Abstract.—Fishing pressure on vermilion snapper, *Rhomboplites aurorubens*, in the Gulf of Mexico has increased since the mid-1970s, and populations are thought to be overfished. We sampled 858 vermilion snapper (192–585 mm TL) from the eastern Gulf of Mexico during 1995 and 1996 to assess their age structure, growth, mortality, spawning season, size and age at maturity, and batch fecundity. The lengths of males and females in our samples were not significantly different, and the overall sex ratio was not significantly different from 1:1. Marginal-increment analysis indicated that one opaque zone is formed on vermilion snapper otoliths during the late spring to early summer of each year. Ages ranged from 1 to 13 years, and von Bertalanffy growth models for males and females were not significantly different. Von Bertalanffy growth model parameters were L_∞ = 298 mm TL, K=0.25/yr, and t_0=−3.9 years for all aged fish. Growth rates in our study were lower than those in previous studies of Gulf of Mexico vermilion snapper, perhaps the result of recent changes in fishing selectivity. Pooled estimates of total instantaneous mortality were 0.480/yr based on recreational landings data and 0.489/yr based on commercial landings data. Most females and all males examined were mature. At 200 mm TL, 90% of the females we examined were mature. Vermilion snapper are summer spawners, and ripe females were caught from May to September. Batch fecundity ranged from 5535 to 22,811 oocytes and was positively correlated with fish weight (batch fecundity=317 × (whole weight) – 3.1624 × 10^4, r^2 = 0.55).

Age, growth, mortality, and reproduction of vermilion snapper, *Rhomboplites aurorubens*, from the eastern Gulf of Mexico

Peter B. Hood

Florida Marine Research Institute, Florida Department of Environmental Protection
100 Eighth Avenue S.E., St. Petersburg, Florida 33701-5095
Present address: Gulf of Mexico Fishery Management Council
　　　　　　　　　3018 U.S. Highway 301 North, Suite 1000
　　　　　　　　　Tampa, Florida 33619-2266
E-mail address: peter.hood@gulfcouncil.org

Andrea K. Johnson

North Carolina State University, Department of Zoology
Box 7617
Raleigh, North Carolina 27695-7617

The vermilion snapper, *Rhomboplites aurorubens*, is a small, subtropical lutjanid that occurs from North Carolina to Rio de Janeiro but is most abundant off the southeastern United States and in the Gulf of Campeche (Vergara, 1978). In the Gulf of Mexico (GOM), vermilion snapper are usually found near hard bottom areas off the west-central Florida coast, the Florida Middle Ground, and the Texas Flower Gardens (Smith et al., 1975; Smith, 1976; Nelson, 1988). Faunal surveys in the South Atlantic Bight (SAB) have indicated that vermilion snapper are most common over inshore live-bottom habitats and over shelf-edge, rocky-rubble, and rock-outcrop habitats (Grimes et al., 1977, 1982; Barans and Henry, 1984; Chester et al., 1984; Sedberry and Van Dolah, 1984).

Vermilion snapper are an important component of the reef fish fishery on the west coast of Florida. In 1995 and 1996, total commercial landings of vermilion snapper on Florida's west coast was 1.6 million pounds and had an estimated dockside value of $4.5 million (Marine Fisheries Information System[1]). Over the same period, 1.8 million vermilion snapper were landed by anglers in Florida (MRFSS[2]). Charter boats or headboats accounted for most (90%) of the angler-caught fish (Goodyear and Schirripa[3]; Schirripa[4]).

The Gulf of Mexico stock of vermilion snapper is showing signs of being overfished. Schirripa[4] reported in an analysis of GOM vermilion snapper landings data that 1) overall landings were declining, 2) the fishery was consolidating to the most productive fishing areas, 3) the mean size of fish in the commercial catch was decreasing, 4) the catch per unit of effort was decreas-

[1] Marine Fisheries Information System. 1997. Florida Department of Environmental Protection, 100 8th Avenue S.E., St. Petersburg, FL. Unpubl. data.

[2] MRFSS (Marine Recreational Fishery Statistics Survey). 1997. Fisheries Statistics Division, National Marine Fisheries Service, Department of Commerce, Silver Springs, MD. Unpubl. data.

[3] Goodyear, C. P., and M. J. Schirripa. 1991. A biological profile for vermilion snapper with a description of the fishery in the Gulf of Mexico. Miami Laboratory, Southeast Fisheries Center, National Marine Fisheries Service, NOAA, Miami, FL. Contribution rep. MIA-90/91-78.

[4] Schirripa, M. J. 1996. Status of the vermilion snapper fishery of the Gulf of Mexico: assessment 3.0. Miami Laboratory, Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., NOAA, Miami, FL. Contribution rep. MIA-95/96-61.

ing, and 5) the estimated number of age-1 fish in the population was declining. Goodyear and Schirripa[3] also noted that large differences in estimates of length-at-age and estimates of fecundity made it difficult to assess confidently conditions of the stock by using standard assessment models.

Existing age and growth data for this species in the GOM are inadequate and dated. Zastrow (1984) and Nelson (1988) used scales to age GOM vermilion snapper collected in the early 1980s. The maximum age reported was 7 years. However, using scales to determine age has proven to be problematic. Studies in the SAB have shown that as age increases, the readability of the scales decreases (Grimes, 1978; Collins and Pinckney, 1988). Barber (1989) used whole otoliths and scales to age GOM fish and was able to count up to 18 rings in scales and 26 rings in whole otoliths. Although he did not directly compare ages from both structures, his scale- and otolith-based estimates of length at age and growth were very different. In addition, his attempt to validate whole-otolith-based ages was unsuccessful.

Growth of vermilion snapper may be affected by changes in fishing. Zhao et al. (1997) found that mean and predicted sizes-at-age of SAB fish had declined between 1979 and 1993 and associated this change with size-selective fishing. They suggested that fishing is removing faster-growing fish from the population and may have genetic or physiological consequences in the life history of this species.

Information on the reproductive biology of vermilion snapper in the GOM is limited. Sex ratio appears to be dependent on location. Sex ratios from the GOM and Puerto Rico are approximately 1:1 (Boardman and Weiler, 1979; Zastrow, 1984; Collins[5]) although Nelson (1988) reported that males outnumbered females 1.2:1. In the SAB, females consistently outnumbered males, and sex ratios ranged from 1.6:1 to 1.7:1 (Grimes and Huntsman, 1980; Collins and Pinckney, 1988; Cuellar et al., 1996; Zhao and McGovern, 1997). Nelson (1988) examined spawning period, fecundity, and sex ratios of fish caught in the western GOM. His results were similar to findings reported for the SAB (Grimes and Huntsman, 1980; Cuellar et al., 1996). In both regions, spawning occurs during the summer and early fall. Nelson (1988) estimated that vermilion snapper batch fecundities in the GOM range from 61,600 to 392,000 eggs. Fecundity has been found to have a positive relationship with fish size (Grimes and Huntsman, 1980; Nelson, 1988; Cuellar et al., 1996). Vermilion

snapper are thought to spawn in aggregations. Boardman and Weiler (1979) and Grimes and Huntsman (1980) found large numbers of fish in the same reproductive state in single collections.

Basic life-history information is needed to properly assess vermilion snapper stocks in the GOM. Accurate ages are needed to develop age-length keys, develop growth models, and estimate total mortality. In addition, the annual periodicity of ring deposition in otoliths has not been validated in the GOM. With the increasing reliance on estimates of spawning-potential ratios to describe a stock's condition, information on maturation schedules, sex ratios, and size-specific fecundities are also needed. The purpose of this study was to accurately age eastern GOM vermilion snapper to develop age-length keys, develop growth models, construct catch curves for deriving estimates of total mortality, and to describe the reproductive biology of this species.

Methods

Eastern GOM vermilion snapper were sampled from October 1995 to September 1996. Samples were obtained from headboat fishermen, commercial catches, and a Florida Department of Environmental Protection trawl survey. Total length (TL), fork length (FL), and standard length (SL) were measured to the nearest millimeter. Whole weight or gutted weight (or both) were measured to the nearest gram. The relationships between lengths and log_{10}-transformed total lengths and weights were determined by least-squares regression (SAS Institute, Inc., 1985). Male and female regression lines of log_{10}-transformed total lengths and weights were compared by using analysis of covariance (Snedecor and Cochran, 1971).

