over artificial reef sites off Ala-

bama. Red snapper shorter than the legal size limit (380 mm total length [TL] for most of the study) were randomly sampled from undersize fish caught during research cruises to tag red snapper. Fish longer than the legal size limit were either randomly sampled from recreational catches or sampled opportunistically at spearfishing or hook-and-line fishing tournaments. Total length and fork length (FL) were measured to the nearest mm for all fish, and whole weight was measured to the nearest 0.1 g. Sex was determined for most fish by macroscopic examination of the gonads. Both sagittae were removed from each sampled individual, rinsed of any adhering tissue, and stored in paper coin envelopes until processing.

Otoliths were sectioned in a transverse plane following the methods of Cowan et al. (1995) and were read under transmitted light with either a Micro Design® model 925 microfiche projector or an Optimas® image analysis system (Media Cybernetics, 1999). Otoliths were read independently by two readers. Blind counts of opaque zones of each sectioned otolith were made along the ventral margin of the sulcus acousticus from the core to the proximal surface; marginal increments were scored following Beckman et al. (1991) (Table 1, Fig. 2). Otoliths for which counts of opaque zones differed between readers were read a second time. Precision among readers was evaluated with the coefficient of variation (CV) (Chang, 1982), index of precision (D) (Chang, 1982), and average percent error (APE) (Beamish and Fournier, 1981).

Age was estimated from the number of opaque zones in otolith sections, timing of opaque zone formation, assumed birthdate, and sampling date. It was assumed that opaque

Table 1

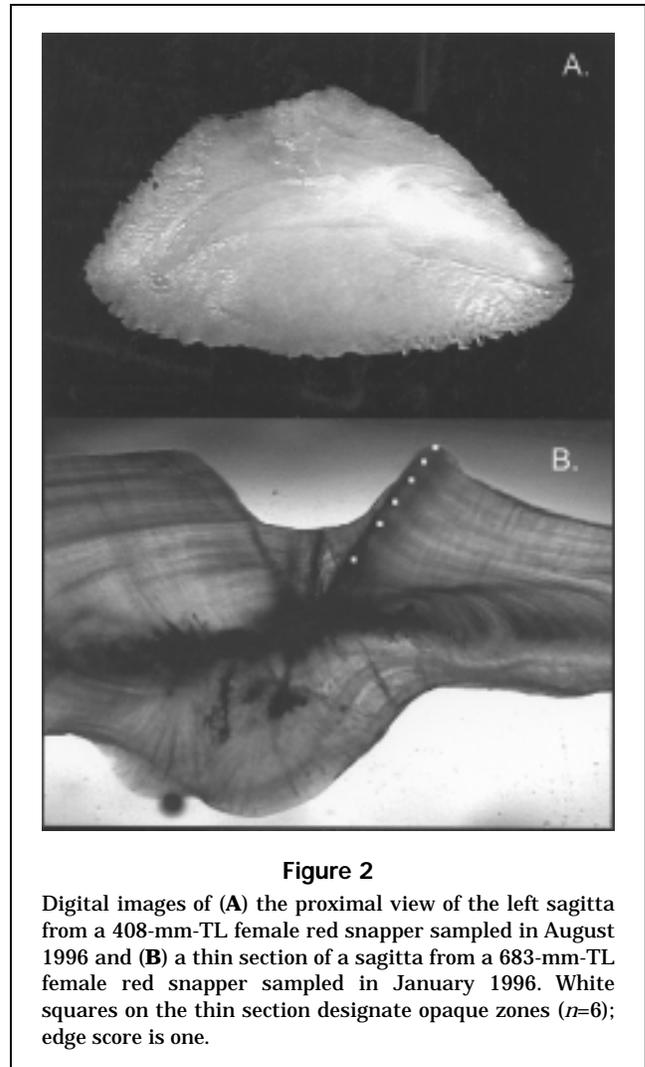
Scale used in determining condition of red snapper otolith marginal increments.

Margin score	Margin description
1	Opaque zone begins to form at edge; zone is $<1/3$ the thickness of the previous opaque zone.
2	Opaque zone at edge is between $1/3$ and $2/3$ the thickness of the previous opaque zone.
3	Opaque zone at edge is $>2/3$ the thickness of the previous opaque zone.
4	Translucent zone begins to form at edge; zone is $<1/3$ the thickness of the previous translucent zone.
5	Translucent zone at edge is between $1/3$ and $2/3$ the thickness of the previous translucent zone.
6	Translucent zone at edge is $>2/3$ the thickness of the previous translucent zone.

zones constitute annuli and that annulus formation begins 1 January (see "Results" section). The birthdate for red snapper in the north central GOM was assumed to be 1 July, which follows the convention of Goodyear (1995a) and is based on the peak in red snapper spawning in the north central and northeastern GOM (Collins et al., 1996; Szedlmayer and Conti, 1999). According to these assumptions, young-of-the-year northern GOM red snapper form their first annulus in sagittae beginning in January when fish are approximately 0.5 yr old. Therefore, the opaque zone closest to the otolith core represents only 0.5 yr of life, which was accounted for in the aging algorithm.

Age (in d) was estimated (for most fish) by first subtracting one opaque zone from the total number of opaque zones in a given otolith and multiplying the difference by 365 d. Next, 182 d was added to the product to account for the first 0.5 yr of life. Finally, the day of year (number of days since 1 January) the fish was sampled was added to account for the number of days in the sampling year that the fish was alive. The result was divided by 365 d to estimate age in years. Age was estimated similarly for fish that were sampled in November and December and had already begun forming opaque margins, except two was subtracted from the total number of opaque zones before multiplying by 365 d in order to assign fish to the correct year class. For fish that were sampled in January that did not have an opaque margin, zero was subtracted from the total number of opaque zones.

