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AGE, GROWTH, AND REPRODUCTION OF THE RED SNAPPER, *LUTJANUS CAMPECHANUS*, FROM THE ATLANTIC WATERS OF THE SOUTHEASTERN U.S.

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ABSTRACT

Otoliths and gonadal tissue were taken from red snapper collected from fishery-independent and fishery-dependent sources between Cape Lookout, North Carolina and Key West, Florida during 1979–2000. The mean size of red snapper from fishery-dependent samples was 594 mm TL and ranged from 70–976 mm TL. Fish sampled with fishery-independent gear had a significantly smaller mean TL (426 mm, range = 121–866 mm) than fishery-dependent samples. The mean size of red snapper was significantly smaller in the 1980s when compared to the 1990s, regardless of gear type. Mean marginal increment analysis showed that opaque zone formation is annual with deposition occurring from June through August. The age range for fishery-independent samples was 1–22 yrs with a mean age of 3.1 yrs, and 1–45 yrs with a mean age of 4.2 yrs for fishery-dependent samples. Von Bertalanffy growth curves revealed that red snapper from commercial catches approach asymptotic size at around age 10, however, no asymptote is apparent for those fish sampled with fishery-independent gear. The overall sex ratio for red snapper was not significantly different from the expected 1:1, regardless of gear type. The smallest mature female was 287 mm TL and the largest immature female was 435 mm TL, with an estimate of length at 50% maturity (L50) of 378 mm TL. The smallest mature male was 200 mm TL and the largest immature male was 378 mm TL, with an L50 for males of 223 mm TL. Histological examination of the gonads indicated that female red snapper were in spawning condition from May through October, with a peak between June and September. The gonadosomatic index (GSI) for females ranged from a low of 0.35 in November and December to a high of 2.67 in June. Males were found to be in spawning condition throughout the year.

The red snapper, *Lutjanus campechanus* (Poey, 1860), is a large lutjanid associated with deep reef habitats along the southeastern U.S., from North Carolina around the Gulf of Mexico to the Yucatán Peninsula (Nelson and Manooch, 1982; Manooch and Potts, 1997). Red snapper occur in depths ranging from a few meters as juveniles, to over 600 m as adults (Camber, 1955; Bradley and Bryan, 1975). This species is generally associated with limestone outcroppings and live-bottom habitat (Powles and Barans, 1980) in temperate and tropical waters (Moseley, 1966; Nelson and Manooch, 1982).

Commercial landings of red snapper increased from 1950 through the 1960s (North Carolina to eastern Florida), reaching a peak in 1968 of 1,043,000 lbs. (454 mt) (Manooch et al., 1998; National Marine Fisheries Service (NMFS) Fish Statistics and Economic Division, pers. comm.). From 1975 through 1998, annual landings fell from 721,100 to 60,949 lbs. (Fig. 1). Eastern Florida landings dominated the catch through the middle 1970s after which a precipitous decline occurred (Fig. 1). During 1990–2001, 58% of the red snapper were landed in Florida (east coast), 6% in Georgia, 25% in South Carolina, and 11% in North Carolina. Recreational landings of red snapper peaked in 1985 at 619,000 lbs. In 2002, recreational fishermen landed 390,908 lbs. of red snapper (NMFS Fish Statistics and Economic Division, pers. comm.).

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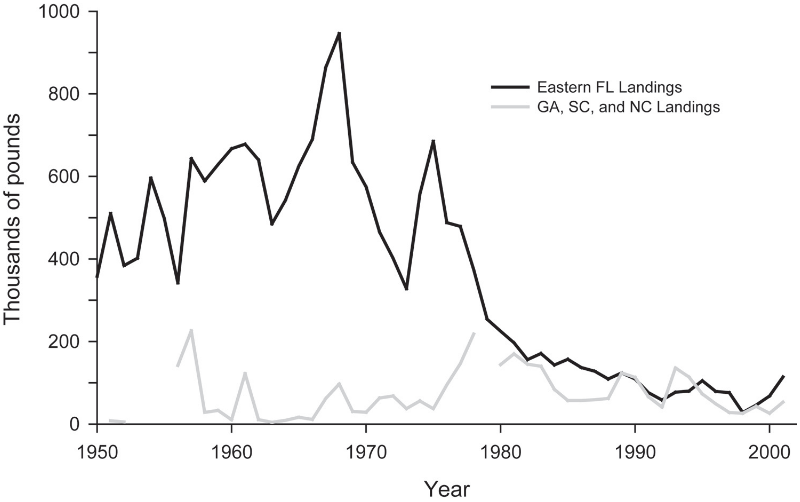

Figure 1. Commercial landings of red snapper in eastern Florida, Georgia, South Carolina, and North Carolina.

This rapid decline of commercial and recreational landings of red snapper off the southeastern U.S. prompted the South Atlantic Fishery Management Council (SAFMC) to establish a minimum size limit of 12″ and a 10 snapper bag limit for commercial and recreational anglers in 1983 (SAFMC, 1983). In 1991, with landings of red snapper still declining, the SAFMC increased the minimum size limit to 20″ and the snapper bag limit of 10 fish was restricted to only two red snappers (SAFMC, 1991). Manooch et al. (1998) reported a spawning potential ratio (SPR) of 24% for red snapper from 1986–1991 and 32% for red snapper from 1992–1995, indicating that the stock may be responding to management actions.

The complete life history of red snapper has been studied in the Gulf of Mexico (Camber, 1955; Moseley, 1966; Bradley and Bryan, 1975; Futch and Bruger, 1976; Nelson and Manooch, 1982; Baker and Wilson, 2001; Collins et al., 2001; Patterson III et al., 2001; Wilson and Nieland, 2001), but there is no published information on the reproductive biology of red snapper from the Atlantic waters of southeastern U.S., thus there is also a dearth of age and growth information as it relates to reproduction for red snapper from the Atlantic. Despite the commercial and recreational importance of this species, the only studies that examined aspects of the age and growth of red snapper from the study area were conducted by Nelson and Manooch (1982) and Manooch and Potts (1997). Nelson and Manooch (1982) used 2151 scales (Gulf of Mexico and Atlantic) and 142 sectioned otoliths (Atlantic only) to examine the growth and mortality of red snapper along the southeastern U.S. and the northern Gulf of Mexico. Based on 537 sectioned otoliths from red snapper collected off the southeastern U.S. from 1990–1996, Manooch and Potts (1997) found that red snapper length-at-age was considerably smaller than the length-at-age of red snapper collected during 1974–1978 (Nelson and Manooch, 1982). The reduction in length-at-age may be due to a variation in sample sizes, differences in interpretation of the sectioned otoliths by the investigators, of sustained heavy fishing pressure that has selectively removed, over many generations, the larger faster growing individuals in the population. Sustained exploitation has been implicated as a cause of a decrease in the size-at-age of fish in wild populations (Harris and McGovern, 1997;

Zhao et al., 1997) along the southeastern U.S., as well as captive populations (Conover and Munch, 2002).

There is currently insufficient life history information on which to base a management strategy for red snapper along the southeastern U.S. Collins et al. (2001) found that red snapper from the northeastern Gulf of Mexico are indeterminant spawners with a spawning season from May through early October. Other studies that examined aspects of the life history of red snapper in the Gulf of Mexico used dated techniques in assessing age and reproductive condition (Moe, 1963; Moseley, 1966; Bradley and Bryan, 1975).

The temporal decrease in the length-at-age of red snapper together with a precipitous decline in landings, and a low SPR of 24–32% (SAFMC, 2001) suggest that this species may be overfished. This study provides updated information on age, growth, and reproduction of red snapper found along the U.S. Atlantic coast.

Materials and Methods

Sampling.—Otoliths and gonadal tissue were taken from red snapper specimens collected from coastal and offshore waters between Cape Lookout, North Carolina, and Key West, Florida between 1979 and 2000 (Fig. 2). Specimens were collected during standard sampling by the Marine Resources Monitoring, Assessment, and Prediction (MARMAP) program (fishery-independent) using chevron traps, Florida traps, blackfish traps, and hook-and-line gear (Harris and McGovern, 1997). Additional red snapper specimens were obtained from commercial catches (fishery-dependent; Table 1).

Samples were obtained monthly to validate the annual nature of otolith increment formation and to assess spawning seasonality. Whole red snapper were weighed to the nearest gram (g) and measured (total length, TL; fork length, FL; standard length, SL) to the nearest mm. The left and right (when possible) sagittal otoliths were removed from all fish and stored dry prior to processing.