Thin sections of sagittae (hereafter referred to generally as otoliths) were used to determine the ages of fish. Otoliths were removed and stored dry in culture wells. The left otolith was serially sectioned across its anterior–posterior midpoint at 0.5-mm intervals by making a transverse cut with an Isomet diamond saw. Mounted sections were placed on a black field, illuminated with reflected light, and examined with a binocular dissecting microscope. The magnified images of otolith sections were transmitted by means of video camera to a video monitor and were analyzed with a computer-driven data-acquisition software package (Optimas Corp., 1996). The number of opaque zones and the radial measurements from the core to the last opaque band and to the edge of the otolith (otolith radius, Fig. 1) were recorded. Marginal increments were measured as the distance between the last opaque band and the edge of the otolith.

[5] Collins, A. 1997. Southeast Fisheries Science Center, Natl. Mar. Fish. Serv., 3500 Delwood Beach Road., Panama City, FL 32407. Personal commun.

To determine the precision of vermilion snapper otolith opaque zone counts, otoliths collected during the first four months of sampling (*n*=200) were read independently by two investigators. After the first reading, readers examined the sections together and compared counts to form a consensus about what constituted an opaque zone. The two readers then re-examined the sectioned otoliths independently, and counts were compared again. Because agreement between readers was 100%, one reader read the remaining otoliths to determine age. Each of the remaining otolith sections was read three times, and opaque zone counts were accepted for ages only if at least two of the three separate readings were the same. To validate annulus periodicity, marginal increments and their medians were plotted by month for each age and compared for consistent temporal patterns.

Age in years was estimated as the number of opaque zones. Therefore, length at age included any growth that occurred after the last opaque ring was formed. Mean length at age was calculated for males, females, and all aged fish. Age and observed length data were fitted to a von Bertalanffy growth model by using a nonlinear regression (SAS Institute, Inc., 1985). Growth curves were fitted separately for males, females, and all aged fish. The estimated parameters for male and female curves were compared by using likelihood-ratio tests (Kimura, 1980; Cerrato, 1990). We calculated an adjusted r^2 for the resulting curves by using methods described by Helland (1987).

We used age-frequency data from this study to estimate mortality rates from the commercial and recreational length data. Because the numbers of vermilion snapper measured in fishery sampling programs were low, we pooled the most recent years where data were available. Length data from commercial landings were obtained from the TIPS[6] from 1992 to 1994, and in 1996. Length data from recreational landings were obtained from the MRFSS[2] and pooled for years 1990–96. Instantaneous mortality and survivorship were estimated by the Chapman-Robson method (Youngs and Robson, 1978). Age at full recruitment was estimated from the catch curve as the next oldest age from the age with the greatest catch.

Reproductive analyses were based on gonad weights and a histological examination of gonadal tissue. Whole gonads were weighed to the nearest 0.1 g, fixed in 10% buffered formalin for approximately one week, rinsed in water, and then transferred to 70% ethanol. A sample was taken from the middle of the pre-
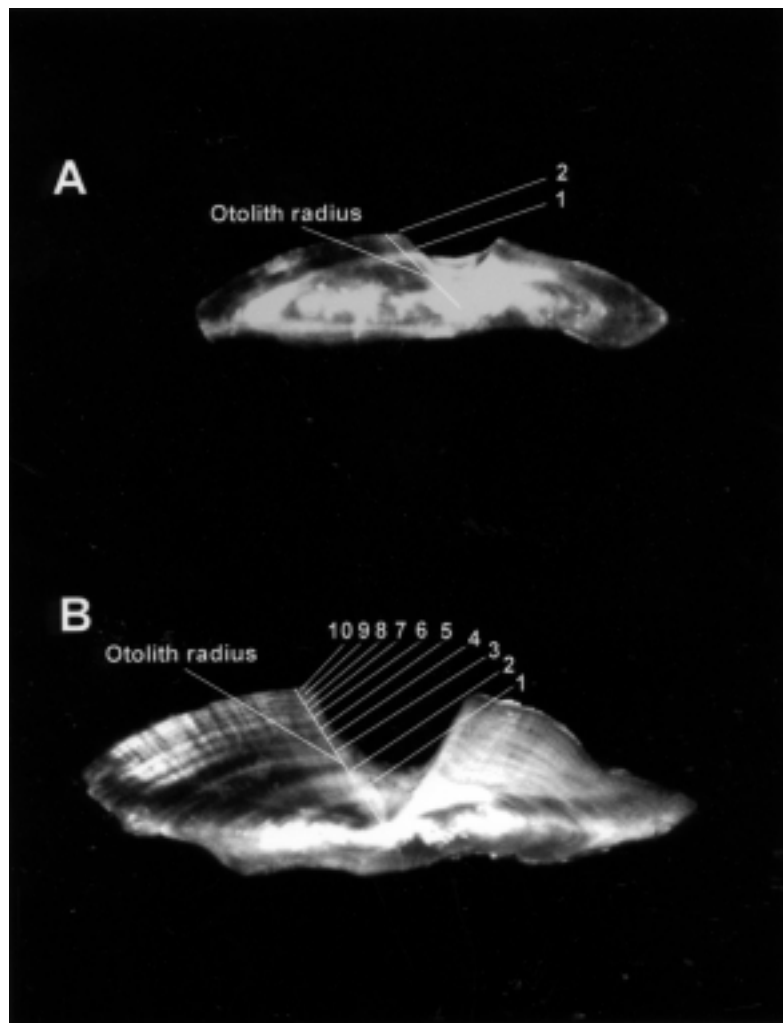

Figure 1

Sectioned saggitae from (**A**) a 2-year-old (204-mm-TL) and (**B**) a 10-year-old (184-m-TL) vermilion snapper. Both fish were caught in the eastern Gulf of Mexico in July 1996.

---

[6] TIPS (Trip Interview Program). 1997. Florida Department of Environmental Protection, 100 8th Avenue, S. E., St. Petersburg, FL. Unpubl. data.

Table 1
Gonad development classes for vermilion snapper.

Class	Ovary	Testes
Immature	Only primary growth oocytes present.	Spermatogonia and spermatocytes in the central lobules; no tailed sperm in the lumen of the lobule.
Resting	Primary growth oocytes and atretic bodies present.	Mostly spermatogonia and spermatocytes in the central lobules. Free spermatozoa in the lumen of the lobule, and brown bodies (Grier, 1987) may be present.
Early developing	Primary growth and cortical alveoli (yolk vesicle) oocytes present. Atretic bodies may be present.	
Developing	Primary growth, cortical alveoli, and vitellogenic oocytes present.	Mostly spermatocytes and spermatids in the central lobules, free spermatozoa in the lumen of the lobule.
Ripe	Primary growth, cortical alveoli, vitellogenic, and late-stage vitellogenic or hydrated oocytes present. Postovulatory follicles (POFs) may be present.	Mostly spermatozoa found in the central lobules and in the lumen of the lobule.
Spent	Primary growth oocytes present. Possibly some cortical alveoli oocytes present. Vitellogenic oocytes undergoing massive atresia.	Few free spermatozoa in the lumen of the lobule; early stages of spermatogenesis in the peripheral lobules.

served gonad and embedded in paraffin. We cut a 5.0-μm section from the sample, stained it with Harris's haematoxylin, counterstained it with eosin (Humason, 1972), and examined it under a compound microscope to determine sex and gonad developmental state. In addition, the frequency of oocyte developmental stages (including atretic bodies and postovulatory follicles) was tabulated for approximately 300 oocytes from each ovary by using a computer-driven data-acquisition software package (Optimas Corp., 1996). Gonadal development classes (Table 1) were determined by using modified classification schemes developed from West (1990) and Wallace and Selman (1981) for females and from Hyder (1969) for males.

Reproductive seasonality was determined by examining the monthly changes in gonad classes, the monthly distribution of oocyte stages, and the monthly changes in the gonadosomatic index (GSI). The GSI was calculated by the following equation:

$$GSI = gonad\ weight/(whole\ weight - gonad\ weight).$$

If whole weight was not available, it was estimated from TL. Batch fecundity was estimated by counting hydrated oocytes following the gravimetric method described by Hunter et al. (1985). The relation between fish weight and batch fecundity was examined for a significant correlation by means of least-squares regression analysis (SAS Institute, Inc., 1985).