Von Bertalanffy (1938, 1957) growth functions (VBGFs) were fitted to TL-at-age data with Proc NLIN in SAS (SAS Institute, Inc., 1996). Von Bertalanffy growth functions were fitted separately for males and females and a likelihood ratio test was used to test for difference in growth

**Figure 2**

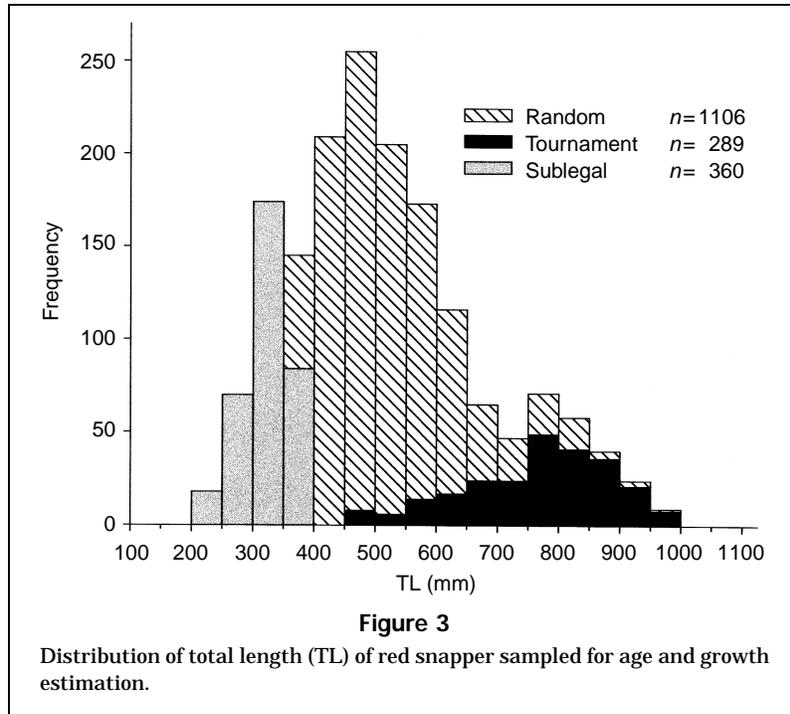
Digital images of (A) the proximal view of the left sagitta from a 408-mm-TL female red snapper sampled in August 1996 and (B) a thin section of a sagitta from a 683-mm-TL female red snapper sampled in January 1996. White squares on the thin section designate opaque zones ($n=6$); edge score is one.

between sexes (Kimura, 1980; Cerrato, 1990). Von Bertalanffy growth functions also were fitted for the complete data set and for the complete set excluding tournament sampled fish.

Weight-TL relationships were modeled with non-linear regression for females and males following Ricker (1975). The functions were computed with Proc NLIN in SAS (SAS Institute, Inc., 1996). Sex-specific weight-TL relationships were made linear by taking the log of weight and TL, and difference between sexes was tested with an analysis of covariance (ANCOVA) on the log-transformed data (SAS Institute, Inc., 1996). Lastly, a weight-TL nonlinear regression was computed for females and males combined with Proc NLIN in SAS (SAS Institute, Inc., 1996).

Mark-Recapture

A tagging study of adult red snapper was conducted off Alabama from March 1995 to August 1999. Fish were caught with hook and line over nine artificial reef tagging sites in the Hugh Swingle general permit area for arti-



ficial reef deployment (labeled 1986 in Fig. 1). Each fish was measured to TL and FL, tagged with a yellow Floy® (Seattle, WA) internal anchor tag, and released. Individuals were recaptured on subsequent tagging trips or were recovered by recreational and commercial fishermen. Red snapper recaptured on tagging trips were measured to TL and FL and recovered fish were measured when fishermen retained carcasses of tagged fish.

To corroborate red snapper age estimates, VBGF parameters estimated from otolith-aged fish were incorporated into Fabens' (1965) length increment model to predict TL at recapture of tagged fish (Labelle et al., 1993; Thompson et al., 1999). Solving for TL at recapture, Fabens' model is computed as

$$TLR_i = TL_i + (L_\infty - t_i) (1 - e^{-k\Delta t_i}), \quad (1)$$

where TLR_i = predicted TL at recapture of individual i ;

TL_i = TL at release of individual i ;

L_∞ = TL asymptote from VBGF estimated from otolith-aged fish;

K = growth coefficient from VBGF estimated from otolith-aged fish; and

t_i = time at liberty of individual i .

Predicted TL at recapture from Fabens' method was plotted against observed TL at recapture to compare growth model predictions to observed values.

Growth of tagged red snapper was estimated by regressing their change in TL on days at liberty (SAS Institute, Inc., 1996). A linear regression also was computed on TL-at-age data over the size range of recaptured individuals from the tagging study (SAS Institute, Inc., 1996). Slopes

of resultant regressions were compared to assess if estimated growth rates were different between tagged and otolith aged fish.

Results

Age and growth

Sagittae were collected from 1755 red snapper, including 360 fish shorter than the minimum size limit (380 mm TL) caught on tagging cruises, 289 fish from tournaments, and 1106 fish randomly sampled from recreational catches (Fig. 3). Sex was not determined for 279 fish, of which 61 individuals were immature. Mean TL (\pm SE) was 518.3 (\pm 5.04) mm for males and 529.5 (\pm 5.96) mm for females. Total length of immature individuals ranged from 208 to 309 mm.

Of the 1755 otoliths sectioned for age determination, reader 1 and reader 2 agreed on the number of opaque zones for 1610 (91.7%) fish after the first reading; opaque zones in 23 otoliths were deemed not interpretable owing to sample preparation. Count disagreement between readers was the following: one opaque zone for 123 fish, two zones for 18 fish, and three zones for four fish. Otoliths were read a second time if reader counts were not in agreement and second otoliths were sectioned and read of the 23 fish for which otoliths were rejected after the first reading. After the second reading, agreement was reached for 1676 (95.6%) otoliths, including all 23 otoliths that were second sections. Disagreement between readers after the second reading was as follows: one opaque zone for 71 fish, two zones for 7 fish, and three zones for one fish; fish for

which agreement was not reached after the second reading were not assigned ages or included in the growth estimation. Precision estimates were 1.25% for APE, 0.90% for CV, and 0.64% for D after the second reading.

A clear pattern exists in the marginal increment scores, demonstrating that one opaque zone is formed annually in winter (Fig. 4). Most otoliths had opaque margins by January and had translucent margins by June, thus, timing of opaque zone formation appears to be from January through May for most fish. Eight fish (of 118) sampled in November (1997) and six fish (of 66) sampled in December (1996) had opaque margins. Four fish (of 47) sampled in January (1997) had translucent margins.