Age Determination.—In the laboratory, the left otolith was embedded in West System 105® epoxy resin, sectioned dorsoventrally (40 μm), and mounted on glass microscope slides using Accu-mount 60 mounting medium (Baxter Scientific Products®). One to three otolith sections were examined with transmitted light under a dissecting microscope (magnification: 20×) that was equipped with a Hitachi® KP-C550 video camera and monitor, a personal computer with a Matrox frame grabber and Optimus® image analysis software.

Counts and measurements were taken along the *sulcus acousticus* from the core of each otolith to the outer edge of each opaque zone and to the edge of the otolith. Sections were examined independently by two readers and reexamined jointly when differences in age estimation occurred. If disagreement persisted, the specimen was eliminated from age analyses. Marginal increment analysis was used to determine the periodicity of increment formation. Standardized monthly means of MI/MI_{max}, where MI=the marginal increment and MI_{max}=the maximum marginal increment in each age class, were plotted for all years. A unimodal plot would indicate that increment formation occurs annually for each age class (Manooch and Potts, 1997). A subsample (n = 100) of the red snapper otoliths was aged by an independent laboratory (NMFS-Panama City, Florida) for age verification.

An analysis of variance was used to determine temporal differences in lengths of red snapper sampled from 1979–1991 and 1992–2000. (Samples collected in 2000 were from January–June only). Differences in mean length-at-age between fishery-independent samples and fishery-dependent samples were examined using a General Linear Model (GLM) with a Tukey studentized range test. The linear relationship between lengths (TL, FL) and the curvilinear relationship between TL and body weight were determined with Least square linear regressions.

Least square linear regressions were used to illustrate the relationship between otolith radius and total length for both fishery-independent and fishery-dependent samples. Slopes and elevations of the aforementioned regressions were compared using an analysis of covariance (AN-

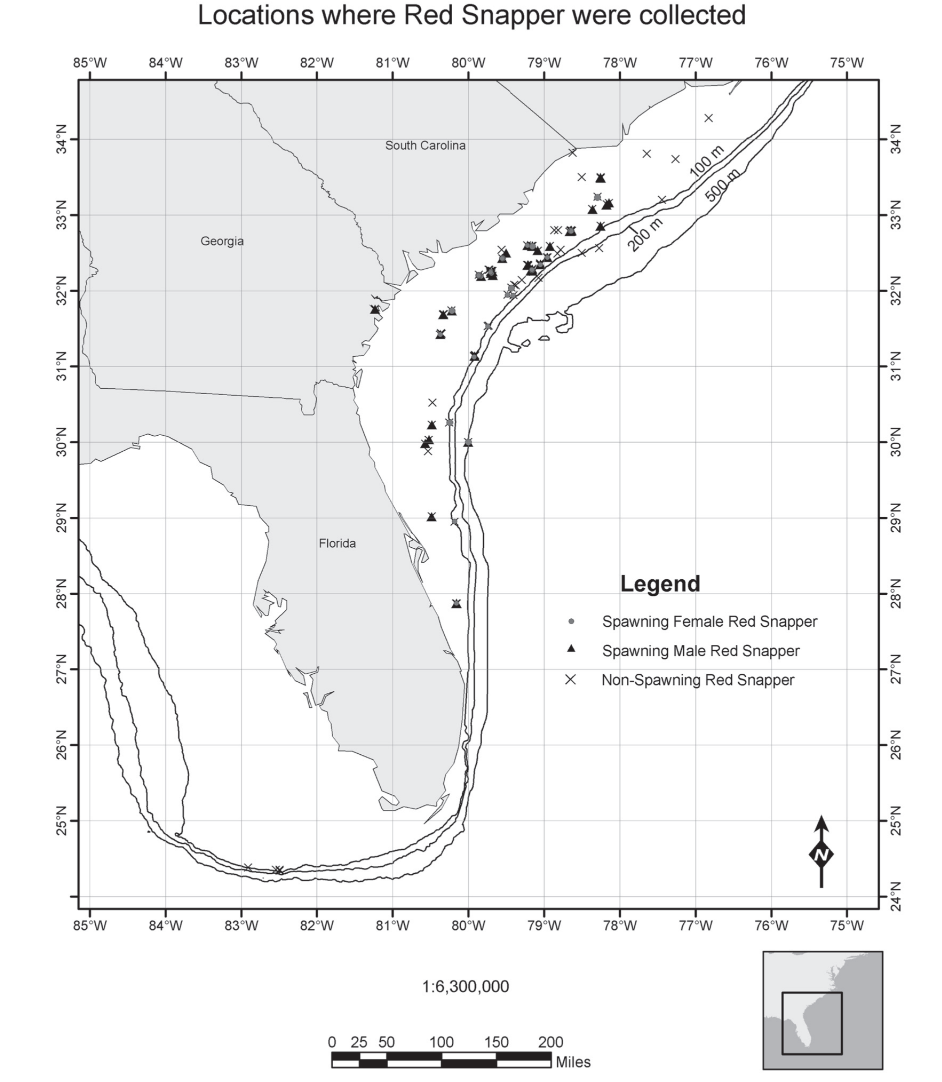

Figure 2. Locations where specimens of red snapper were collected including spawning red snapper. Spawning defined as ripe males and females, and females with postovulatory follicles.

COVA) to determine if separate back-calculations were needed. Back-calculated lengths-at-age were computed using the body proportional hypothesis (Francis, 1990): $TL_i = [(c + dS_i)/(c + dS_c)]TL_c$ where TL_i = length at time of formation of ith increment; c = intercept of fish length on otolith radius regression; d = slope of fish length on otolith radius regression; S_i = increment measurement at time of capture; S_c = otolith measurement at time of capture; TL_c = fish length at time of capture.

The Sigmaplot curve-fitting module based on the Marquart-Levenburg algorithm (Jandel, 1995) was used to fit von Bertalanffy growth curves (von Bertalanffy, 1938) to mean back-calculated lengths at age and mean observed lengths at age.

The potential effect of depth (7–282 m) and latitude (24°21′N–34°17′N) on length-at-age was examined using a general linear model (GLM) with a Tukey studentized range test. Depth data were recorded using the vessel's onboard fathometer or by plotting fishing location on a chart. All statistical analyses were performed using SAS, rejection of the null hypothesis was based on an

Table 1. The number of red snapper collected in this study from fishery-independent and fishery-dependent sampling.

Years	Fishery-independent	Fishery-dependent
1979–1983	51	81
1984–1988	74	10
1989–1993	119	15
1994–1998	154	226
1999–2000	74	499
Total	472	831
Grand total	1,303	

alpha of 0.05, and F tests in ANCOVA were based on a type III sum of squares (SAS Institute, Inc. 1990).

Reproductive Biology.—Sections from the posterior portions of collected gonadal tissues were fixed in 10% seawater- formalin solution for 7–14 d and transferred to 50% isopropanol for 7–14 d. Tissue samples were processed in an Auto-Technicon 2A Tissue Processor® or Modular Vacuum Tissue Processor® and blocked in paraffin. Three transverse sections (6–8 μm) were cut from each sample with a rotary microtome, mounted on glass slides, stained with double-strength Gill hematoxylin, and counterstained with eosin-y.

Two readers independently determined sex and reproductive state using histological criteria (Table 2). When assignments differed, the readers reexamined the section simultaneously to determine reproductive state. To confirm that resting and immature stages were assigned correctly the length-frequency histogram of these stages was compared to the histogram of all sexually mature stages (e.g., developing, spawning, spent, and resting). If there was little or no overlap between histograms representing mature and immature individuals, we concluded that resting and immature stages were assigned correctly. A gonadosomatic index (GSI) was calculated to verify the spawning season for females (GSI = gonad weight/total body weight × 100; Nikolsky, 1963). Females were considered to be in spawning condition if they possessed hydrated oocytes and/or postovulatory follicles (POFs). Sex ratio data were analyzed using a Chi-square goodness of fit test with Yates correction for continuity to determine if these ratios differed among size classes from an expected 1:1 (Zar, 1984). To estimate length at 50% maturity (L_{50}) and age at 50% maturity (A_{50}) the PROBIT procedure (SAS Institute, Inc., 1990) was used. The LOGISTIC procedure was used to determine which model (gompit, logit, or normit) provided the best fit to maturity data.