Results

Collections

We sampled 858 vermilion snapper that ranged from 192 to 585 mm TL. Most fish (87%) were between 201 and 325 mm TL. Relationships between lengths, between lengths and weights, and between weights are seen in Table 2. Male and female data were pooled for the weight-length relationship because no significant difference was found between slopes and y-intercepts of sex-specific regression equations (analysis of covariance, P=0.47 and 0.08, respectively). Most fish came from the recreational fishery (n=661) and ranged in length from 192 to 400 mm TL (Fig. 2). Fish from the commercial fishery (n=168) ranged from 225 to 585 mm TL. The mean length of recreationally caught fish (256 mm TL, SE=29) was significantly less than the mean length of commercially caught fish (324 mm TL, SE=90; t-test, P<0.001). The length-frequency distributions for commercially and recreationally caught fish were significantly different (χ^2=216, df=5, P<0.001). Fish obtained from the trawl survey (n=27) were small and ranged in length from 205 to 253 mm TL.

The mean length of males (256 mm TL, SE=4) was not significantly different from that of females (261 mm TL, SE=3; t-test, P=0.315). Males (n=392) ranged in length from 199 to 585 mm TL and females (n=430) from 192 to 518 mm TL (Fig. 2). The overall sex ratio of males to females was 1:1.1 and was not signifi-

Table 2

Linear relationships ($Y=a+bX$) between length and length, length and weight, and weight and weight for vermilion snapper from the eastern Gulf of Mexico. SL is standard length (mm); FL is fork length (mm), TL is total length (mm); WT is whole weight (gm); GWT is gutted weight (gm). n is the number of fish sampled, and standard error is in parentheses.

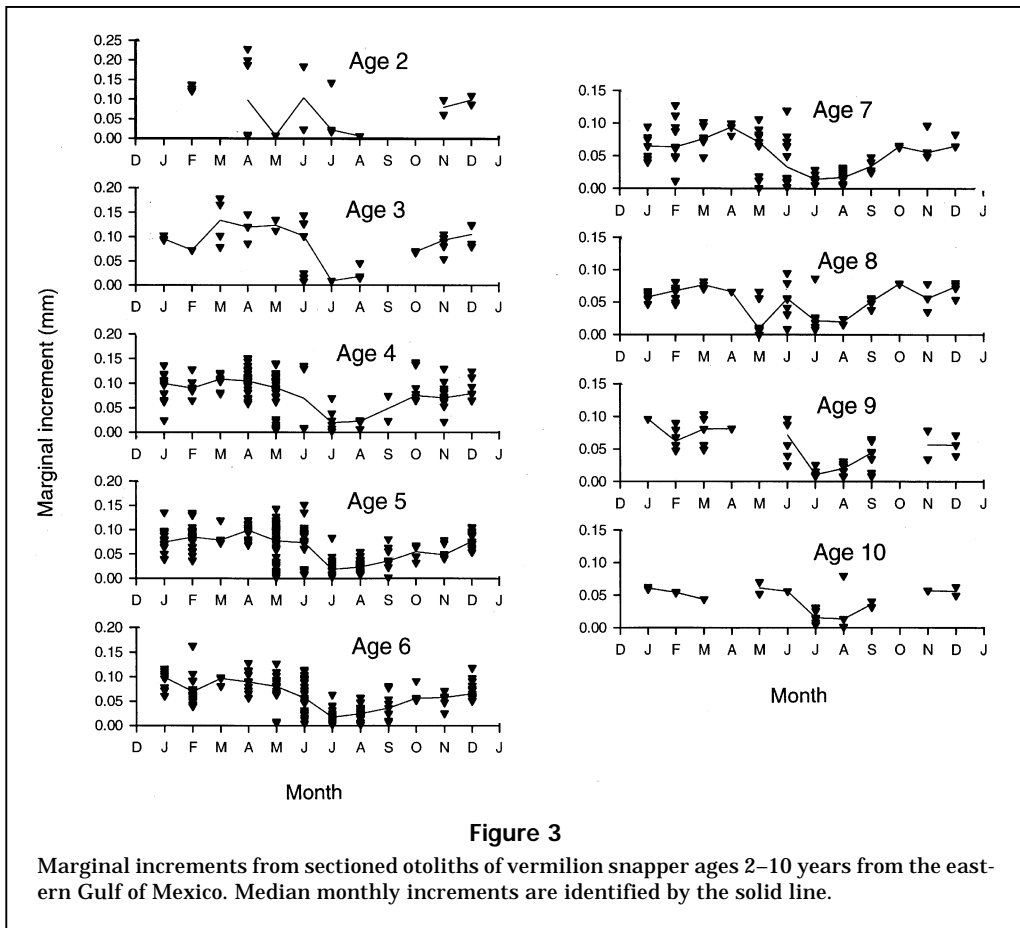| Y	X	n	a	b	r^2
SL	FL	857	7.5 (0.8)	0.82 (0.003)	0.99
SL	TL	869	10.5 (1.0)	0.72(0.004)	0.98
FL	SL	857	−5.5 (1.1)	1.20 (0.005)	0.99
FL	TL	854	3.4 (0.6)	0.88 (0.002)	0.995
TL	SL	869	−8.4 (1.4)	1.36(0.007)	0.98
TL	FL	854	−2.6 (0.6)	1.13 (0.003)	0.995
WT	GWT	89	−11.8(2.3)	1.15 (0.012)	0.99
$\log_{10}$WT	$\log_{10}$TL	646	−4.60(0.084)	2.87 (0.035)	0.91
$\log_{10}$GWT	$\log_{10}$TL	170	−5.01(0.05)	3.03(0.02)	0.99
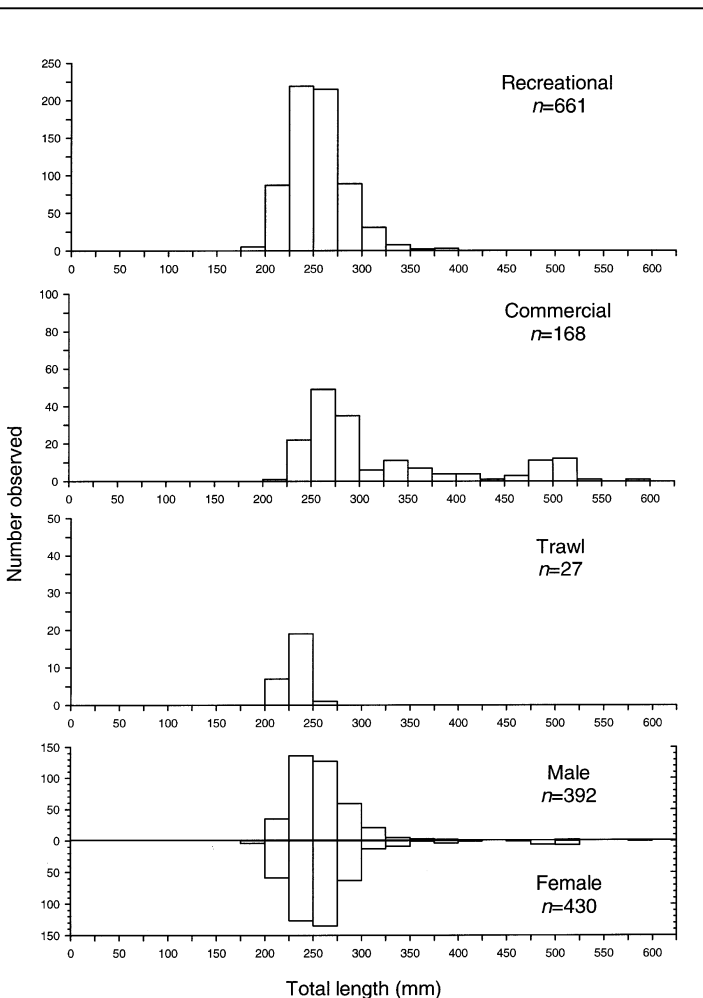
Figure 2

Total lengths of vermilion snapper from the eastern Gulf of Mexico by sampling source and by sex.

cantly different from 1:1 (χ^2=1.175, df=1, P>0.05). Seasonal sex ratios based on three-month intervals (December–February, March–May, June–August, September–November) ranged from 1:1 to 1:1.2 and were not significantly different from 1:1 (χ^2=0.017 to 1.045, df=1, P>0.05).