The oldest female sampled was 34.1 yr old and the oldest male sampled was 33.2 yr old. The female to male ratio was 1.1:1 overall but was 1.5:1 for fish between 10 and 20 yr old and 3.4:1 for fish greater than 20 yr old (Fig 5, A and B). Von Bertalanffy growth functions for females and males modeled separately were

Females: $TL = 976(1 - e^{-0.191(t-0.051)})$
 $(F_{3;735} = 21,952; P < 0.001; r^2 = 0.99)$

Males: $TL = 956(1 - e^{-0.194(t+0.054)})$
 $(F_{3;726} = 19,058; P < 0.001; r^2 = 0.99).$

Computed VBGFs were not significantly different between males and females (likelihood ratio test; $P > 0^2_{df=1} = 0.2879$), therefore, sexes were modeled together. Von Bertalanffy growth functions computed for all fish and excluding tournament sampled fish were

All fish: $TL = 969(1 - e^{-0.192(t-0.020)})$
 $(F_{3;1,672} = 47,690; P < 0.001; r^2 = 0.99)$ (Fig. 6)

Excluding tournament fish: $TL = 1181(1 - e^{-0.120(t+0.652)})$
 $(F_{3;1,461} = 43,550; P < 0.001; r^2 = 0.99).$

The growth model including all fish was similar to other VBGFs estimated for GOM and southeast U.S. Atlantic red snapper (Fig. 7, Table 2).

Weight-TL nonlinear regression models for females and males modeled separately were

Females: $Weight = (4.46 \times 10^{-9})TL^{3.18}$
 $(F_{1;73} = 42,577; P < 0.001; r^2 = 0.98)$

Males: $Weight = (5.18 \times 10^{-9})TL^{3.16}$
 $(F_{1;728} = 43,956; P < 0.001; r^2 = 0.99).$

Log-transformed weight-TL relationships were not significantly different between males and females (ANCOVA test for equal slopes; $F_{1;1,465} = 1.54, P = 0.2145$; ANCOVA test for equal intercepts; $F_{1;1,465} = 1.49, P = 0.2226$), therefore, sexes were modeled together. The resultant nonlinear regression model was

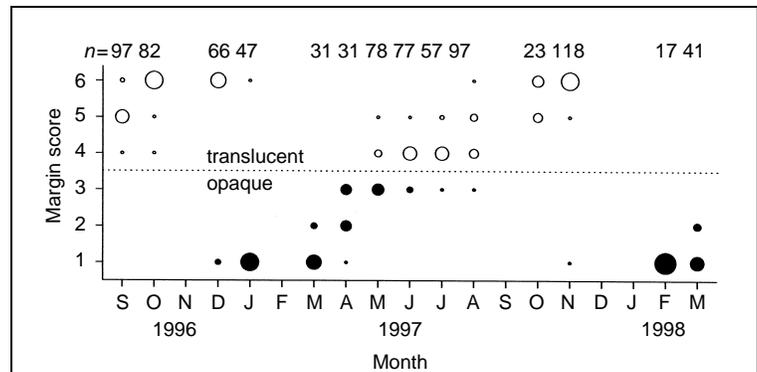


Figure 4

Plot of monthly margin edge scores of red snapper sagittae. Symbol size is relative to the percentage of fish with the corresponding margin edge score. Monthly sample size is given.

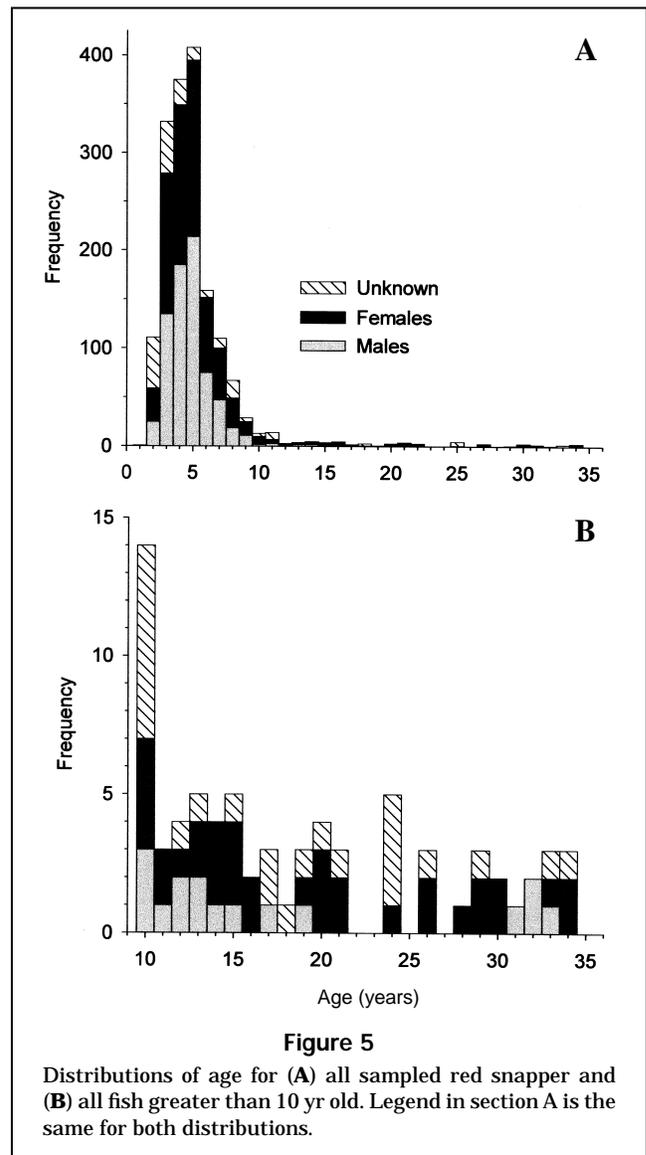
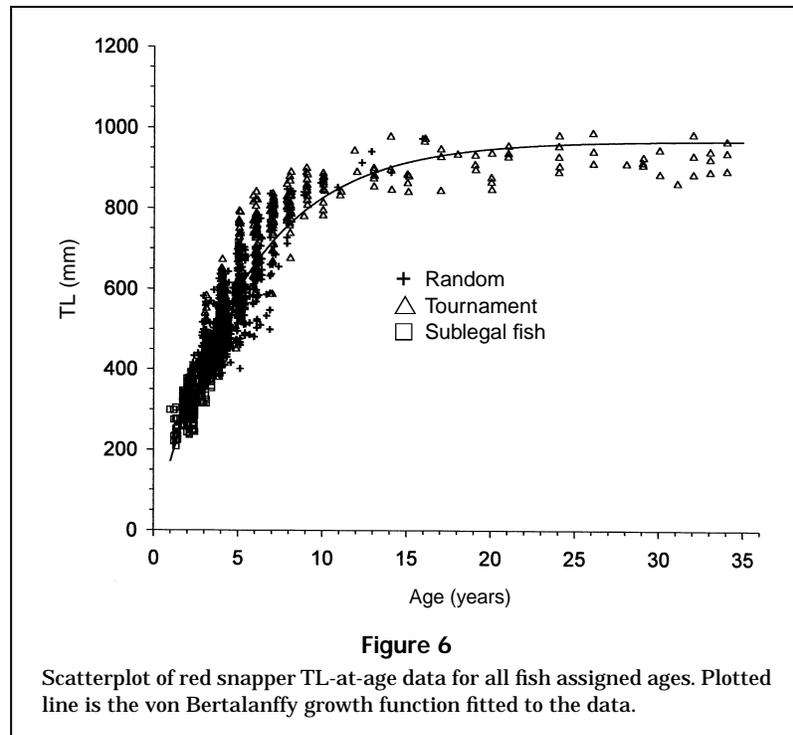