Results

Age Determination.—The total number of red snapper specimens (n =1303) collected for this study included specimens from fishery-dependent (n = 831) and fishery-independent sources (n = 472). Red snapper sampled by MARMAP (Fig. 3A) had a significantly smaller mean TL (mean = 426 mm; range: 121–866 mm; ANOVA; P > 0.0001, df = 1) than fishery-dependent samples. The mean size of fish from fishery-dependent samples was 594 mm TL and ranged from 70–976 mm TL (Fig. 3B). Total length was strongly related to FL and total body weight (TBW) regardless of gear type (Table 3). The mean size of red snapper sampled by MARMAP was significantly smaller in the 1980s (381 mm TL) than in the 1990s (453 mm TL; ANOVA; P > 0.0001, df = 1; Fig. 4). The mean size of red snapper sampled by fishery-dependent gear was also significantly larger in the 1990s (610 mm TL) than specimens collected in the 1980s (486 mm TL; ANOVA; P > 0.0001, df = 1; Fig. 5). Ages could be determined for 90% (n = 966) of the sectioned otoliths examined (n = 1073). Initial agreement between readers was 48% (n = 508), with 84% (n = 896) of the age estimates ± 1 yr. Of those specimens

Table 2. Histological criteria used to determine reproductive state in red snapper *Lutjanus campechanus*; modified from Wallace and Selman (1981); Hunter and Macewicz (1985); Hunter et al. (1986); Wenner et al. (1986); West (1990); Davis and West (1993).

Reproductive stage	Male	Female
1-Immature	Small transverse section compared to resting male; spermatogonia and little or no spermatocyte development.	Oogonia and primary growth oocytes only (< 60 μm), no evidence of atresia. Relative to resting female, area of transverse section of ovary is smaller, lamellae lack muscle and connective tissue bundles are not as elongate, oogonia are abundant along margin of lamellae, ovarian wall is thinner.
2-Developing	Development of cysts containing primary and secondary spermatocytes through some accumulation of spermatozoa in lobular lumina and ducts.	See below.
3-Running ripe	Predominance of spermatozoa in lobules and ducts; little or no occurrence of spermatogenesis.	Completion of yolk coalescence and hydration in most advanced oocytes; zona radiata becomes thinner.
4-Spent	No spermatogenesis; some residual spermatozoa in shrunken lobules or ducts.	More than 50% of vitellogenic oocytes undergoing alpha or beta atresia.
5-Resting	Larger transverse section compared to immature male; little or no spermatocyte development; empty lobules and ducts; some recrudescence (spermatogonia through primary spermatocytes) possible at end of stage.	Oogonia and primary growth oocytes (> 60 μm), traces of all stages of atresia. Relative to immature female, area of transverse section of ovary is larger, lamellae more elongate, oogonia are less abundant along margin of lamellae, bundles of connective and muscle tissue present, ovarian wall is thicker.
2B-Developing, recent spawn		Vitellogenic oocytes predominant and POFs (postovulatory follicles) <12 hr old (sensu Hunter et al., 1986).
2C-Developing, recent spawn		Vitellogenic oocytes predominant and POFs 12–24 hr old (sensu Hunter et al., 1986).
2D-Developing, recent spawn		Vitellogenic oocytes predominant and POFs >24 hr old (sensu Hunter et al., 1986)
2E-Early developing, cortical alveoli		Most advanced oocytes in cortical-alveoli stage. Cortical alveoli form in peripheral cytoplasm. Oil droplets form around germinal vesicle.
2F-Developing, vitellogenesis		Most advanced oocytes in yolk-granule or yolk-globule stage.
2G-Final oocyte maturation		Most advanced oocytes in migratory-nucleus stage. Partial coalescence of yolk globules. Nucleus has moved away from center of cell, being replaced by coalescing oil droplets. By the time of ovulation, one large oil droplet is present.

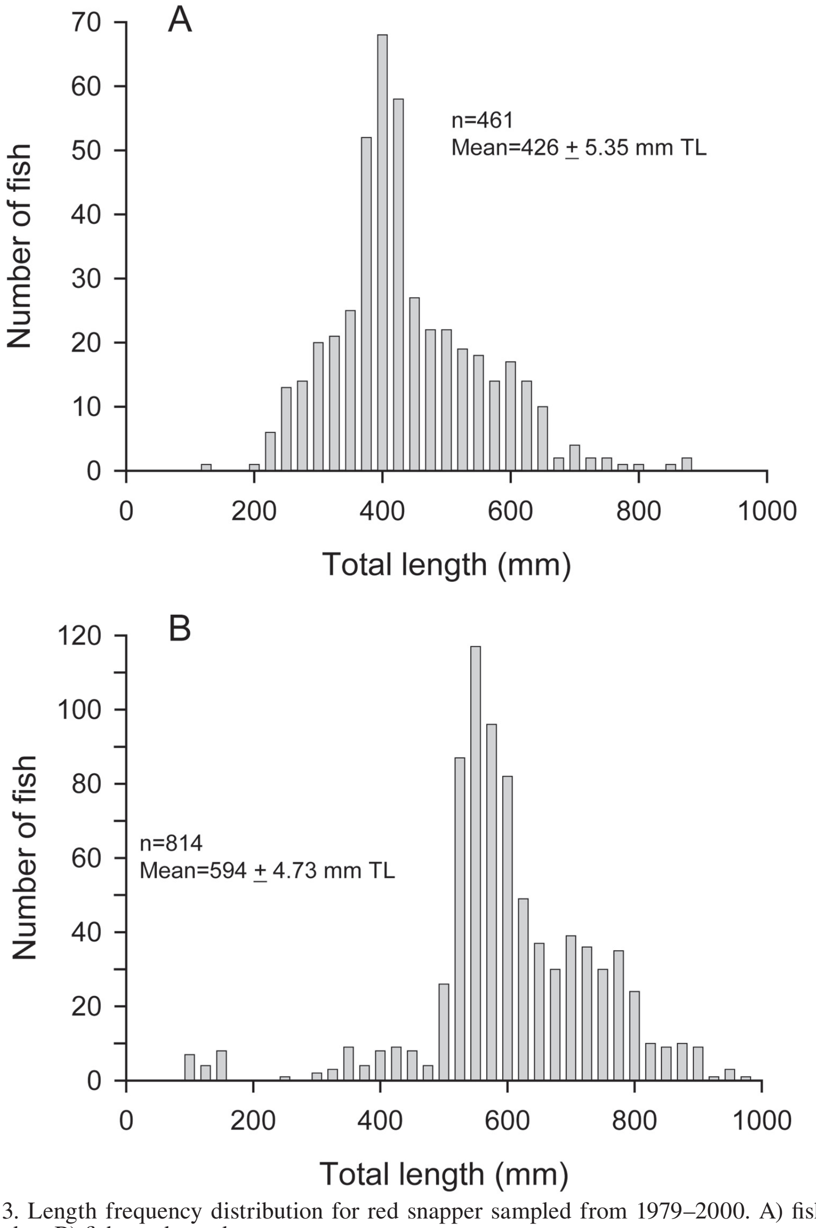

Figure 3. Length frequency distribution for red snapper sampled from 1979–2000. A) fishery-independent B) fishery-dependent.

aged, 74% (n = 789) were utilized for marginal increment analysis. The mean marginal increment indicated that opaque zone formation is unimodal, occurring one time per year, during June through August (Fig. 6). Examination of daily growth rings in five age 0 (59–133 TL mm) specimens collected with trawl by SEAMAP (Southeastern Atlantic Monitoring Assessment & Prediction) confirmed that assignment of the first annulus was correct. These five specimens were excluded from analyses. Independent laboratory readings of our otolith samples was 58% absolute agreement, and 86% in agreement