Age and growth

Under reflected light, alternating opaque (white) and translucent (dark) zones were evident on vermilion snapper otoliths (Fig. 1). Two readers examined a subsample of 200 otoliths, and 57% of their readings were in agreement. Most of the disagreements (82.6%) differed by only one opaque zone. A second independent reading of the subsample by the two readers resulted in complete agreement (100%). Of 858 sectioned otoliths examined, 841 (98%) could be assigned ages. Of the otoliths that could be aged, measurements for marginal-increment analyses could not be made for 50 individuals (5.9%) because of broken or occluded areas along the otolith radius.

Analyses of marginal-increment data for fish ages 2 to 10 suggested that opaque zones were formed once a year during the late spring to early summer (Fig. 3). During this time, the widest increments (opaque zone formation was imminent) and the narrowest increments (opaque zone formation was just completed) were present. In addition, monthly median marginal increments for ages 2 to 10 had a consistent yearly pattern of high me-

Figure 3

Marginal increments from sectioned otoliths of vermilion snapper ages 2–10 years from the eastern Gulf of Mexico. Median monthly increments are identified by the solid line.
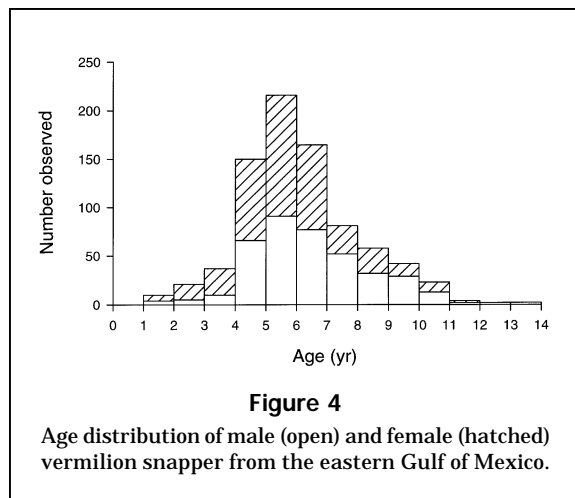
dian values from January to May and low values in July and August (Fig. 3).

Ages ranged from 1 to 13 years. Most males (74%) and females (77%) were found to be between ages 4 and 7 (Fig. 4). Initial growth of vermilion snapper was rapid, and fish attained a mean length of 211 mm TL during their second year (age 1, Table 3). However, subsequent increases in length were low (<33 mm). Likelihood ratio tests did not show a difference between the male and female von Bertalanffy growth models (χ^2=0.92, df=3, P>0.5). The estimated von Bertalanffy growth parameters (standard error) for all aged fish (n=841) were L_∞=298(5.0), K=0.25 (0.04), and t_0=−3.9 (0.85). Predicted lengths at age were similar to mean lengths at age (Table 3; Fig. 5); however, because of high variability in length-at-age data, the correlation coefficient for estimated growth was low (adjusted r^2=0.26), suggesting that age is not a good predictor of length.

Mortality

Catch length-frequency data were transformed into age frequencies by using age-length keys constructed

Figure 4

Age distribution of male (open) and female (hatched) vermilion snapper from the eastern Gulf of Mexico.
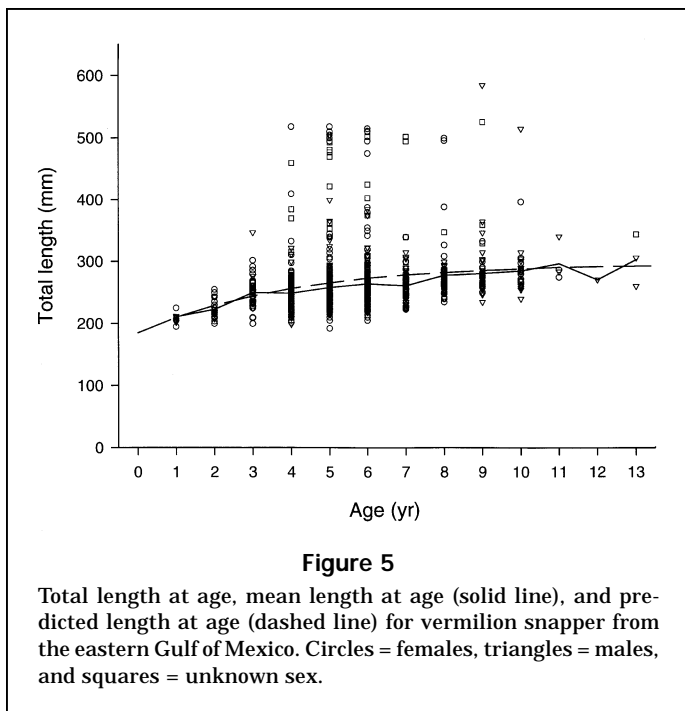
from our ages. Full recruitment into both the recreational and commercial fisheries occurred at age 6. Survivorship (standard error) estimates determined by using the Chapman-Robson method were 0.619 (0.0002) and 0.613(0.0001), respectively. Instantaneous mortality estimates (Z=−ln survivorship) were

Table 3

Mean empirical and predicted total lengths (mm TL) of female, male, and all vermilion snapper sampled from the eastern Gulf of Mexico. Standard error is in parentheses, and *n* is number of fish examined.

	Female			Male			All Fish			
Age	*n*	Mean empirical	Range	*n*	Mean empirical	Range	*n*	Mean empirical	Range	Predicted
1	6	214(13.1)	195–225	4	207(4.6)	202–212	11	211(10.1)	195–225	210
2	16	224(16.3)	200–255	5	221(13.4)	208–243	21	223(15.4)	200–255	229
3	27	249(24.7)	200–302	10	253(36.1)	225–347	37	250(27.8)	200–347	245
4	83	253(41.9)	202–518	66	245(23.8)	199–322	154	253(41.5)	199–518	257
5	124	267(60.5)	192–518	91	262(41.5)	215–505	225	270(60.8)	192–518	266
6	88	275(60.1)	205–515	76	262(29.7)	218–385	171	274(56.9)	205–515	273
7	29	263(23.7)	223–340	52	259(21.0)	225–315	85	267(43.1)	223–502	278
8	26	294(67.7)	235–500	32	270(14.8)	241–300	59	282(48.1)	235–500	283
9	13	277(21.8)	250–333	29	288(63.6)	325–585	45	293(64.4)	235–585	286
10	10	294(38.1)	267–397	13	295(69.6)	240–515	24	294(55.7)	240–515	289
11	2	281(8.5)	275–287	2	313(40.3)	284–341	4	297(29.9)	275–341	291
12				2	271(0)		2	271(0)		292
13				2	284(32.5)	261–307	3	304(42.1)	261–345	294

Figure 5

Total length at age, mean length at age (solid line), and predicted length at age (dashed line) for vermilion snapper from the eastern Gulf of Mexico. Circles = females, triangles = males, and squares = unknown sex.

0.480 for the recreational fishery and 0.489 for the commercial fishery.

Reproduction

Our sample contained no immature males and only 23 immature female vermilion snapper. Testes either contained tailed sperm, suggesting the potential for spawning, or contained brown bodies, suggesting previous spawning. The smallest male examined was 199 mm TL; therefore males must reach maturity at a smaller size than do females. For females, 80% were sexually mature at age 1, and 100% were sexually mature by age 7. More than 90% of the females were mature at 200 mm TL, and 100% were mature at 325 mm TL.

Vermilion snappers in the eastern GOM spawn from May to September. Ripe females were observed during this time period (with the exception of June) (Fig. 6). These fish contained late-stage vitellogenic oocytes, hydrated oocytes, and postovulatory follicles (Fig. 7). Through the rest of the year, there was a progression from mostly resting ovaries during October to mostly early developing ovaries during December. Ripe males were observed throughout the year; they were most common (>60% of testes) from March to September and in January (Fig. 6). For both sexes, median GSIs were low from October to April (<0.01 for females and <0.005 for males, Fig. 8). In May, GSIs increased dramatically (medians equaled 0.034 for females and 0.020 for males) and then gradually decreased through September.