Figure 5

Distributions of age for (A) all sampled red snapper and (B) all fish greater than 10 yr old. Legend in section A is the same for both distributions.



$$\text{Weight} = (4.68 \times 10^{-9}) TL^{3.17}$$

$$(F_{1;1,467} = 85,961; P < 0.001; r^2 = 0.98).$$

Mark-Recapture

A total of 2932 adult red snapper were tagged. Total length at recapture was measured for 288 of 519 recaptured individuals. Mean TL (\pm SE) of recaptures was 344 (\pm 4.1) mm (range: 183–660 mm) at release and 423 (\pm 5.6) mm (range: 253–726 mm) at recapture, and mean time at liberty (\pm SE) was 334 (\pm 16.3) d (range: 12–1501 d). Predicted TL from Faben's method corresponded well to observed TL at recapture for tagged fish (Fig. 8). The linear regression of change in TL on days at liberty was statistically significant ($F_{1;286} = 631.0$, $P < 0.001$, $r^2 = 0.76$) and had a slope of 0.238 mm/d (Fig. 9A). The range in estimated ages of otolith-aged fish for the linear regression of TL on age was 356–2599 d (approximately one to seven years). The model was statistically significant ($F_{1;1,541} = 6309$, $P < 0.001$, $r^2 = 0.80$) and had a slope of 0.240 mm/d (Fig. 9B).

Discussion

Validating the periodicity of opaque zone formation in otoliths as annual is imperative for age and growth studies where otoliths are used as aging structures (Beamish and McFarlane, 1983, 1987). Annual formation of opaque zones in otoliths has been validated for several tropical and subtropical lutjanids (Manooch, 1987; Fowler, 1995; Cappo et al., 2000), and annual formation of opaque zones in red snapper sagittae has been reported from the northwestern GOM

and the southeastern U.S. Atlantic (Render, 1995; Manooch and Potts, 1997; Wilson and Nieland, 2001). Our marginal increment analysis of red snapper otoliths demonstrates that opaque zones in adult red snapper sagittae also are formed annually in the north central GOM. The pattern of monthly marginal increment scores reveals that some fish begin opaque zone formation as early as November and some do not have translucent margins until midsummer; however, the general pattern of opaque zone formation is from January through May. Render (1995) and Wilson and Nieland (2001) have reported a similar pattern for adult red snapper in the northwestern GOM, and opaque zone formation in winter–spring has been shown for sagittae of several other teleosts in the northern GOM (Maceina et al., 1987; Beckman et al., 1989, 1990, 1991; Thompson et al., 1999).

Because relatively few old red snapper were sampled in our study, and samples of old fish came mostly from tournaments in summer months, we were unable to validate ages beyond 8 years. Baker (1999) compared age estimates of otolith-aged GOM red snapper with age estimates from radiometric dating of their otolith cores and reported that age estimates from the two methods were highly correlated for fish up to 37 yr old, thus corroborating otolith-based estimates of age for older fish. Therefore, despite lack of annulus validation for older red snapper ages in our study, we are confident that otolith-based age estimates of older individuals are accurate.

Age and growth

Red snapper are long-lived reef fish; we observed a maximum age of 34 yr for females and 33 yr for males. Other

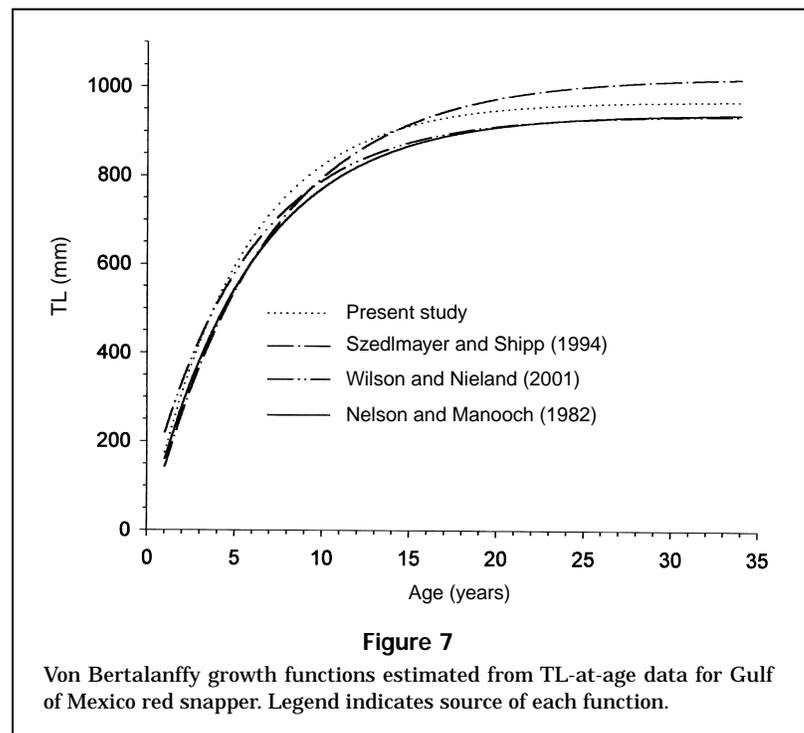
Table 2
Results from previous studies of the age and growth of Gulf of Mexico and southeastern U.S. Atlantic red snapper.