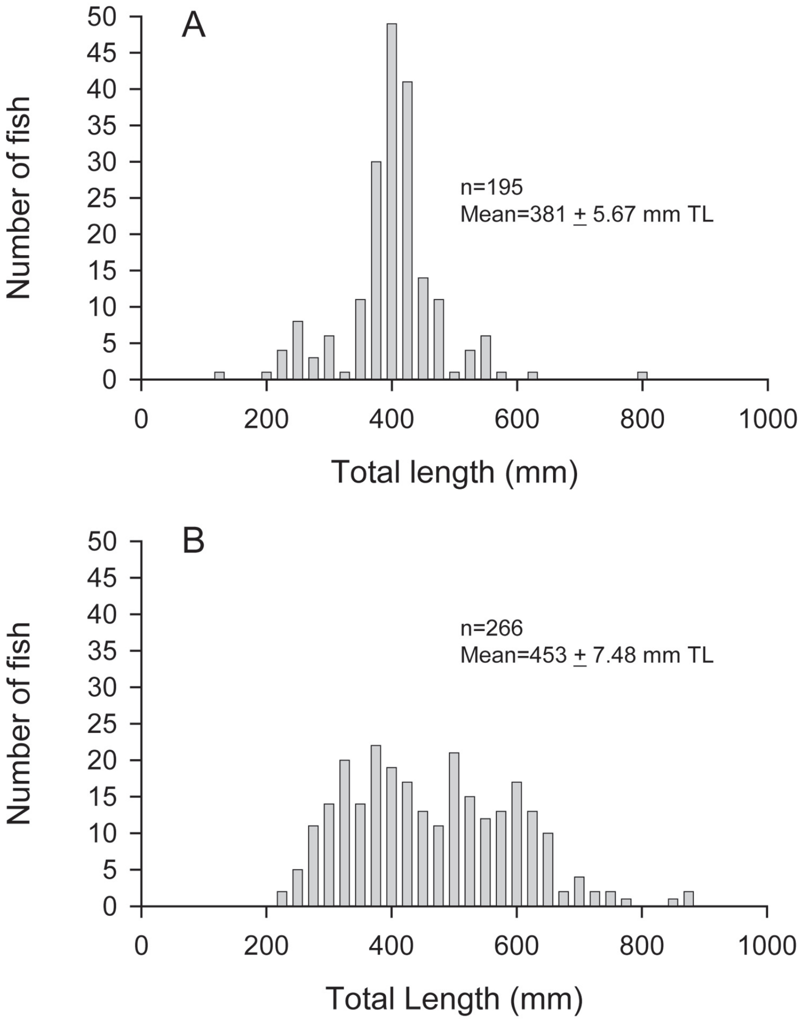

Figure 4. Length frequency distribution for red snapper from fishery-independent samples. A) 1979–1991 B) 1992–2000.

within 1 yr of our age estimates (G. Fitzhugh, NMFS, pers. comm.). The coefficient of variation (CV%) between laboratory comparisons was 12%, with relative bias at zero.

The age range for fishery-independent samples was 1–22 yrs with a mean age of 3.1 yrs, and 1–45 yrs with a mean age of 4.2 yrs for fishery-dependent samples (Fig. 7). All data were combined to generate an age-length key (Table 4). Due to differences in size and age between fishery-independent and fishery-dependent samples, further age analyses were performed on separate data sets. Size-at-age did not vary significantly with depth or latitude.

There was a strong correlation between otolith radii and fish lengths indicating that otolith radius increased as fish length increased (Fig. 8). Fishery-independent slopes and elevations from the linear regressions of TL on OR were significantly steeper than fishery-dependent samples (ANCOVA; $P < 0.0001$, df = 1; Fig. 8). Observed and back-calculated lengths-at-age indicated that red snapper from fishery-independent sampling were smaller at younger ages than fish from commercial sampling (fishery-dependent;

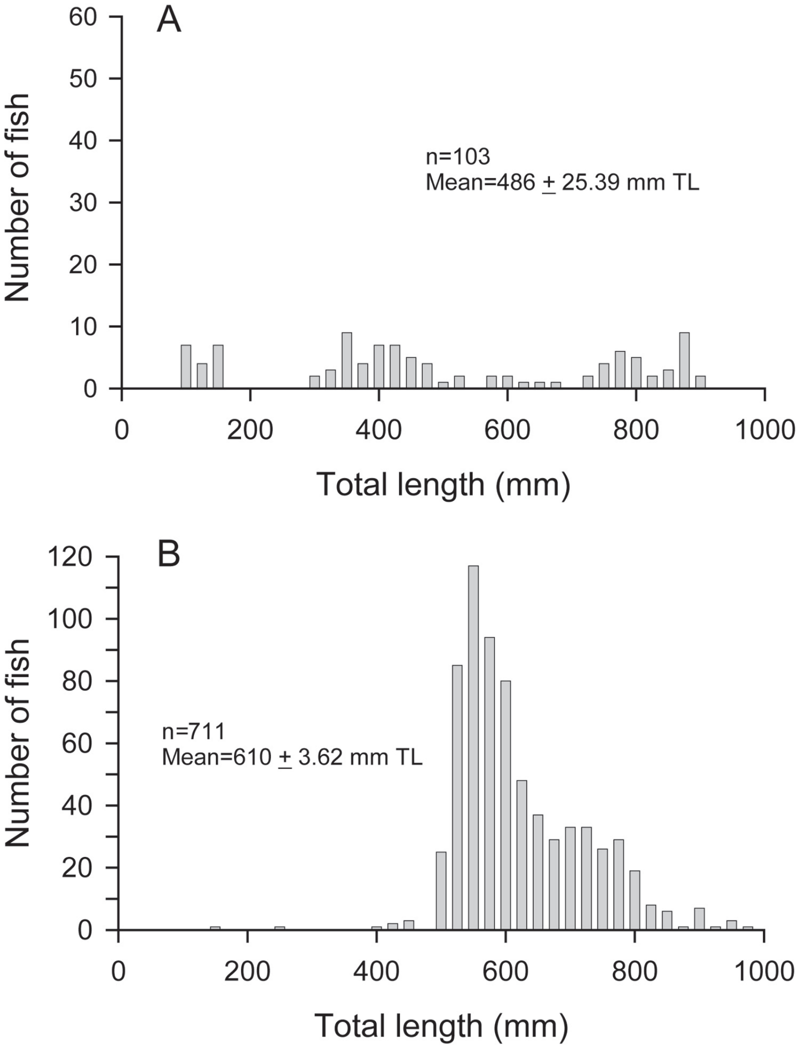

Figure 5. Length frequency distribution for red snapper from fishery-dependent samples. A) 1979–1991 B) 1992–2000.

Fig. 9). Age 1 red snapper from fishery-dependent samples, both observed and back-calculated, were significantly larger than age 1 red snapper from fishery-independent samples (ANOVA; P = 0.0116, df = 1).

The von Bertalanffy growth curves and parameters derived from mean back-calculated and observed lengths-at-age demonstrated that red snapper from commercial catches approached asymptotic size at around age 10, however, no asymptote is apparent for those fish sampled with fishery-independent gear (Fig. 10; Table 5). The results also demonstrated that red snapper collected with fishery-dependent gear attain a larger size-at-age than those fish sampled with fishery-independent gear. Growth curves were only calculated to age 12 to facilitate comparisons between fishery-independent and dependent samples.

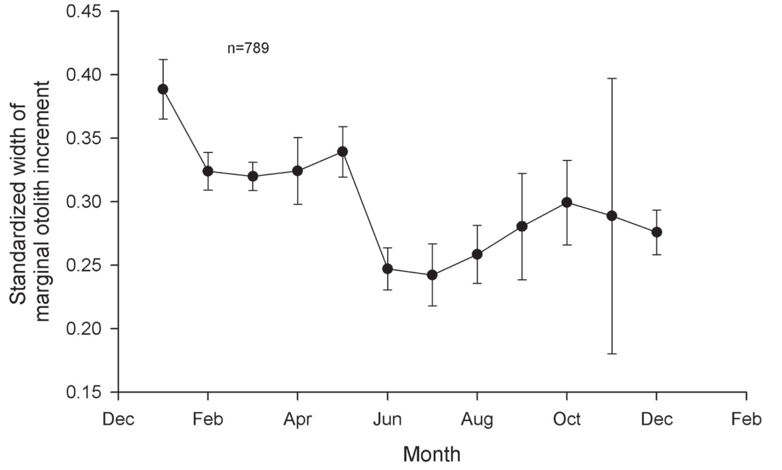

Figure 6. Mean monthly-standardized marginal increment (± 1 SE) for red snapper. There were few samples collected in November.

The observed mean lengths-at-age of red snapper from the present study were considerably larger than red snapper sampled by Manooch and Potts (1997) but similar to the results of Nelson and Manooch (1982) (Fig. 11).

Reproductive Biology.—Red snapper gonads were sampled from 1981–2000 during MARMAP cruises (n = 423) and 1979–2000 from commercial fish houses (n = 604). Approximately 97% (n = 996) of the gonads collected were successfully assigned a sex and reproductive state. There was very little overlap in the length distributions of immature or resting red snapper and substantial overlap of resting and definitely mature individuals, indicating that maturity stages were assigned correctly for both sexes (Fig. 12). The overall sex ratio by size class for red snapper was not significantly different from the expected 1:1 regardless of sampling regime (Tables 6,7). In both fishery-independent and fishery-dependent samples, however, more females were present in the larger length classes ($\geq$ 701 mm TL; Tables 6,7). The sex ratio has remained 1:1 since 1986.