Vermilion snapper batch fecundities ranged from 5535 to 86,811 oocytes from fish measuring 210–298 mm TL (*n*=27). The relationship between batch fecundity and length was batch fecundity = 317 × (whole weight) − 3.1624×10^4, r^2=0.55.
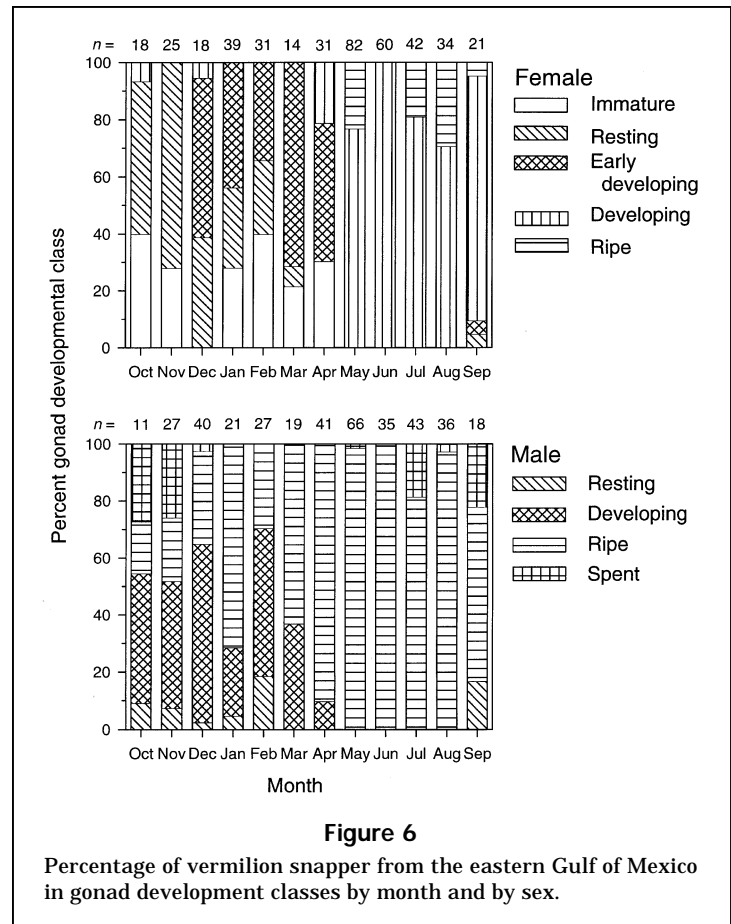
Discussion

Collections

The vermilion snapper that we sampled from the eastern GOM were smaller than those collected during the 1980s from the western GOM. Most hook-and-line-caught fish that we sampled (88%) were between 201 and 325 mm TL and were smaller than fish collected from the Texas Flower Gardens by Zastrow (1984) and Nelson (1988). The fish they sampled were mostly (75%) between 269 and 474 mm TL and 262 and 517 mm TL, respectively. Gear bias is probably not responsible for the differences in length distributions. As in our study, both Zastrow (1984) and Nelson (1988) examined fish caught principally with hook-and-line gear. Furthermore, Nelson (1988) examined the length distributions of vermilion snapper caught with different hook sizes (Mustad no. 2–no. 4/0) and noted no differences in the size of fish caught.

Other factors, such as depth and movement, probably cannot explain the differences between the size distribution of fish caught in our study and that of fish caught in the western GOM. Nelson (1988) caught most vermilion snapper from depths between 60 and 90 m. We do not know the depth at which the fish we sampled were captured; however, the mean depth at which vermilion snapper were caught by the eastern GOM commercial fishery in 1995 was 80 m (Schirripa[4]) and is within the depth range given by Nelson (1988). The presence of larger fish in the western GOM could be the result of larger fish moving from the eastern to western GOM. However, this movement seems unlikely because tagging data suggest that vermilion snapper are residents of reefs and do not travel long distances (Beaumariage, 1964; Fable, 1980; Grimes et al., 1982).

Increases in fishing pressure may have reduced the average size of fish caught by the fishery. Schirripa[4] reported that the average size of fish in the GOM commercial fishery dropped from a high of 371 mm TL in 1984 to a low of 320 mm TL in 1993. Over this same time, commercial landings increased from 1.6 million pounds in 1984 to 2.5 million pounds in 1993, and recreational landings increased from 0.2 million fish in 1984 to 1.2 million fish in 1993.

The sex ratio of GOM vermilion snapper is different from the sex ratio reported for snapper from the SAB. In the GOM, female-to-male sex ratios were not significantly different from 1:1 (Zastrow, 1984; Collins[3]; this study), or they significantly favored

Figure 6

Percentage of vermilion snapper from the eastern Gulf of Mexico in gonad development classes by month and by sex.
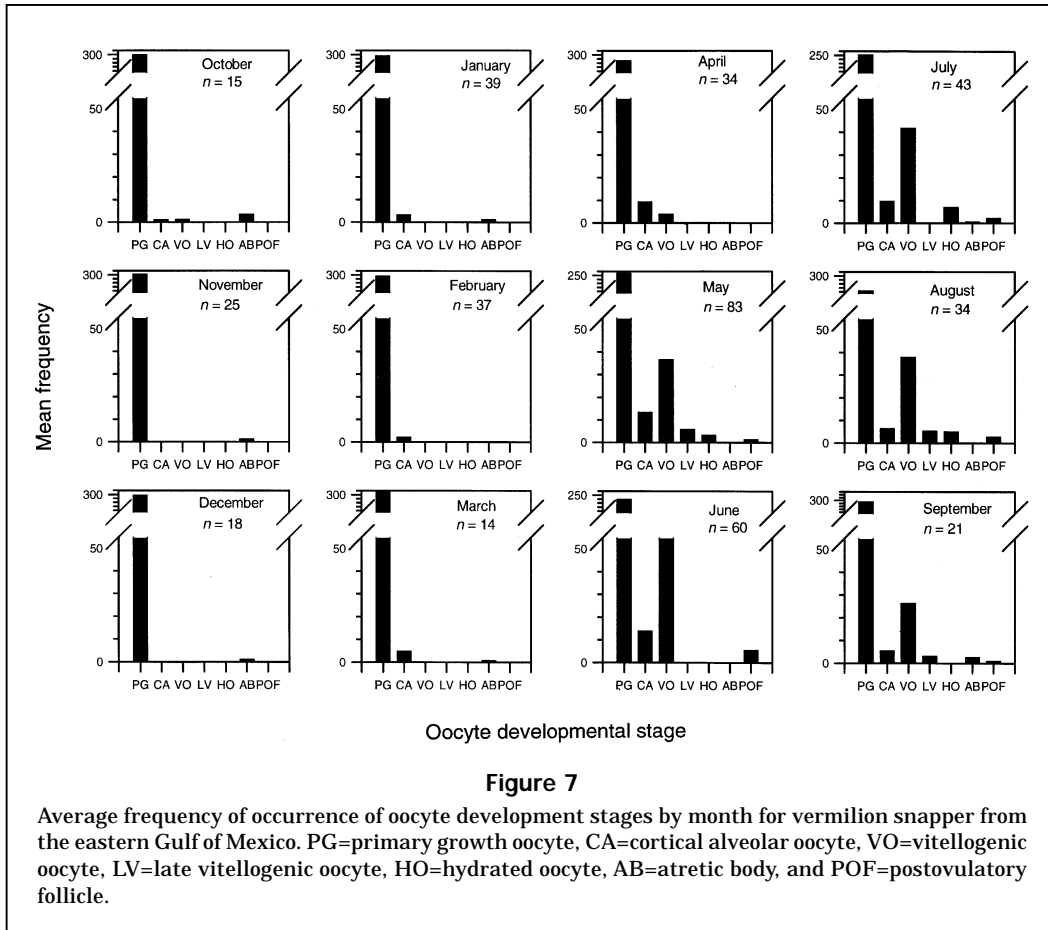
males (1:1.2; Nelson, 1988). In the SAB, females significantly outnumbered males, and sex ratios ranged from 1.6:1 to 1.7:1 (Grimes and Huntsman, 1980; Cuellar et al., 1997; Zhao and McGovern, 1997). Zhao and McGovern (1997) partitioned sex ratios from the SAB by depth, fish size, sampling year, gear type, and latitude. Of these, only gear type and latitude significantly affected the sex ratio. Females were proportionally more common in trap and hook-and-line collections than in trawl collections. Although Zhao and McGovern (1997) were cautious about attributing decreases in the proportion of females to changes in latitude, 1:1 sex ratios reported in the GOM (Zastrow, 1984; Collins[3]; our study) and from Puerto Rico (Boardman and Weiler, 1979) are consistent with this hypothesis. We did not find any significant differences in sex ratios by season; however, Zastrow (1984) and Nelson (1988) reported an increase in the proportion of males in the summer in the western GOM.