Study and location	Aging structure	Maximum age (yr)	L_{∞} mm (TL)	K	t_0
Szedlmayer and Shipp (1994); north central GOM	sectioned otoliths	42	1025	0.150	not reported
Wilson and Nieland, 2001; northwest GOM	sectioned otoliths	53	938	0.175	-0.530
Nelson and Manooch (1982); GOM	scales and sectioned otoliths	15	941	0.170	-0.10
Nelson and Manooch (1982); southeast U.S. Atlantic	scales and sectioned otoliths	15	975	0.160	0.00
Manooch and Potts (1997); southeast U.S. Atlantic	sectioned otoliths	25	955	0.146	0.182

authors have reported fish over 40 yr old (Szedlmayer and Shipp, 1994; Render, 1995; Wilson and Nieland, 2001) and the oldest fish aged to date is 53 yr old (Render, 1995; Wilson and Nieland, 2001). Among western Atlantic lutjanids for which maximum age has been reported, GOM red snapper has the greatest longevity (Acosta and Appeldoorn, 1992; Manickchand-Heileman and Phillip, 1996; Potts et al., 1998; Hood and Johnson, 1999). Maximum ages of 30+ and 40+ yr have been reported for several species of Pacific lutjanids (reviewed in Rocha-Olivares, 1998).

Overall, the numbers of sampled males and females were nearly equal, but females were predominant in samples greater than 10 yr old. A similar pattern was observed in Pacific red snapper, *Lutjanus peru*, where the female-to-male ratio was essentially equal (1.1:1) for fish less than 10 yr old and 2.4:1 for fish older than 10 yr (Rocha-Olivares, 1998, Fig. 6). Rocha-Olivares (1998) concluded from catch curve analyses that differences in sex-specific numbers at age for *L. peru* resulted from males experiencing a higher mortality rate. Differential mortality between sexes is not unusual in lutjanids (Grimes, 1987) and the predominance of female GOM red snapper in older age classes may result from a higher mortality rate for males.

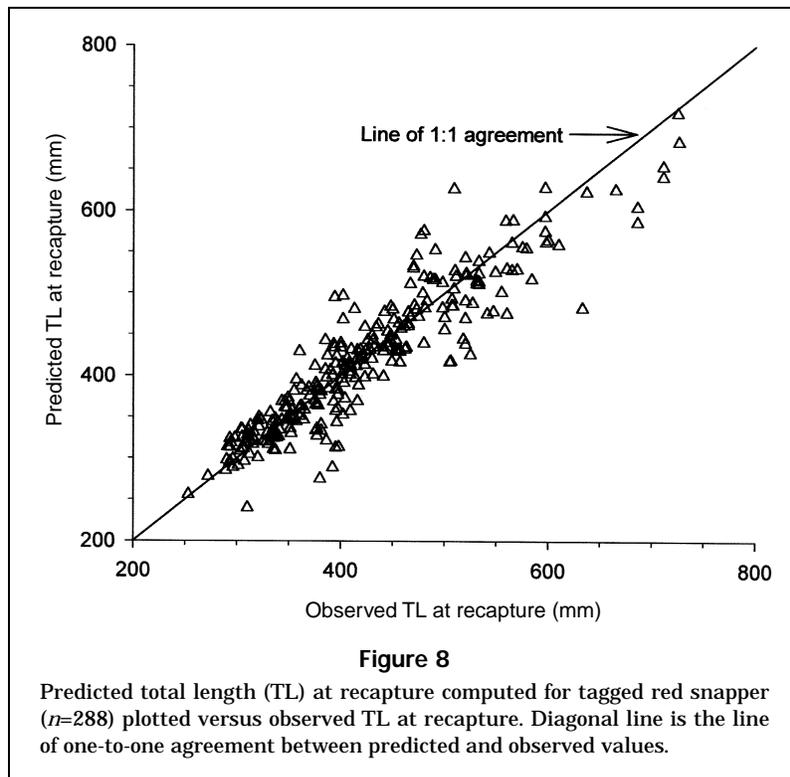
Fish sampled from tournaments were included in growth estimation because few large, old individuals were sampled randomly from the recreational catch. The inclusion of tournament sampled fish could bias growth estimates because tournament anglers target large fish; thus the potential exists for them to catch or spear the fastest growing individuals at a given age (Ottera, 1992; Vaughan and Burton, 1993; Goodyear, 1995b). Without the fish sampled from tournaments, however, the VBGF did not reach an asymptote; therefore growth parameters were poorly esti-



mated (Hirschhorn, 1974). We feel that excluding the tournament fish from growth function estimation introduced far greater bias than including them.

Mark-Recapture

Comparisons between estimated growth of tagged red snapper and otolith-aged fish corroborate otolith aging methods. Predicted TL of tagged individuals obtained with Fabens' (1965) method and VBGF parameters estimated from otolith-aged fish are coincident with observed TL at recapture because predicted and observed values corresponded well to the line of 1:1 agreement. Although ours



was a graphical rather than a statistical exercise (Labelle et al., 1993; Thompson et al., 1999), results corroborate otolith-based estimates of growth.