The smallest mature female was 287 mm TL and the largest immature female was 435 mm TL, with an estimate of L_{50} of 378 mm TL (Gompertz model; 95% confidence interval (CI) = 364–389 mm) and A_{50} of 1.62 yr (Logit model; 95% CI = 1.21–1.87 mm). The smallest mature male was 200 mm TL and the largest immature male was 378 mm TL, with an L_{50} for males 223 mm TL (Logit model; 95% CI = 147–258 mm). Age at 50% maturity (A_{50}) for male red snapper was not calculated due to the abrupt transition

Table 3. Least square linear regressions relating fork length (FL) in mm to total length (TL) in mm and total body weight (TBW) in grams to TL for fishery-independent (fi) and fishery-dependent (fd) red snapper. Samples without all measurements were excluded from analyses.

Fork length equations:		
$FL_{fi} = 0.918\ (TL) + 6.570$	N = 442	$r^2 = 0.99$
$FL_{fd} = 0.931\ (TL) + 1.570$	N = 770	$r^2 = 0.99$
Total body weight equations:		
$TBW_{fi} = \log_{10}(TBW) = -4.838 + (3.001 \times \log_{10}(TL))$	N = 436	$r^2 = 0.97$
$TBW_{fd} = \log_{10}(TBW) = -4.681 + (2.950 \times \log_{10}(TL))$	N = 359	$r^2 = 0.98$

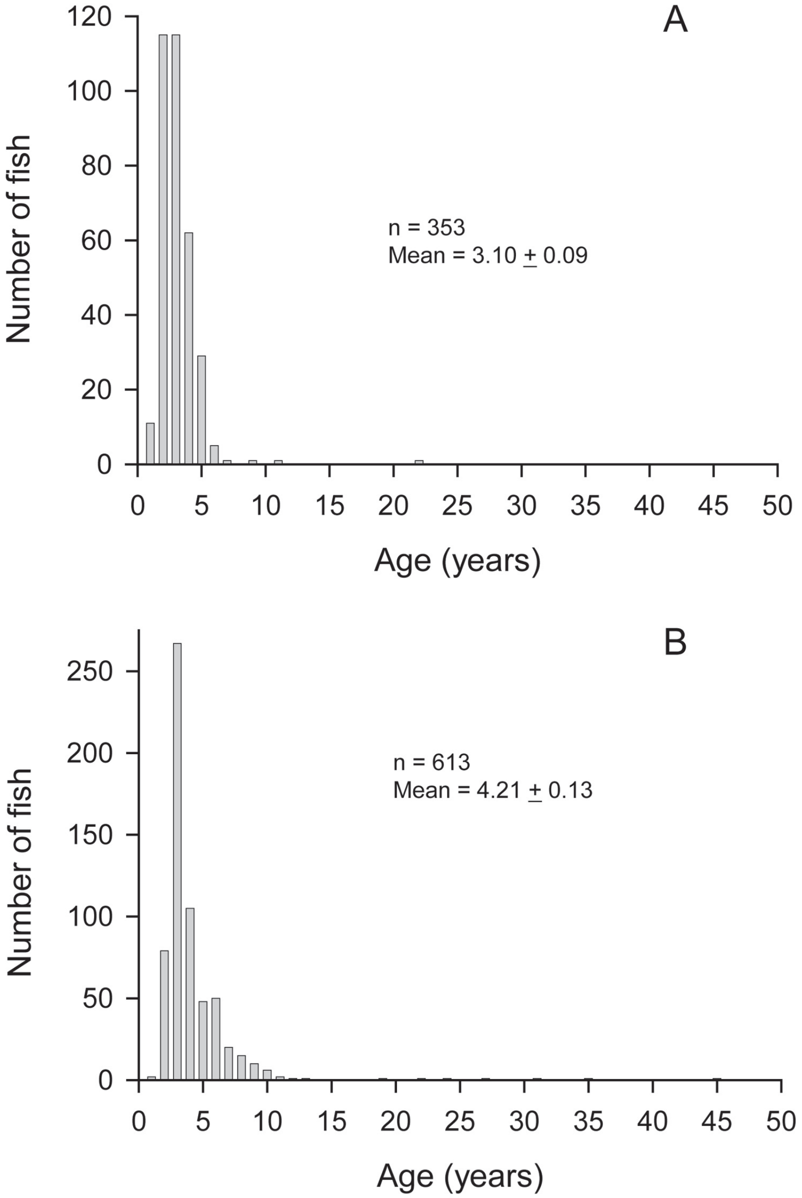

Figure 7. Age frequency distribution for red snapper samples from 1979–2000. A) fishery-independent B) fishery-dependent.

to maturity (Trippel and Harvey, 1991). Mature females were present in 0% of the age 1 class, 53% of age 2, 92% of age 3, 96% of age 4, and 100% of females age 5 or older (Table 8). Mature males were present in 86% of the age 1 class, 91% of age 2, 100% of age 3, 98% of age 4, and 100% of males age 5 or older (Table 8).

The majority of female red snapper were in spawning condition from May through October (Fig. 13A), with a peak in activity occurring between June and September. The GSI for females ranged from a low of 0.35 to a high of 2.67 in mature individuals (Fig.

Table 4. Age-length (TL, mm) key for red snapper collected from Atlantic waters of the southeastern U.S. (n = 966). Number of fish and proportion of length class in parentheses.

Length class (TL, mm)		Age					
		1	2	3	4	5	6
	N						
200	1			1 (1)			
225	5	1 (0.20)	4 (0.80)				
250	11	3 (0.27)	5 (0.46)	3 (0.27)			
275	12	2 (0.17)	8 (0.67)	1 (0.08)	1 (0.08)		
300	18	5 (0.28)	9 (0.50)	3 (0.17)	1 (0.05)		
325	19	1 (0.05)	11 (0.58)	6 (0.32)	1 (0.05)		
350	19	1 (0.05)	9 (0.47)	7 (0.37)	2 (0.11)		
375	35		13 (0.37)	21 (0.60)	1 (0.03)		
400	53		20 (0.38)	28 (0.53)	4 (0.07)	1 (0.02)	
425	44		20 (0.45)	20 (0.45)	3 (0.07)	1 (0.03)	
450	24		15 (0.63)	5 (0.20)	4 (0.17)		
475	25		7 (0.28)	8 (0.32)	7 (0.28)	3 (0.12)	
500	37		8 (0.22)	15 (0.40)	11 (0.30)	3 (0.08)	
525	82		24 (0.30)	45 (0.55)	10 (0.12)	2 (0.02)	1 (0.01)
550	111		22 (0.20)	76 (0.68)	11 (0.10)	2 (0.02)	
575	95		9 (0.09)	53 (0.56)	21 (0.22)	11 (0.12)	
600	89		7 (0.08)	48 (0.54)	24 (0.27)	8 (0.09)	2 (0.02)
625	53		3 (0.06)	24 (0.45)	13 (0.25)	10 (0.19)	2 (0.03)
650	41		1 (0.02)	7 (0.17)	19 (0.46)	9 (0.22)	5 (0.12)
675	25			4 (0.16)	12 (0.48)	5 (0.20)	4 (0.16)
700	34			4 (0.12)	12 (0.35)	3 (0.09)	9 (0.26)
725	29			1 (0.03)	4 (0.14)	9 (0.31)	7 (0.24)
750	29			1 (0.03)	3 (0.10)	6 (0.21)	8 (0.28)
775	28		1 (0.04)	1 (0.04)	5 (0.18)	4 (0.14)	9 (0.32)
800	18					2 (0.11)	9 (0.50)
825	9						1 (0.11)
850	7						
875	3						
900	7						1 (0.14)
925	0						
950	2						
975	0						
1,000	1						
N		13	196	382	169	79	58

14). Males in spawning condition were found throughout the year, however, the majority of spawning activity occurred from May through September (Fig. 13B).

Spawning red snapper were captured throughout the sampling range south of Cape Fear, North Carolina (Fig. 2).

Table 4. Continued.