Age and growth

Sectioned otoliths can be used to age eastern GOM vermilion snapper and produce higher readability

Figure 7

Average frequency of occurrence of oocyte development stages by month for vermilion snapper from the eastern Gulf of Mexico. PG=primary growth oocyte, CA=cortical alveolar oocyte, VO=vitellogenic oocyte, LV=late vitellogenic oocyte, HO=hydrated oocyte, AB=atretic body, and POF=postovulatory follicle.

and agreement rates than scales or whole otoliths can produce. Our readability rates were high (98%) and were similar to rates reported by Zhao et al. (1997), who were able to read 96% of sectioned otoliths from SAB vermilion snapper. The use of whole otoliths has produced mixed results. Barber (1989) had a high agreement rate between readings (84%) and was able to count as many as 26 zones. However, Grimes (1978) found that whole otoliths were difficult to interpret at ages greater than 7. Scales have been used with limited success by Grimes (1978), Zastrow (1984), Nelson (1988), and Collins and Pinckney (1988). Agreement rates between readings in these studies have ranged from 44% to 85% and were lower than reported in this study (100%) and by Zhao et al. (1997) (96%). Grimes (1978) found that counts from scales and whole otoliths from the same fish were similar and reported an agreement rate of 75%.

Marginal-increment analyses suggest that vermilion snapper form one opaque band per year in the late spring and summer. This pattern has also been noted for vermilion snapper captured from the SAB. Zhao et al. (1997) found that opaque zones formed in

June for fish age one year and in July for fish ages two to six years. Barber (1989) attempted to use marginal-increment analyses to validate annulus formation in whole otoliths from snapper from the GOM; however, he was unable to show an annual pattern. Grimes (1978) observed that the hyaline layer was formed in November in the SAB. Because hyaline and opaque bands alternate, Grimes's (1978) findings imply that an opaque band is formed once a year before November.

Vermilion snapper are considered long-lived, slow-growing fish (Manooch, 1987). The oldest individual we aged was 13 years old, similar to the SAB maximum age of 12 years reported by Zhao et al. (1997), who also used sectioned otoliths. However, our maximum age was older than the scale-based maximum ages reported for the western GOM of age 7 by Zastrow (1984) and age 10 by Nelson (1988). Those using scales to age fish typically underestimate the ages of older fish (Beamish and McFarlane, 1987). As fish approach their asymptotic size, little or no increase in fish size occurs and this is reflected as little or no increase in scale size. Therefore, rings at the scale edge of older (larger) fish become difficult

to interpret. Barber (1989) reported that otolith-based ages were on average three years greater than scale-based ages for GOM vermilion snapper, although he did not directly compare otoliths and scales from the same fish. Our maximum age was less than the 26 years reported by Barber (1989). His older ages are surprising because he used whole otoliths to estimate age. Grimes (1978) noted that one disadvantage to aging vermilion snapper by using whole otoliths is that rings are difficult to interpret in fish older than age 7. Although we did not compare whole otoliths to sectioned otoliths of vermilion snapper, for gag (*Mycteroperca microlepis*), annuli at the edge of the otolith are more readily observed in sectioned otoliths than in whole otoliths (Collins et al., 1987; Hood and Schlieder, 1992).

Empirical mean lengths and predicted lengths at age were less for our vermilion snapper than for snapper from the western GOM (Table 4; Fig. 9). At age 1, the mean length of fish from our study (211 mm TL) is similar to that of fish from studies by Zastrow (1984; 207 mm TL) and Nelson (1988; 207 mm TL); however, by age 4, the mean length in our study (253 mm TL) is at least 100 mm less than mean lengths in their studies (353 and 357 mm TL, respectively; Fig. 9). If scale-based ages underestimate actual age, then mean length at age and growth rates will be over-estimated (Beamish and McFarlane, 1987). However, because scales generally give good estimates of age for younger fish and because the mean length of our fish at age 1 is similar to lengths given by Zastrow (1984) and Nelson (1988), differences in length could reflect differences in growth as opposed to bias from aging structures.

Our estimates of empirical mean lengths and predicted lengths at age, which were lower than those estimates for vermilion snapper from the western GOM, could also be the product of changes in fishing pressure. Schirripa[4] summarized GOM landings data and noted that annual commercial and recreational landings have increased 3- to 4-fold from the mid-1970s to the early 1990s. If larger fish are more vulnerable to capture, then faster-growing fish within an age class will be selectively removed from the population. The result of this type of selection will be a depression of mean size at age for older age classes and an underestimation of the biologically realistic L_∞ (Pitcher and Hart, 1982). This pattern was noted by Zhao et al. (1997) for vermilion snapper in the SAB. Their estimates of growth based on ages from sectioned otoliths for 1979–81 were similar to growth estimates (scale-based ages) by Grimes (1978) from the mid-1970s, when fishing pressure
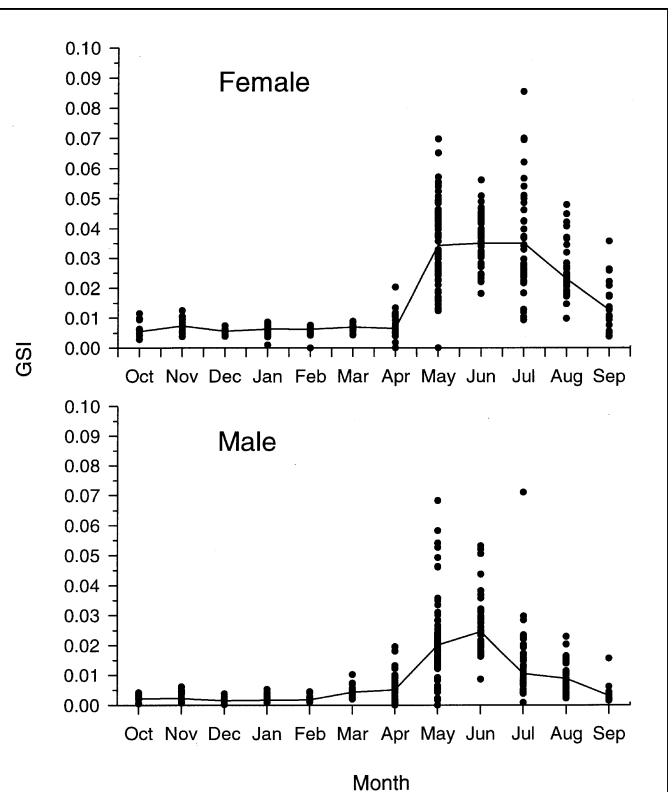

Figure 8

Monthly gonosomatic indices (GSI) for female and male vermilion snapper from the eastern Gulf of Mexico. Median values are connected by the solid line.

was low. Zhao et al.'s (1997) estimates of size at age and of L_∞ then decreased over time. Estimates of L_∞ dropped from 629 mm TL (1979–81) to 365 (1982–84) and 333 mm TL (1985–93) (Table 4). They could not attribute declines in size at age or L_∞ to gear selectivity, sampling regime, depth, or latitude and concluded their observed changes were due to selective fishing for faster-growing individuals within all age classes.

Similar decreases in observed lengths at age have been reported for red porgy, a species often found in the same habitats as vermilion snapper (Grimes et al., 1982; Barans and Henry, 1984; Chester et al., 1984; Sedberry and Van Dolah, 1984; Nelson, 1988) and sought by the same fisheries (Grimes et al, 1982; Nelson, 1988; Collins and Sedberry, 1991). Average total length of GOM red porgy reported by Hood and Johnson[7] at age 6 years was 348 mm and was over

---

[7] Hood, P. B., and A. K. Johnson. 1997. Age, growth, mortality, and reproduction of red porgy (*Pagrus pagrus*) from the eastern Gulf of Mexico. Florida Marine Research Institute, Florida Department of Environmental Protection, 100 Eighth Avenue S.E., St. Petersburg, Florida. Manuscript in prep.

100 mm less than the average length of 464 mm reported by Nelson (1988). In the SAB, the average total length of 6-year-old fish had decreased from 451 mm in 1972–74 (Manooch and Huntsman, 1977) to 363 mm in 1991–94 (Harris and McGovern, 1997). Both Harris and McGovern (1997) and Hood and Johnson[7] concluded that the observed decrease in average length at age was likely due to size selective fishing.