Direct comparison of linear growth functions computed for tagged fish and otolith-aged fish provides further support for otolith-based estimates of growth (slopes from the two equations differed by only 0.002 mm/d). Francis (1988) cautioned against direct comparison of age-based growth estimates with growth estimates from tagging data because different information results from the different data types. The linear model fitted to length-at-age data predicts TL of fish for a given age (in d), whereas the linear model fitted to tagging data predicts the increment of growth expected of a fish at liberty for a given number of days. However, because the relationship between TL and age is linear over the range of TL from the tagging data (Szedlmayer and Shipp, 1994), we submit that the slopes can be compared as estimates of mean growth. The slope of the age-based linear model is an estimate of the population growth rate of young fish, whereas the slope of the length-based linear model is an estimate of the mean growth of tagged individuals. That growth estimates for otolith-aged and tagged red snapper are very similar corroborates the aging method with otoliths and indicates that on average tagging did not affect fish growth.

Red snapper off Alabama

The red snapper fishery off Alabama is unique in several ways. Despite the reported lack of high-relief natural reef

structures on the continental shelf off Alabama (Parker et al., 1983; Shultz et al., 1987; Schroeder et al., 1989), fishermen land a disproportionately high percentage of the annual GOM red snapper harvest from Alabama coastal waters (Schirripa and Legault, 1999). Although Alabama red snapper landings have accounted for approximately 11% of total GOM landings from 1981 to 1998, the recreational fishery off Alabama accounted for mean (\pm SE) 21.1 (\pm 2.25)% of GOM recreational landings from 1981 to 1998 and 26.5 (\pm 1.83)% of recreational landings from 1990 to 1998 (Schirripa and Legault, 1999). Total landings of red snapper from the U.S. GOM averaged 3.5×10^3 metric tons from 1981 to 1998, with commercial and recreational landings essentially equal; however, 94% of Alabama red snapper landings from 1990 to 1998 came from the recreational sector of the fishery (Schirripa and Legault, 1999).

The red snapper fishery off Alabama is also unique because it is prosecuted almost entirely over artificial reefs (Minton and Heath, 1998; Shipp, 1999). Artificial reef construction began in the 1950s when charter boat operators gained permission from the Marine Resources Division of the Alabama Department of Conservation to place 250 car bodies on the sea floor off Alabama (Hosking and Swingle, 1989; Minton and Heath, 1998). Since the 1950s, artificial reefs have been constructed of a variety of materials including car bodies, liberty ships, army tanks, kitchen appliances, newspaper bins, and most recently, prefabricated concrete structures. Reef building increased dramatically in the 1980s with the creation (by permit) of artificial reef areas that now encompass a total of 3100 km²,

and it is estimated that over 15,000 artificial reefs currently exist off Alabama (Hosking and Swingle, 1989; Szedlmayer and Shipp, 1994; Minton and Health, 1998; Havard¹).

The correlation of catch rates with artificial reef construction has caused some to conclude that artificial reefs off Alabama have increased the production of red snapper, as opposed to merely aggregating fish from surrounding areas (Szedlmayer and Shipp, 1994; Minton and Health, 1998). Among the evidence cited in support of this conclusion was that red snapper grew faster, attained larger sizes, and lived longer over artificial reefs off Alabama than other places throughout their range (Szedlmayer and Shipp, 1994). More recent data, including those from the current study, indicate that GOM red snapper off Alabama grow similarly to and reach similar sizes as fish from the northwestern GOM and the Atlantic (Render, 1995; Manooch and Potts, 1997; Wilson and Nieland, 2001). It is also apparent that the maximum longevity of fish off Alabama is no greater than that of fish of other locations in the GOM (Szedlmayer and Shipp, 1994; Render, 1995; Wilson and Nieland, 2001).

These results have important implications for management of GOM red snapper. That growth of fish off Alabama is similar to growth of fish in the northwestern GOM is consistent with the management paradigm that northern GOM red snapper constitute a single stock (Goodyear, 1995a) and contrary to the hypothesis that fish off Alabama are unique (Szedlmayer and Shipp, 1994). Moreover, if fishing mortality rates are higher off Alabama than other places in the northern GOM but growth is the same, production of red snapper may be lower off Alabama than in other areas. Furthermore, if red snapper recruit to artificial reefs off Alabama from other areas in the northern GOM, Alabama's red snapper fishery may serve as a net sink for stock-specific production. Future research is needed to compare mortality as well as growth of fish from different areas in the northern GOM and to estimate the source of recruits to Alabama's artificial reefs.

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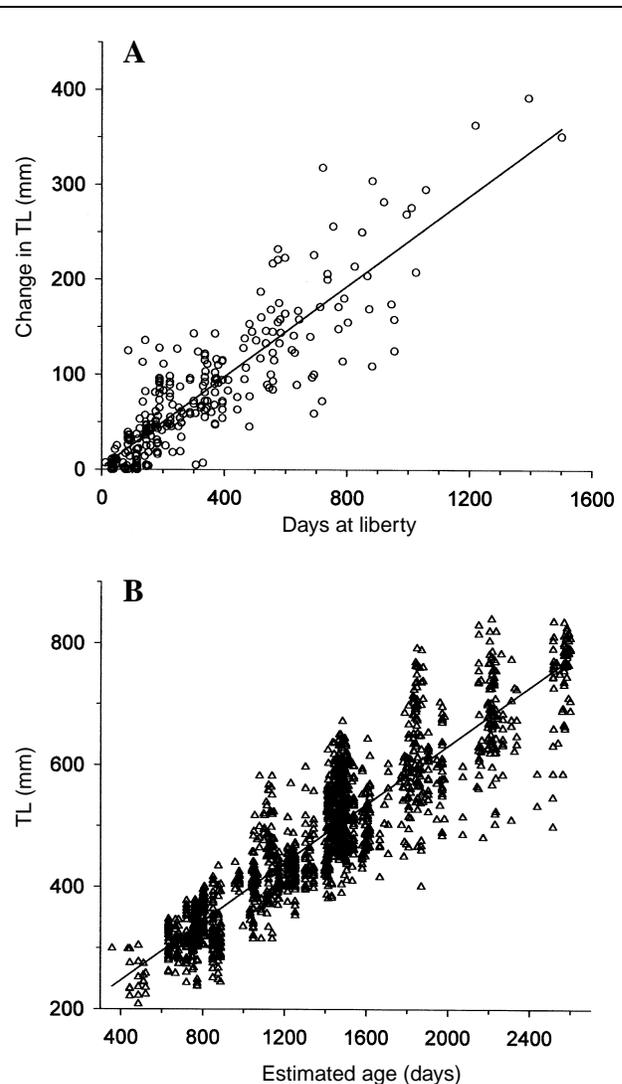


Figure 9

Linear regressions fitted to (A) change in total length (TL) versus days at liberty for recaptured red snapper ($n=288$) from the tagging study and (B) TL-at-age data for otolith-aged red snapper in the size range of fish from the tagging study ($n=1543$).

and recreational fishermen who reported recaptured fish. Lastly, we thank Amada Gonzales for collecting data from fishermen who reported recaptured fish.