Length Class (TL, mm)		Age					
		7	8	9	10	11	12+
	N						
200	1						
225	5						
250	11						
275	12						
300	18						
325	19						
350	19						
375	35						
400	53						
425	44						
450	24						
475	25						
500	37						
525	82						
550	111						
575	95						1 (0.01)
600	89						
625	53	1 (0.02)					
650	41						
675	25						
700	34	5 (0.15)	1 (0.03)				
725	29	6 (0.21)	1 (0.03)	1 (0.03)			
750	29	6 (0.21)	2 (0.07)	2 (0.07)	1 (0.03)		
775	28	1 (0.04)	3 (0.11)	3 (0.11)		1 (0.04)	
800	18	2 (0.11)	1 (0.06)	3 (0.17)			1 (0.06)
825	9	2 (0.22)	4 (0.44)		1 (0.11)		1 (0.11)
850	7		2 (0.29)		2 (0.29)	1 (0.14)	2 (0.29)
875	3			1 (0.33)		1 (0.33)	1 (0.33)
900	7		1 (0.14)	1 (0.14)	1 (0.14)		3 (0.43)
925	0						
950	2				1 (0.50)		1 (0.50)
975	0						
1,000	1						1 (1)
N		23	15	11	6	3	11

Discussion

Our marginal increment analysis demonstrated that one increment was deposited each year with opaque zone formation occurring between June and August for red snapper along the southeast Atlantic coast. Goodyear (1995) reported that annual opaque zone formation also occurred during June–August for red snapper from the Gulf of Mexico. In contrast, Manooch and Potts (1997) found that red snapper from Atlantic waters deposited an opaque zone between March and May. Using scales, Nelson and Manooch (1982) found that red snapper from the Atlantic formed opaque zones during April through

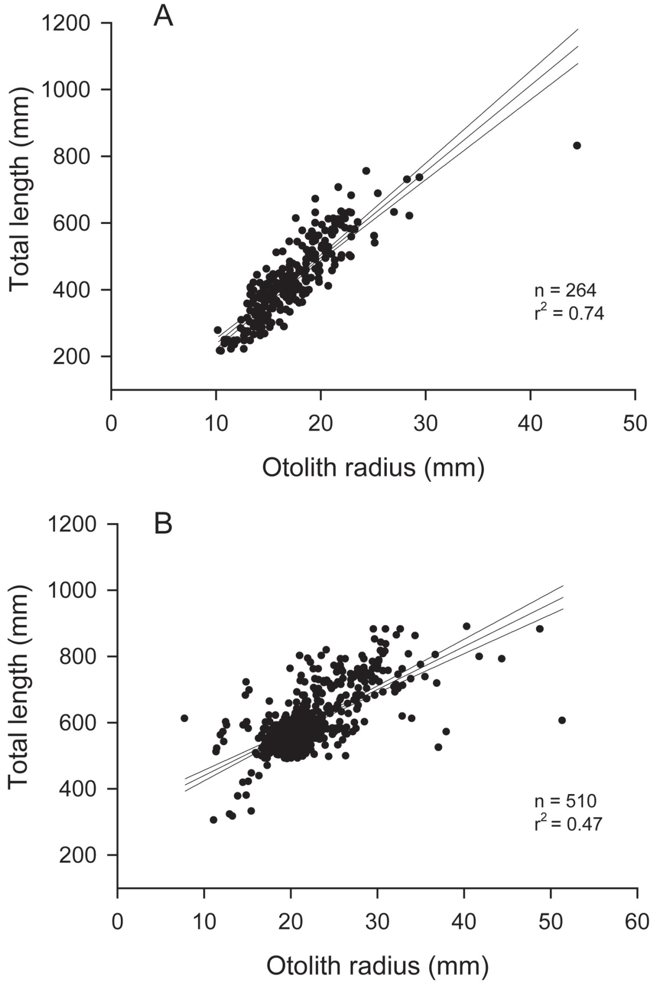

Figure 8. Length vs. otolith radius for red snapper from 1979–2000. A) fishery-independent B) fishery-dependent. Specimens with missing measurements were excluded from analyses.

May, while red snapper from the Gulf of Mexico formed opaque zones during June through July. Contrasting ageing techniques (scales and cut sections, Nelson and Manooch (1982); ground sections, Manooch and Potts (1997); and cut sections, this study) could account for the temporal differences of opaque zone formation between studies. Nelson and Manooch (1982) suggested that opaque zone formation in red snapper is correlated with spawning activity. The formation of an annulus in immature fish could be related to the same innate physiological rhythm, along with environmental factors (i.e., temperature, moon phase), that stimulate spawning (Nelson and Manooch, 1982).

Goodyear (1995), Wilson and Nieland (2000), Baker and Wilson (2001), and Wilson and Nieland (2001), found that red snapper from the Gulf of Mexico live for at least 53–55 yrs. Wilson and Nieland (2000) and Baker and Wilson (2001) used radiocarbon dating techniques as well as traditional otolith aging methods. The oldest age previously reported for red snapper along the southeast Atlantic was 25 yrs (Manooch and Potts, 1997). We aged red snapper to 45 yrs, similar to Goodyear's (1995) ages, suggesting that Atlantic red snapper are much longer lived than previously thought. Only five specimens

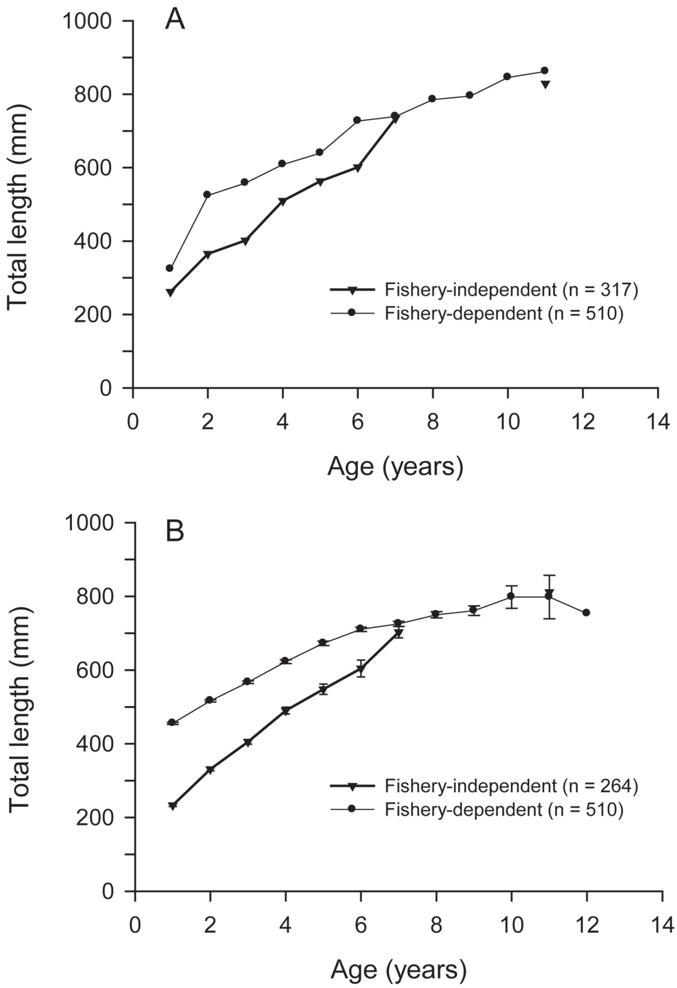

Figure 9. Mean size-at-age for fishery-independent and fishery-dependent red snapper data. A) observed B) back-calculated. Specimens with missing measurements were excluded from analyses.

less than age 1 were sampled in this study, as juvenile red snapper are infrequently captured by commercial or recreational fishing gear in the Atlantic waters of the southeastern U.S. (Stender and Barans, 1994; SEAMAP, 2000). In the Gulf of Mexico, red snapper juveniles are frequently taken as by-catch in shrimp trawls (Bradley and Bryan, 1975; Gutherz and Pellegrin, 1988).

The mean size of red snapper collected via fishery-independent sampling has increased from the 1980s to the 1990s. This increase in mean size may be a result of the alterations in MARMAP gear (see Collins, 1990), however, it is more likely due to changes in size limits and bag limits implemented by the SAFMC in 1991 (size limit increased from 12–20″, bag limit decreased from 10–2).