Mortality

The age of full recruitment to both the recreational and commercial fisheries has increased since the early 1980s. Zastrow (1984) and Nelson (1988) reported the age at full recruitment to be 4 years, less than our estimate of 6 years. The reported age of full recruitment to the SAB hook-and-line fishery was 4 years before 1981 (Grimes, 1978; Huntsman et al., 1983; Zhao et al., 1997) but increased to 6 years by 1993 (Cuellar et al., 1996; Zhao et al., 1997). This increase in age of recruitment has been associated with a decrease in length at age attributed to selective fishing on faster-growing members of each age group (Zhao et al., 1997). Our estimates of mortality (0.469–0.489) are within the range given by Schirripa[4] for the years 1986–1995 in the GOM (0.466–0.791) and less than the estimate from the SAB headboat fishery (0.67) reported by Huntsman et al. (1983).

Reproduction

Our observed sizes of maturation were less than those reported by Nelson (1988) for the western GOM. We found that most females were sexually mature at 200 mm TL (age 1), and we did not examine any immature males (the smallest male we sampled was 199 mm TL). The smallest mature female and male reported by Nelson (1988) were 234 mm TL and 291 mm TL, respectively. In the SAB, Collins and Pinckney (1988) found that at 160 mm TL, 60% of females and 90% of males were mature. Cuellar et al. (1996) sampled females as small as 186 mm TL and males as small as 197 mm TL and did not find any immature fish in their samples. These lengths at maturity are in contrast to the results of Grimes and Huntsman (1980) who found that SAB vermilion snapper matured between 186 and 324 mm TL (ages 3 and 4). There is an indication that increasing fishing pressure may depress vermilion snapper size and age at maturity. Zhao and McGovern (1997) noted a decrease in the size at maturity for males and females in the SAB from 1970 to 1992. Before 1982, 31% of males and 5% of females were mature
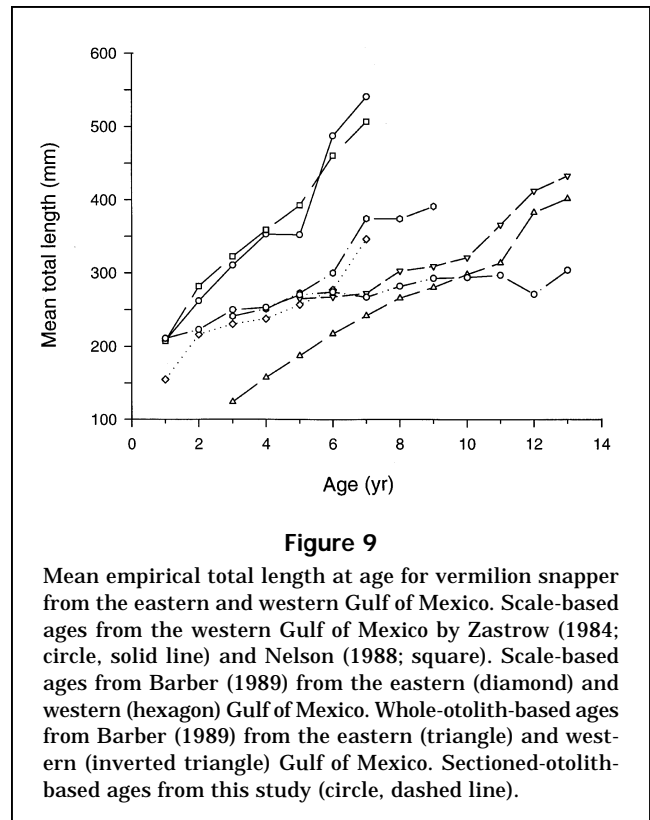

Figure 9

Mean empirical total length at age for vermilion snapper from the eastern and western Gulf of Mexico. Scale-based ages from the western Gulf of Mexico by Zastrow (1984; circle, solid line) and Nelson (1988; square). Scale-based ages from Barber (1989) from the eastern (diamond) and western (hexagon) Gulf of Mexico. Whole-otolith-based ages from Barber (1989) from the eastern (triangle) and western (inverted triangle) Gulf of Mexico. Sectioned-otolith-based ages from this study (circle, dashed line).

at 140 mm TL. After 1982, all males and 37% of females were mature at 140 mm TL. They suggested that this change may have been caused by the increasing and selective fishing pressure that occurred during the 1980s.

On the basis of the presence of ripe females and increases in GSI, we believe that vermilion snapper in the GOM spawn from May to September. Nelson (1988) and Collins[5] also reported summer spawning. In our samples, ripe gonads were present from late spring to early fall but were most common from May to July. In addition, GSIs were highest during the summer months. Spawning seasonality in the GOM is similar to that reported for the SAB, where fish spawn from the late spring to early fall (Grimes and Huntsman, 1980; Cuellar et al., 1996). Boardman and Weiler (1979) found that in Puerto Rican waters, spawning takes place year round.

Batch fecundity was positively correlated with fish length. Nelson (1988) and Collins[5] also found a positive relationship between batch fecundity and length for GOM fish. Their estimates were larger than those obtained in our study (61,600–392,000 and 33,550–415,161 oocytes, respectively); however, the fish sampled were also larger (209–510 and 248–375 mm TL, respectively). Our estimates of batch fecundity were similar to SAB estimates reported by Cuellar

Table 4

Von Bertalanffy growth parameters for vermilion snapper from the Gulf of Mexico (GOM) and South Atlantic Bight (SAB). Table adapted from Goodyear and Schirripa.[3] Our study and the studies of Schirripa[4] and Zhao et al. (1997) were added to the table. L_∞ is the asymptotic TL, K is the von Bertalanffy growth coefficient, t_0 is the time that TL is zero, and n is the sample size.

Study and area	Aging structure	Sex	n	L_∞ (mm)	K	t_0
Current study						
Eastern GOM	otoliths	Combined	841	298	0.25	−3.9
Schirripa[1]						
GOM	scales and otoliths	Combined	586	535	.203	−0.94
Nelson (1988)						
Flower Gardens, TX	scales	Combined	906	554	0.22	−0.30
Barber (1989)						
St. Petersburg, FL	scales	Combined	34	936	0.05	−3.37
Pensacola, FL		Combined	194	344	0.16	−3.356
Galveston, TX		Combined	799	561	0.10	−2.81
Port Aransas, TX		Combined	270	428	0.15	−2.78
Brownsville, TX		Combined	779	477	0.16	−2.32
St. Petersburg, FL	otoliths	Combined	1113	469	0.09	−1.16
Pensacola, FL		Combined	600	511	0.08	−1.44
Galveston, TX		Combined	799	554	0.08	−1.46
Port Aransas, TX		Combined	270	657	0.07	−1.18
Brownsville, TX		Combined	779	603	0.09	−0.87
Grimes (1978)						
SAB	scales	Combined	815	627	0.20	−0.13
Zhao et al. (1997)						
1979–81	otoliths	Combined	195	629	0.202	−0.117
SAB 1982–84		Combined	265	365	0.315	−0.361
1985–93		Combined	766	333	0.271	−0.899

[1] Schirripa, M. J. 1992. Analysis of age and growth of vermilion snapper with an assessment of the fishery in the Gulf of Mexico. National Marine Fisheries Service, Southeast Fisheries Center, Miami Laboratory, Miami, FL. CRD-91/92-

et al. (1996; 4000 to 90,000 oocytes from fish 186–340 mm TL).

Summary

Recent stock assessments of vermilion snapper suggest that vermilion snapper stocks in the GOM are overfished (Schirripa[4]). Our study, when compared to previous studies of vermilion snapper, suggests that size-selective mortality coupled with overfishing may be responsible for changes in life history parameters (decreases in the mean length at age, estimated L_∞, and length and age of maturation). If these changes are not taken into consideration, estimates of the yield-per-recruit, mortality, and spawning potential ratios that use the above life history parameters in their calculations could be biased. Consequently, erroneous conclusions about the health of the stock of GOM vermilion snapper could be made in future stock assessments.