Literature cited

- Acosta, A., and R. S. Appeldoorn.
1992. Estimation of growth, mortality, and yield per recruit for *Lutjanus synagris* (Linnaeus) in Puerto Rico. *Bull. Mar. Sci.* 50:282-291.
- Baker, M. S., Jr.
1999. Radiometric age validation of red snapper, *Lutjanus campechanus*, and red drum, *Sciaenops ocellatus*, from

¹ Havard, R. 1999. Personal commun. Alabama Department of Conservation, Marine Resources Division, P.O. Box 189, Dauphin Island, AL 36528.

- the northern Gulf of Mexico. Master's thesis, Louisiana State Univ., Baton Rouge, LA, 59 p.
- Beamish, R. J., and D. A. Fournier.
1981. A method for comparing the precision of a set of age determinations. *Can. J. Fish. Aquat. Sci.* 38:982-983.
- Beamish, R. J., and G. A. McFarlane.
1983. The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc.* 112:735-743.
1987. Current trends in age determination methodology. *In* Age and growth of fish (R. C. Summerfelt and G. E. Hall, eds.), p. 15-42. Iowa State Univ. Press, Ames, IA.
- Beckman, D. W., A. L. Stanley, J. H. Render, and C. A. Wilson.
1990. Age and growth of black drum in Louisiana waters of the Gulf of Mexico. *Trans. Am. Fish. Soc.* 119:537-544.
1991. Age and growth of sheepshead *Archosargus probatocephalus* in Louisiana waters using otoliths. *Fish. Bull.* 89:1-8.
- Beckman, D. W., C. A. Wilson, and A. L. Stanley.
1989. Age and growth of red drum, *Sciaenops ocellatus*, from offshore waters of the northern Gulf of Mexico. *Fish. Bull.* 87:17-28.
- Camper, J. D., R. C. Barber, L. R. Richardson, and J. R. Gold.
1993. Mitochondrial DNA variation among red snapper (*Lutjanus campechanus*) from the Gulf of Mexico. *Mol. Mar. Biol. Biotech.* 2:154-161.
- Cappo, M., P. Eden, S. J. Newman, and S. Robertson.
2000. A new approach to validation of periodicity and timing of otolith opaque zone formation in the otoliths of eleven species of *Lutjanus* from the central Great Barrier Reef. *Fish. Bull.* 98:474-488.
- Cerrato, R. M.
1990. Interpretable statistical tests for growth comparisons using parameters in the von Bertalanffy equation. *Can. J. Fish. Aquat. Sci.* 47:1416-1426.
- Chang, W. B.
1982. A statistical method for evaluating the reproducibility of age determination. *Can. J. Fish. Aquat. Sci.* 39:1208-1210.
- Collins, L. A., A. G. Johnson, and C. P. Kiem.
1996. Spawning and annual fecundity of the red snapper (*Lutjanus campechanus*) from the northeastern Gulf of Mexico. *ICLARM Conf. Proc.* 48:174-188.
- Cowan, J. H., Jr, R. L. Shipp, H. K. Bailey IV, and D. W. Haywick.
1995. Procedure for rapid processing of large otoliths. *Trans. Am. Fish. Soc.* 124:280-282.
- Fabens, A. J.
1965. Properties and fitting of the von Bertalanffy growth curve. *Growth* 29:265-289.
- Fowler, A. J.
1995. Annulus formation in otoliths of coral reef fish—a review. *In* Recent developments in fish otolith research (D. H. Secor, J. M. Dean, and S. E. Campana, eds.), p. 45-63. Univ. South Carolina Press, Columbia, SC.
- Francis, R. I. C. C.
1988. Are growth parameters estimated from tagging and age-length data comparable? *Can. J. Fish. Aquat. Sci.* 45:936-942.
- Gold, J. R., F. Sun, and L. R. Richardson.
1997. Population structure of red snapper from the Gulf of Mexico as inferred from analysis of mitochondrial DNA. *Trans. Am. Fish. Soc.* 123:386-396.
- Goodyear, C. P.
1995a. Red snapper in U.S. waters of the Gulf of Mexico. Stock assessment report MIA-95/96-05. Miami Laboratory, Southeast Fisheries Science Center, Miami, FL.
1995b. Mean size at age: an evaluation of sampling strategies using simulated red grouper data. *Trans. Am. Fish. Soc.* 124:746-755.
- Grimes, C. B.
1987. Reproductive biology of Lutjanidae: a review. *In* Tropical snappers and groupers: biology and fisheries management (J. J. Polovina and S. Ralston, eds.), p. 239-294. Westview Press, Inc., Boulder, CO.
- GMFMC (Gulf of Mexico Fishery Management Council).
1989. Amendment number 1 to the reef fish fishery management plan. GMFMC, Tampa, FL. 356 p.
- Heist, E. J., and J. R. Gold.
2000. DNA microsatellite loci and genetic structure of red snapper in the Gulf of Mexico. *Trans. Am. Fish. Soc.* 129:469-475.
- Hirschhorn, G.
1974. Effect of different age ranges on von Bertalanffy parameters in three fishes and one mollusk of the north-eastern Pacific Ocean. *In* The aging of fish (T. Bagenal, ed.), p.192-199. Unwin Brothers, Ltd., London.
- Hoesel, H. D., and R. H. Moore.
1998. Fishes of the Gulf of Mexico, 2nd ed. Texas A&M Press, College Station, TX, 422 p.
- Hood, P. B., and A. K. Johnson.
1999. Age, growth, mortality, and reproduction of vermilion snapper, *Rhomboplites aurorubens*, from the eastern Gulf of Mexico. *Fish. Bull.* 97:828-841.
- Hosking, W., and H. A. Swingle.
1989. Alabama's artificial reefs. MS-AL Sea Grant Publ. 9-019, Mobile, AL, 6 p.
- Kimura, D. K.
1980. Likelihood methods for the von Bertalanffy growth curve. *Fish. Bull.* 77:765-776.
- Labelle, M., J. Hampton, K. Bailey, T. Murray, D. A. Fournier, and J. R. Sibert.
1993. Determination of age and growth of south Pacific albacore (*Thunnus alalunga*) using three methodologies. *Fish. Bull.* 91:649-663.
- Maceina, M. J., D. N. Hata, T.L. Linton, and A. M. Landry Jr.
1987. Age and growth analysis of spotted seatrout from Galveston Bay, Texas. *Trans. Am. Fish. Soc.* 116:54-59.
- Manickchand-Heileman, S. C., and D. A. T. Phillip.
1996. Reproduction, age, and growth of Caribbean red snapper (*Lutjanus purpureus*) in waters off Trinidad and Tobago. *ICLARM Conf. Proc.* 48:137-149.
- Manooch, C. S., III.
1987. Age and growth of snappers and groupers. *In* Tropical snappers and groupers: biology and fisheries management (J. J. Polovina and S. Ralston, eds.), p. 329-373. Westview Press, Inc., Boulder, CO.
- Manooch, C. S., III, and J. C. Potts.
1997. Age and growth of red snapper, *Lutjanus campechanus*, Lutjanidae, collected along the southeastern United States from North Carolina through the east coast of Florida. *J. Elisha Mitchell Sci. Soc.* 113:111-122.
- Media Cybernetics.
1999. Optimas, version 6.5. Media Cybernetics, Silver Spring, MD.
- Minton, R. V., and S. R. Health.
1998. Alabama's artificial reef program: building oases in the desert. *Gulf of Mex. Sci.* 16:105-106.
- Moseley, F. N.
1966. Biology of the red snapper, *Lutjanus aya* Bloch, of the northwestern Gulf of Mexico. *Publ. Inst., Mar. Sci. Univ. Texas* 11:90-101.
- Nelson, R. S., and C. S. Manooch.
1982. Growth and mortality of red snappers in the west-central Atlantic ocean and northern Gulf of Mexico. *Trans. Am. Fish. Soc.* 111:465-475.