Observed and back-calculated lengths-at-age for red snapper were smaller at younger ages in fishery-independent samples relative to fishery-dependent samples. This difference in length-at-age is attributable to the current size limits imposed on red snapper. The minimum size limit of 20″ (508 mm) exacerbates the tendency of the commercial

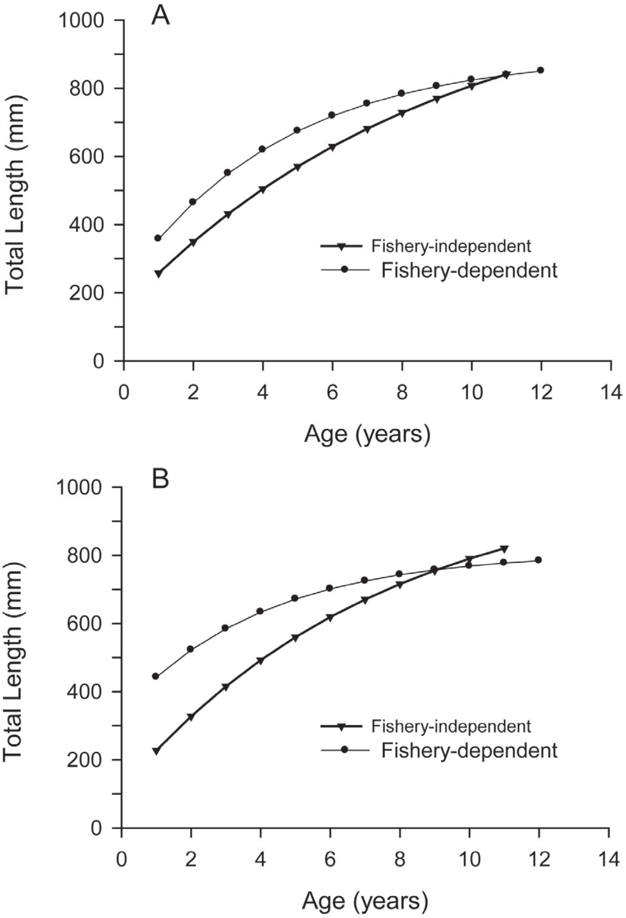

Figure 10. The von Bertalanffy growth curves derived for fishery-independent and fishery-dependent red snapper data. A) observed B) back-calculated.

fishery to select those fish predisposed to rapid growth, particularly at younger ages. This resultant larger length-at-age for younger fish, caused a low theoretical maximum length and a flat growth curve, and therefore is not a good representation of growth in red snapper. Fishery-independent sampling includes both slow and fast growing individuals and thus reflects a more accurate estimate of growth in the population of red snapper. Harris and McGovern (1997), Zhao et al. (1997), and Conover and Munch (2002) found that in heavily exploited populations a size-selective fishery may lead to smaller lengths-at-age over time.

The overall mean lengths-at-age of this study were similar to Nelson and Manooch (1982) but slightly larger than Manooch and Potts (1997). This difference may be attributed to dissimilar methodologies in otolith preparation or in assignment of the first increment. Assessment of age by an independent laboratory (Panama City, Florida) confirmed the assignment of ages in this study.

Red snapper from the Atlantic waters of the southeastern U.S. spawn May–October with peak spawning occurring June through September. This is very similar to the spawning period reported for red snapper from the Gulf of Mexico: June–September (Moseley, 1966); June–July with a probable fall spawn (Bradley and Bryan, 1975); July–

Table 5. Von Bertalanffy growth equation parameters derived from the mean observed and back-calculated total length for fishery-independent and fishery-dependent data for this study. Von Bertalanffy growth equation parameters derived from back-calculated total length from Nelson & Manooch (1982)* and Manooch & Potts (1997) presented for comparison.

Parameter	Fishery independent (observed)	Fishery independent (back-calculated)	Fishery dependent (observed)	Fishery dependent (back-calculated)	Nelson & Manooch, 1982 (back-calculated)	Manooch & Potts, 1997 (back-calculated)
k	0.112	0.133	0.220	0.245	0.160	0.150
L_4	1,124.4	1,034.5	898.7	808.6	975	955
t_0	−1.328	−0.871	−1.309	−2.230	0.000	0.180

* used scales to calculate age

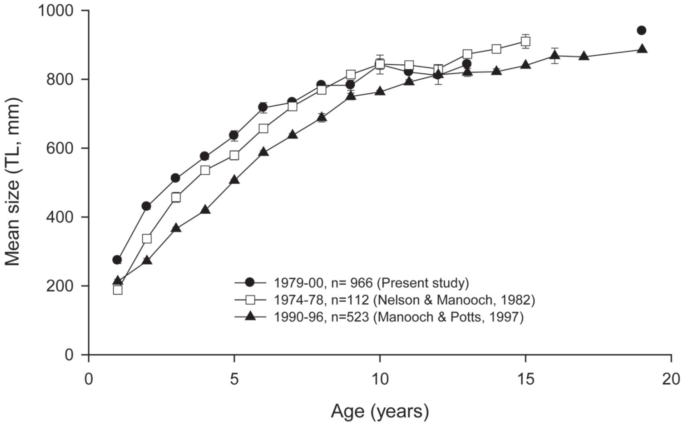

Figure 11. Mean observed size at age of red snapper, based on three studies. Ages > 20 yrs were excluded from this figure to facilitate comparisons between studies.

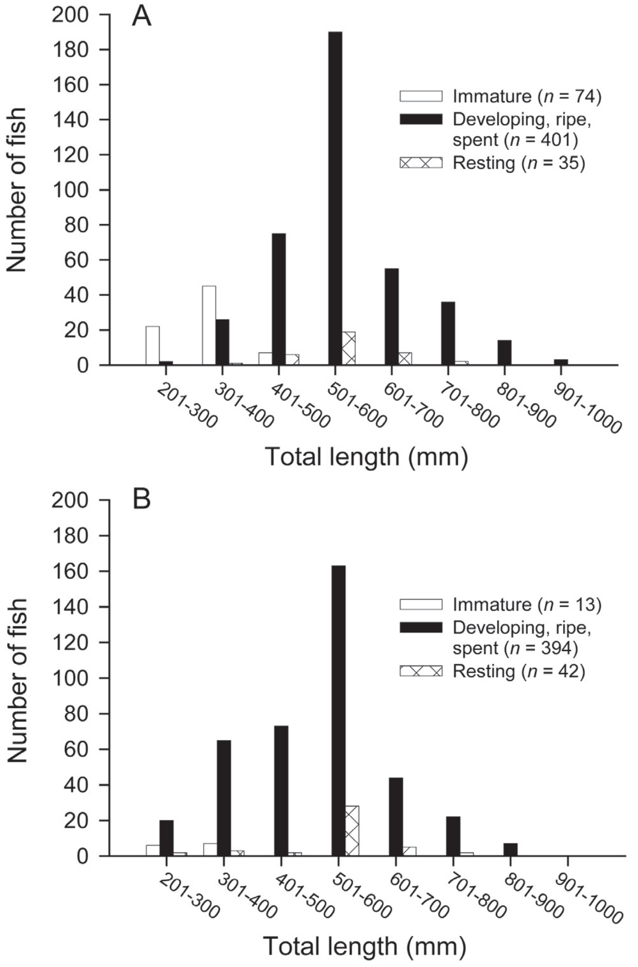

Figure 12. Length histogram for immature, confirmed mature, and resting red snapper from 1979–2000. A) female B) male.

Table 6. Chi-square analysis (with Yates correction for continuity) of sex ratios for red snapper caught with fishery independent gear. H_o: Male to female ratio is 1:1.

Total length (mm)	Males	Females	Male:Female	χ^2	P >
201–250	7	8	1:1.14	0.28	0.50
251–300	20	14	1:0.70	0.37	0.50
301–350	25	17	1:0.68	0.58	0.25
351–400	45	46	1:1.02	0.05	0.75
401–450	35	46	1:1.31	1.03	0.25
451–500	25	17	1:0.68	0.58	0.25
501–550	14	22	1:1.57	1.13	0.25
551–600	16	14	1:0.88	0.02	0.75
601–650	11	12	1:1.09	0.19	0.50
651–700	1	4	1:4	2.08	0.10
701–750	0	3			
751–800	0	1			
801–850	0	1			
851–900	0	2			
Total	199	207	1:1.04	0.06	0.75

October (Futch and Bruger, 1976); April–October (Collins et al., 2001). Arnold et al. (1978) reported that captive red snapper spawn in May and June. With the exception of Futch and Bruger (1976), Collins et al. (1996), Collins et al. (2001), and this study, most red snapper studies have utilized less accurate macroscopic methods, as opposed to histological methods, to assess reproductive state.

Male red snappers mature earlier than female red snappers, a common life history trait found in other snapper species (Domeier et al., 1996; Manickchand-Heileman and Phillip, 1996). Red snapper males reach maturity as early as age 1 or 200 mm TL, with all males mature by age 3 or 378 mm TL. Females can be mature by age 2 or 287 mm TL, with all females mature after age 4 or 435 mm TL. These results are similar to those re-

Table 7. Chi-square analysis (with Yates correction for continuity) of sex ratios for red snapper caught with fishery dependent gear. H_o: Male to female ratio is 1:1.