Acknowledgments

Literature cited

Barans, C. A., and V. J. Henry.
   1984.   A description of the shelf edge groundfish habitat along the southeastern United States.   N.E. Gulf Sci. 7:77–96.
Barber, R. C.
   1989.   Age and growth of vermilion snapper (*Rhomboplites aurorubens*) in the northern Gulf of Mexico.   M.S. thesis, Texas A&M Univ., College Station, TX, 87 p.
Beamish, R. J., and G. A. McFarlane.
   1987.   Current trends in age determination methodology.   *In* R. C. Summerfelt and G. E. Hall (eds.), Age and growth of fish, p. 15–42.   Iowa State Univ. Press, Ames, IA
Beaumariage, D. S.
   1964.   Returns from the 1973 Schlitz tagging program.   Fla. State Board Conserv. Tech. Ser. 43, 34 p.
Boardman, C., and D. H. Weiler.
   1979.   Aspects of the life history of three deepwater snappers around Puerto Rico.   Proc. Gulf Caribb. Fish. Inst. 32:158–182.
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.
Chester, A. J., G. R. Huntsman, P. A. Tester, and C. S. Manooch.
   1984.   South Atlantic Bight reef fish communities as represented in hook-and-line catches.   Bull. Mar. Sci. 34:267–279
Collins, M. R., and J. L. Pinckney.
   1988.   Size and age at maturity for vermilion snapper (*Rhomboplites aurorubens*) (Lutjandidae) in the South Atlantic Bight.   N.E. Gulf Sci. 10:51–53.
Collins, M. R., and G. R. Sedberry.
   1991.   Status of vermilion snapper and red porgy stocks off South Carolina.   Trans. Am. Fish. Soc. 120:116–120.
Collins, M. R, C. W. Waltz, W. A. Roumillat, and D. L. Stubbs
   1987.   Contribution to the life history and reproductive biology of gag, *Mycteroperca microlepis* (Serranidae), in the south Atlantic Bight.   Fish. Bull. 85:648–653.
Cuellar, N., G. R. Sedberry, and D. A. Wyanski.
   1996.   Reproductive seasonality, maturation, fecundity, and spawning frequency of the vermilion snapper, *Rhomboplites aurorubens*, off the southeastern United States.   Fish. Bull. 94:635–653.
Fable, W. A.
   1980.   Tagging studies of red snapper (*Lutjanus campechanus*) and vermilion snapper (*Rhomboplites aurorubens*) off the south Texas coast.   Contrib. Mar. Sci. 23:115–121.
Grier, H. J.
   1987.   Brown bodies in the gonads of the black sea bass, *Centropristis striatus*.   *In* Proc. 3rd Int. Symp. Reprod. Biol. Fish, 199 p.
Grimes, C. B.
   1978.   Age, growth, and length-weight relationship of vermilion snapper, *Rhomboplites aurorubens,* from North Carolina and South Carolina waters.   Trans. Am. Fish. Soc. 107:454– 456.

Grimes, C. B., and G. R. Huntsman.
   1980.   Reproductive biology of the vermilion snapper, *Rhomboplites aurorubens*, from North Carolina and South Carolina.   Fish. Bull. 78:137–146.
Grimes, C. B., C. S. Manooch, and G. R. Huntsman.
   1982.   Reef and rock outcropping fishes of the outer continental shelf of North Carolina and South Carolina. And ecological notes on the red porgy and vermilion snapper.   Bull. Mar. Sci. 32:277–289.
Grimes, C. B., C. S. Manooch, G. R. Huntsman, and R. L. Dixon.
   1977.   Red snappers of the Carolina coast.   Mar. Fish. Rev. 39:12–15.
Harris, P. J., and J. C. McGovern.
   1997.   Changes in the life history of red porgy, *Pagrus pagrus*, from the southeastern United States, 1972–1994.   Fish. Bull. 95:732–747.
Helland, I. S.
   1987.   On the interpretation and use of r^2 in regression analysis.   Biometrics 43:61–69.
Hood, P. B., and R. A. Schlieder.
   1992.   Age, growth, and reproduction of gag, *Mycteroperca microlepis* (Pisces: Serranidae), in the eastern Gulf of Mexico.   Bull. Mar. Sci. 51:337–352.
Humason, G. L.
   1972.   Animal tissue technique.   W.H. Freeman and Co., San Francisco, CA, 641 p.
Hunter, J. R., N. C. Low, and R. J. H. Leong.
   1985.   Batch fecundity in multiple spawning fishes.   *In* U.S. Dep. Commer., NOAA Tech. Rep. NMFS. 36, p. 63–66.
Huntsman, G. R., C. H. Manooch, and C. B. Grimes.
   1983.   Yield per recruit models of some reef fishes of the U.S. South Atlantic Bight.   Fish. Bull. 81:679–695.
Hyder, M.
   1969.   Histological studies on the testis of *Tilapia leucosticta* and other species of the genus *Tilapia* (Pisces: Teleostei).   Trans. Am. Microsc. Soc. 88:211–231.
Kimura, D. K.
   1980.   Likelihood methods for the von Bertalanffy growth curve.   Fish. Bull. 77:765–776.
Manooch, C. S.
   1987.   Age and growth of snappers and groupers.   *In* J. J. Polovina and S. Ralston (eds.), Tropical snappers and groupers biology and management.   Westview Press, Inc., Boulder, CO, p. 329–373.
Manooch, C. S., and G. R. Huntsman.
   1977.   Age, growth, and mortality of the red porgy, *Pagrus pagrus* (Pisces:Sparidae) in North Carolina.   Trans. Am. Fish. Soc. 106:26–33.
Nelson, R. S.
   1988.   A study of the life history, ecology, and population dynamics of four sympatric reef predators (*Rhomboplites aurorubens*, *Lutjanus campechanus*, Lutjanidae; *Haemulon melanurum*, Haemulidae; and *Pagrus pagrus*, Sparidae) on the east and west Flower Garden Banks, northwestern Gulf of Mexico.   Ph.D. diss., North Carolina State University, Raleigh, NC, 197 p.
Optimas Corp.
   1996.   Optimas 5.0 user's manual.   Optimas Corp., Bothell, WA.
Pitcher, T. J., and P. J. B. Hart.
   1982.   Fisheries ecology.   AVI Publishing Co., Westport, CT, 414 p.
SAS Institute, Inc.
   1985.   SAS user's guide: statistics.   SAS Institute, Inc., Cary, NC, 956 p.

Sedberry, G. R., and R. F. Van Dolah.
  1984.   Demersal fish assemblages associated with hard bottom habitat in the South Atlantic Bight of the U.S.A. Environ. Biol. Fish. 11:241–258.
Snedecor, G. W., and W. G. Cochran.
  1971.   Statistical methods.   Iowa State University Press, Ames, IA, 593 p.
Smith, G. B.
  1976.   Ecology and distribution of eastern Gulf of Mexico reef fishes.   Fla. Mar. Res. Publ. 19, 78 p.
Smith, G. B., H. M. Austin, S. A. Bortone, R. W. Hastings, and L. H. Ogren.
  1975.   Fishes of the Florida Middle Ground with comments on the ecology and zoogeography.   Fla. Mar. Res. Publ. 9, 14 p.
Vergara, R.
  1978.   Lutjanidae.   *In* vol. 3: FAO species identification sheets for fishery purposes: western central Atlantic (fishing area 31), unpaginated.
Wallace, R. A., and K. Selman.
  1981.   Cellular and dynamic aspects of oocyte growth in teleosts.   Am. Zool. 21:325–343.

West, G.
  1990.   Methods of assessing ovarian development in fishes: a review.   Aust. J. Mar. Freshwater Res. 41:199–222.
Youngs, W. D., and D. S. Robson.
  1978.   Estimation of population number and mortality rates.   *In* T. Bagenal (ed.), Methods for assessment of fish production in fresh waters, p. 137–164.   Blackwell Scientific Publications, Oxford, UK.
Zastrow, C. E.
  1984.   Age and growth of the red snapper, *Lutjanus campechanus*, and the vermilion snapper, *Rhomboplites aurorubens*, from the northwestern Gulf of Mexico.   M.S. thesis, Texas A&M University, Galveston, TX, p. 77.
Zhao, B., and J. C. McGovern.
  1997.   Temporal variation in sexual maturity and gear-specific sex ratio of vermilion snapper, *Rhomboplites aurorubens*, in the South Atlantic Bight.   Fish. Bull. 95:837–848.
Zhao, B., J. C. McGovern, and P. J. Harris.
  1997.   Age, growth, and temporal change in size at age of the vermilion snapper from the South Atlantic Bight.   Trans. Am. Fish. Soc. 126:181–193.