- Ottera, H.
1992. Bias in calculating growth rates in cod (*Gadus morhua* L.) due to size selective growth and mortality. *J. Fish Biol.* 40:465–467.
- Parker, R. O., D. R. Colby, and T. D. Willis.
1983. Estimated amount of reef habitat on a portion of the U.S. south Atlantic and Gulf of Mexico continental shelf. *Bull. Mar. Sci.* 33:67–86.
- Potts, J. C., C. S. Manooch III, and D. S. Vaughan.
1998. Age and growth of vermilion snapper from the southeastern United States. *Trans. Am. Fish. Soc.* 127:787–795.
- Render, J. H.
1995. The life history (age, growth, and reproduction) of red snapper (*Lutjanus campechanus*) and its affinity for oil and gas platforms. Ph. D. diss., Louisiana State Univ., Baton Rouge, LA, 76 p.
- Ricker, W. E.
1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.*, Ottawa, 382 p.
- Rocha-Olivares, A.
1998. Age, growth, mortality, and population characteristics of the Pacific red snapper, *Lutjanus peru*, off the southeast coast of Baja California, Mexico. *Fish. Bull.* 96:562–574.
- SAS Institute, Inc.
1996. Statistics, version 6.11. SAS Institute Inc., Box 8000, Cary, NC.
- Schirripa, M. J., and C. M. Legault.
1999. Status of red snapper in U.S. waters of the Gulf of Mexico updated through 1998. Report SFD-99/00-75, Sustainable Fisheries Division, Miami Laboratory, National Marine Fisheries Service, Miami, FL.
- Schroeder, W. W., A. W. Shultz, and J. J. Dindo.
1989. Inner-shelf hardbottom areas, northeastern Gulf of Mexico. *Trans. Gulf Coast Asso. Geol. Soc.* 38:535–541.
- Schultz, A. W., W. W. Schroeder, and J. R. Abston.
1987. Along-shore and offshore variations in Alabama inner-shelf sediments. In *Coastal sediments and processes*, 9th symposium of coastal sedimentology, p. 141–152. Florida State Univ., Tallahassee, FL.
- Shipp, R. L.
1999. The artificial reef debate: are we asking the right questions? *Gulf of Mex. Sci.* 17:51–55.
- Stanley, D. R., and C. A. Wilson.
1997. Seasonal and spatial variations in the abundance and size distribution of fishes associated with a petroleum platform in the northern Gulf of Mexico. *Can. J. Fish. Aquat. Sci.* 54:1166–1176.
- Szedlmayer, S. T., and J. Conti.
1999. Nursery habitats, growth rates, and seasonality of age-0 red snapper, *Lutjanus campechanus*, in the northeast Gulf of Mexico. *Fish. Bull.* 97:626–635.
- Szedlmayer, S. T., and R. L. Shipp.
1994. Movement and growth of red snapper, *Lutjanus campechanus*, from an artificial reef area in the northeastern Gulf of Mexico. *Bull. Mar. Sci.* 55:887–896.
- Thompson, B. A., M. Beasley, and C. A. Wilson.
1999. Age distribution and growth of greater amberjack, *Seriola dumerili*, from the north-central Gulf of Mexico. *Fish. Bull.* 97:362–371.
- Vaughan, D. S., and M. L. Burton.
1993. Estimation of von Bertalanffy growth parameters in the presence of size-selective mortality: a simulated example with red grouper. *Trans. Am. Fish. Soc.* 123:1–8.
- von Bertalanffy, L.
1938. A quantitative theory of organic growth. II. Inquiries on growth laws. *Human Biol.* 10:181–213.
1957. Quantitative laws in metabolism and growth. *Quart. Rev. Biol.* 32:217–231.
- Wilson, C. A., and D. L. Nieland.
2001. Age and growth of red snapper, *Lutjanus campechanus*, from the northern Gulf of Mexico off Louisiana. *Fish. Bull.* 99:653–664.