Total length (mm)	Males	Females	Male:Female	χ^2	P >
201–250	0	1	0:1	2.00	0.25
251–300	1	1	1:1	0.25	0.50
301–350	4	6	1:1.50	0.45	0.50
351–400	3	5	1:1.67	0.56	0.25
401–450	5	9	1:1.80	0.89	0.25
451–500	10	18	1:1.80	1.45	0.10
501–550	89	98	1:1.10	0.32	0.50
551–600	77	80	1:1.04	0.08	0.75
601–650	27	39	1:1.44	1.28	0.25
651–700	14	14	1:1	0.02	0.75
701–750	14	23	1:1.64	1.59	0.10
751–800	12	13	1:1.08	0.17	0.50
801–850	5	4	1.25:1	0.05	0.75
851–900	2	7	1:3.5	2.45	0.10
901–950	1	2	1:2	1.13	0.25
951–1,000	0	1	0:1	2.00	0.25
Total	264	321	1:1.22	2.58	0.10

Table 8. Percentage of mature specimens by size and age class for red snapper from 1979–2000.

Female Total length (mm)	Age 1		Age 2		Age 3		Age 4		Age 5		Age 6		Age 7+		Totals	
	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*
201–250	0	(3)	0	(3)	0	(1)									0	(7)
251–300	0	(1)	0	(8)	100	(2)	0	(1)							17	(12)
301–350	0	(2)	135	(9)	67	(3)									21	(14)
351–400			50	(12)	50	(18)	50	(2)							44	(32)
401–450			93	(15)	82	(13)	100	(5)	100	(1)					91	(34)
451–500			100	(6)	100	(13)	100	(7)	100	(4)					100	(30)
501–550			100	(23)	100	(59)	100	(7)	100	(3)					100	(92)
551–600			100	(8)	100	(45)	100	(14)	100	(8)					100	(75)
601–650			100	(3)	100	(14)	100	(9)	100	(8)	100	(4)			100	(38)
651–700					100	(2)	100	(2)	100	(4)	100	(5)			100	(13)
701–750					100	(1)	100	(5)	100	(5)	100	(4)	100	(6)	100	(21)
751–800							100	(3)	100	(1)	100	(6)	100	(2)	100	(12)
801–850													100	(5)	100	(5)
851–900													100	(5)	100	(5)
901–950													100	(2)	100	(2)
951–1000													100	(1)	100	(1)
Totals	0	(6)	53	(87)	92	(171)	96	(55)	100	(34)	100	(19)	100	(21)	88	(393)

Table 8. Continued.

Male Total length (mm)	Age 1		Age 2		Age 3		Age 4		Age 5		Age 6		Age 7+		Totals	
	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*
201–250	0	(1)	25	(4)	100	(2)									43	(7)
251–300	100	(6)	88	(8)	100	(2)	0	(1)							88	(17)
301–350			90	(10)	100	(7)	100	(1)							94	(18)
351–400			77	(13)	100	(17)	100	(3)	100	(1)					91	(34)
401–450			100	(18)	100	(9)	100	(2)							100	(29)
451–500			100	(9)	100	(7)	100	(11)	100	(2)					100	(29)
501–550			100	(22)	100	(47)	100	(7)	100	(1)	100	(1)			100	(78)
551–600			100	(8)	100	(48)	100	(20)	100	(8)	100	(1)			100	(85)
601–650					100	(13)	100	(9)	100	(6)	100	(1)			100	(29)
651–700					100	(5)	100	(8)			100	(5)			100	(18)
701–750					100	(1)	100	(2)	100	(3)			100	(1)	100	(7)
751–800					100	(1)			100	(1)	100	(1)	100	(6)	100	(9)
801–850													100	(4)	100	(4)
851–900			100	(1)									100	(2)	100	(3)
901–950																
951–1,000																
Totals	86	(7)	91	(92)	100	(159)	98	(64)	100	(22)	100	(10)	100	(13)	98	(367)

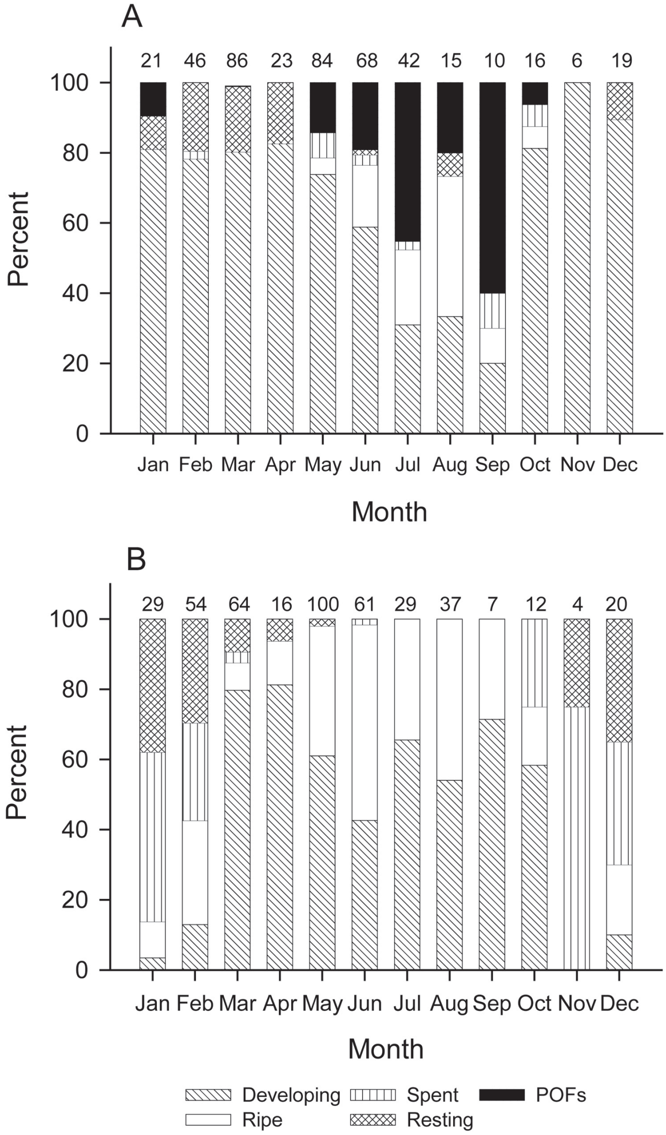

Figure 13. Spawning season for red snapper sampled from 1979–2000. A) female B) male. Number above each bar is sample size. POF = postovulatory follicle.

ported by Collins et al. (1996). The current management regulations allow all red snapper to reach maturity and spawn for 1–3 spawning seasons before being available to the fishery. However, older red snapper have a higher spawning frequency than younger red snapper (Collins et al., 1996), therefore, the harvesting of older fish leaves the younger, less fecund fish (Manooch, 1976) available, resulting in reduced reproductive output for the population.

The life history parameters of the red snapper in the Atlantic waters of southeastern U.S. are very similar to results reported from other parts of its range. The current regulations appear to be appropriate for protecting immature fish. The stable sex ratio, and

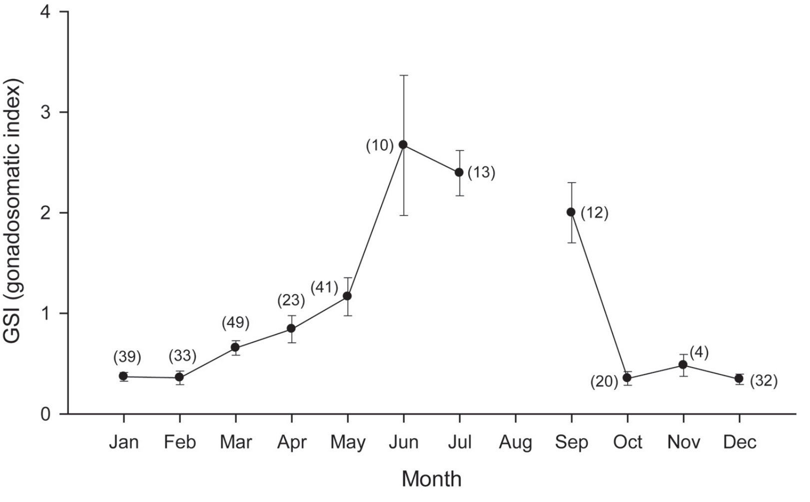

Figure 14. Mean gonadosomatic index (GSI = gonad weight/total body weight) by month for female red snapper from 1979–2000. Error bars represent ± 1 SE.

the increase in spawning potential ratio (SPR) from 24–32% indicates that the Atlantic red snapper stock may be responding to management actions (Manooch et al., 1998), but it may take decades for stocks to return to the abundance of the 1960s and 1970s, and continued monitoring is necessary to assess long term trends.

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